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Observing animal behaviour and movement patterns remotely: A case study using bio-logging technology on free-ranging Eurasian beavers (*Castor fiber*)

Partner

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Dedication

To my grandparents Maria and Robert Hasitzka

Acknowledgements

When I was a kid, I always loved going on ‘expeditions’ with my dad: We would stroll through the forest, build camps with materials we found there, cross small streams by bending hazel branches over them, climb trees and perfect our swing-and-jump from-tree-to-tree skills. Already at this age, I already spent considerable amounts of time close to streams and lakes, but sadly never saw a beaver – they were extinct in my home county, Carinthia, at that time. For this reason (or any other reason – not sure there was a reason), I would rather spend my time collecting snails, building small enclosures for them and trying to stick as many as possible to my face.

Time went by and due to several fortunate coincidences (well, one was that I had an amazing biology teacher which fuelled my passion – thanks Prof. Vouk! – and the other was I was terribly bad in French – yes I started my study career doing translation studies!), I ended up in a biology lecture with my friend Lissi. I was fascinated from the very first moment, and – luckily – enrolled in biology studies shortly after that. But it was not until I was on the search for a topic for my master thesis, that I stumbled across beavers (my snail-passion had slightly faded by then): It was my mum who gave me the momentous call saying that the news was reporting that beavers had returned to Carinthia. This was the beginning of a long love story (yes, it was beaver love!), that still continues and hopefully will do so for a long time. I am very grateful that my parents, Monika and Erwin, always supported me and gave me the freedom to follow my dreams; they even developed a passion for beavers: my dad accompanied me on all my boat trips for mapping beaver field signs during my masters, and my mum joined some of these expeditions to the rivers.

‘Too many cooks spoil the broth’ is usually said when too many people are involved in the same task. Well, I think with this thesis it was just the opposite – I believe I can say that we prepared an exceptionally flavourful ‘bouillon’, with fine and spicy nuances from my three supervisors Frank Rosell, Klaus Hackländer and Rory Wilson. A big thanks for all your help and support, and the amazing time I spend both at the University College of Southeast Norway (HSN) and the University of Natural Resources and Life Sciences Vienna (BOKU), as well as the fabulous visits at Swansea University. At all three institutes, I met nice colleagues, got insights into their research questions and had fruitful discussions – not to mention the great times I

had at social gatherings with them… I did my fieldwork in Norway and want to thank the ‘beaver team’ at HSN for all their help during our nightly fieldwork sessions at the rivers: Frank, Christian, Manuel, Róisín, Hannah, Veronica, Martin, Howard and Frode – this would have never been possible without your help during beaver captures, tagging and recaptures, and not least digging for lost tags! Both the beaver conference and the ‘beaver parties’ in Bø have always been a highlight and wouldn’t have been the same without you. I also thank all the PhD students that have been around during this time, in particular Martin for all the long discussions (and the good cooperation on paper III) and Shane and Eva for statistical help (here another big thanks to Andreas and Prof. Leisch!). I also thank Julia for being such a motivated master student and her contribution to paper II, and also Lea, Elle, Gunn and Manuel, and all my students from the courses I was teaching during my PhD – their feedback helped me develop. I would also like to thank HSN, BOKU, IRSAE, the OeAD and the Austrian Federal Ministry of Science, Research and Economy for financial support during my thesis.

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Abstract

Understanding animal behaviour is a fundamental part of biology and has been revolutionized by the invention of bio-logging units, which can be used to study wild animals in their natural habitats. In this thesis, tri-axial accelerometers and GPS systems were used to examine activity, behaviour and movement patterns of dominant, free-living Eurasian beavers (*Castor fiber*) (n = 33; 19 males, 14 females) in southeast Norway. We investigated whether accelerometry data could be used to study beaver behaviour, and, by using a random forest classifier, were able to identify seven different behaviours (standing, walking, swimming, feeding, grooming, diving and sleeping). Capture and tagging can be stressful, and, thus, changes in activity and movement patterns were examined for the first week after the tagging event. There was a lower post-release activity; however, the small effect size indicated that it was likely minor. We applied these results when studying movement patterns and the diving behaviour of beavers. Movement patterns in water and on land were linked to territory size and individual age. There was a trade-off between foraging and patrolling: beavers in larger territories patrolled more, but stayed closer to the shoreline when foraging, while this relationship was reversed in smaller territories. Movement patterns also changed with increasing age: older beavers spent more time on land and within absolute border zones, which may be linked to increased experience of dominant territory holders with time. Beavers dived during only 2.8% of their active time and the majority of dives where short and shallow. Maximum diving depth and dive durations (total and bottom phase) were defined by the physical effort during the descent and bottom phases and the maximum depth reached, while water temperature had no effect. Lastly, to advance analyses of accelerometry data, we provide researchers with software for visualizing behavioural data coupled with proxies for power use, or any other parameter of interest. This thesis emphasizes the power of accelerometers and GPS systems for determining beaver behaviours, ranging from the construction of ethograms, to evaluating tagging effects, to gaining detailed insights into the beavers' movement patterns and diving performance, and reinforces the field by introducing a new software tool for the analysis of such data.

Keywords: acceleration, activity, behaviour, Castor fiber, Eurasian beaver, GPS, spatial movement

List of papers

Paper I

Graf, P.M., Wilson, R.P., Qasem, L., Hackländer, K. & Rosell, F. (2015). The use of acceleration to code for animal behaviours; a case study in free-ranging Eurasian beavers *Castor fiber*. PLoS One 10:e0136751. doi:10.1371/journal.pone.0136751

Paper II

Graf, P.M., Hochreiter, J., Hackländer, K., Wilson, R.P. & Rosell, F. (2016). Short-term effects of tagging on activity and movement patterns of Eurasian beavers (*Castor fiber*). European Journal of Wildlife Research 62: 725. doi:10.1007/s10344-016-1051-8

Paper III

Graf, P.M., Mayer, M., Zedrosser, A., Hackländer, K. & Rosell, F. (2016). Territory size and age explain varying movement patterns in the Eurasian beaver. Mammalian Biology 81: 587-594. doi:10.1016/j.mambio.2016.07.046

Paper IV

Graf, P.M., Wilson, R.P., Cohen Sanchez, L.G., Hackländer, K. & Rosell, F. (*in preparation*). Diving behaviour in a free-living, semi-aquatic herbivore, the Eurasian beaver *Castor fiber*.

Paper V

Wilson, R. P., Holton, M.D., Walker, J. S., Shepard, E. L. C., Scantlebury, D. M., Wilson, V. L., Wilson, G. I., Tysse, B., Gravenor, M., Ciancio, J., McNarry, M. A., Mackintosh, K. A., Qasem, L., Rosell, F., Graf, P. M., Quintana, F., Gomez-Laich, A., Sala, J.-E., Mulvenna, C. C., Marks, N. J. & Jones, M. W. (2016). A spherical-plot solution to linking acceleration metrics with animal performance, state, behaviour and lifestyle. Movement Ecology 4: 1-11. doi: 10.1186/s40462-016-0088-3

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1. Introduction

Animal behaviour is complex and acts as an interface between an organism, its physiological condition and the environment (Baldwin 1976; Sih et al. 2010). Under natural conditions, animals constantly undergo decision-making processes as they need to trade-off investment of time and energy in certain activities/behaviours to maximize lifetime reproductive success (Mangel and Clark 1986). Through these decisions, animals adapt to the conditions in which they live by, for example, gaining access to food, avoiding predators, finding and selecting mates, rearing offspring and defending territories (Martin and Bateson 2007). The decision to invest into a specific activity can have severe consequences for fitness and survival (Ohgushi 1996; Stearns 1989), and may ultimately even lead to evolutionary change (Duckworth 2009). The study of animal behaviour in natural habitats is thus a fundamental part of biology and delivers important insights into the strategies animals adopt to increase their fitness. Moreover, studies on animal behaviour are substantial to other fields of research, and have important implications for animal welfare (Broom and Fraser 2015; Mench 1998), wildlife management (Martin 1998; Nolet et al. 2016), and conservation actions (Allen and Singh 2016; Sutherland 1998).

In the early years of ethology, field biologists largely relied on direct observations to gain insights into wild animal behaviour (Martin and Bateson 2007). However, human presence might be perceived as a threat by wild animals and thus induce – even subtle – changes in behaviour (Caine 1990; Schneirla 1950). Moreover, direct observations are limited to highly visible species in accessible habitats. In the early 1960, advances in technology led to the development of radio-transmitters, which could be used to remotely track animals in their natural surroundings (Cochran and Lord 1963; White and Garrot 1990). Radio-telemetry became a renowned method in ecological studies and was used to explore movement patterns and space-use, resource selection and even survival (Amlaner and MacDonald 1980; Millspaugh and Marzluff 2001). However, radio-tracking also had limitations, as following animals in difficult terrain could be arduous and time-consuming. Moreover, while radio-tracking enabled investigations on where and when an animal moved, it was still difficult or impossible to determine what the animal was doing (Macdonald 1978; Macdonald and Amlaner 1980).

This gap of knowledge was soon to be closed when the first bio-logging units – small, sensor-equipped electronic tags that could be attached to animals for collecting physical and biological data – were emerging (Kooyman 2004). In pioneering studies on free-living Weddell seals (*Leptonychotes weddelli*), the first time-depth-recorders (TDRs) were deployed to investigate diving depths in hitherto untraceable marine divers (Kooyman 1965). Even though the use of animal-borne bio-logging devices advanced only slowly during the early years, it was clearly the starting point for a new era in wildlife research. Today, finally, behavioural information can be gathered remotely – without the presence of an observer – and linked to movement patterns and physiological measurements of animals (Evans et al. 2013). Increasingly, technological advances are leading to the development of even-more sophisticated, miniaturized tags, which feature a broad suite of sensors for measuring physiological parameters such as temperature and heart rate (Evans et al. 2016; Pongais 2007), social interactions (Cross et al. 2013; Prange et al. 2011), spatial movement (Kays et al. 2015) and body movement and behaviour (Brown et al. 2013; Gómez Laich et al. 2008), and even power use (Wilson et al. 2006). Amongst these sensors, tri-axial accelerometers (hereafter 3D-ACCs) and GPS systems are particularly powerful examples, which enable the determination of animal behaviour and movement patterns, and can be combined with other sensors, e.g. depth transducers to provide remarkable detail on the behavioural ecology of wild animals in an environmental context.

3D-ACCs document 'static acceleration', which represents the angle the device is tilted with respect to the Earth's gravitational field (1 *g* = 9.81 $m.s^{-2}$), and 'dynamic acceleration', which is superimposed on the former signal and stems from the subject motion (Shepard et al. 2008). Attached on an animal, 3D-ACCs measure posture and movement and can thus be used to determine animal activity and behaviour (Shepard et al. 2008; Wilson et al. 2008). Tags containing these sensors are usually mounted so that the three (orthogonal) axes represent the dorso-ventral (heave), the anterior-posterior (surge) and the lateral (sway) body acceleration and thereby body angles. In addition, the dynamic acceleration component can be summed to derive mean overall- or vectorial dynamic body acceleration (ODBA and VeDBA, respectively) according to methods described in Wilson et al. (2006) and Qasem et al. (2012). Dynamic body acceleration – both as ODBA and VeDBA – has been shown to be a good proxy for the rate of oxygen consumption, and is therefore useful for documenting movement-based activity and power use (Halsey et al. 2009; Qasem et al. 2012). Applications of the accelerometry technique have allowed detection of heretofore unknown aspects of wild animal behaviour, ranging from investigations into activity and energy budgets (Gervasi et al. 2006; Wilson et al. 2012), through foraging strategies (Ropert-Coudert et al. 2006; Wilson et al. 2010), to the determination of detailed ethograms (Gómez Laich et al. 2008; McClune et al. 2014). GPS systems are another powerful bio-logging tool for studying spatial movement patterns in free-living animal species. Locating animals with GPS systems has several advantages over other technologies such as radio-tracking or Argos satellite positioning, as it is more accurate, allows for determination of animal positions on the Earth's surface or in the air, provides precise time-stamping and can potentially be used 24 hours (Tomkiewicz et al. 2010). Recording an animal's movement paths in proper space helps elucidate favoured landscapes and, thus, highlights important habitat features relating to e.g. food or other resources selected (Johnson et al. 2002).

Investment in movement – both in terms of non-translational body movement and movement through space – may differ in terms of time, energy and effort used by an animal, and the way animals allocate their individual resources to specific activities is a key parameter in understanding their ecology (Brown et al. 2004). Today, tracing both these movement types is facilitated by the use of bio-logging units such as accelerometers and GPS systems, and has advanced the scientific understanding of vital ecological processes (Kays et al. 2015). For example, accelerometers attached to jaws are used to determine foraging strategies, effort and success in marine predators (Ropert-Coudert et al. 2006; Viviant et al. 2010; 2016) and a combination of accelerometers and GPS systems has revealed that the energy use of pumas (*Puma concolor*) during sneak attacks increases with prey size (Williams et al. 2014). Satellite tracking systems such as GPS units have been used to document migratory movements, destinations and survival of birds (López-López et al. 2014; van Wijk et al. 2012), ungulates (Hebblewhite and Merrill 2007; Mysterud et al. 2011) and marine species (Hoenner et al. 2012). However, the bio-logging technique also has limitations, which are typically related to the size and weight of the units, particularly modulated by battery size which relates to battery-, and therefore, tag-life (Cagnacci et al. 2010; Ropert-Coudert and Wilson 2005). In addition, capture and tagging may affect the behaviour and movement of an animal, and should thus always be considered and investigated when conducting bio-logging studies (Ropert-Coudert and Wilson 2004). The implementation of the accelerometry technique to study animal behaviour and movement is relatively new and, in particular with regard to mammalian species, accelerometers have mainly been deployed on domestic species or captive individuals (Brown et al. 2013).

Capitalizing on the value of bio-logging techniques for understanding the behavioural ecology of elusive animals, we deployed tri-axial accelerometers and GPS units on free-living Eurasian beavers (*Castor fiber*) to study their behaviour and movement patterns. Beavers (both the Eurasian and the North American beaver (*C. canadensis*)) are socially monogamous (Crawford et al. 2008; Syrůčková et al. 2015), semi-aquatic mammals that live in family groups consisting of the dominant pair, the young of the year, yearlings, and subdominants (Campbell et al. 2005). Beavers inhabit freshwater bodies such as rivers and streams, lakes and ponds (Rosell et al. 2005). They are nocturnal and the family spends the daytime inside lodges or bank dens (Barnes and Dibble 1988; Wilsson 1971). Beavers are highly territorial and announce territory occupation by scent-marking (Rosell et al. 1998). Belonging to the 3-5 % of mammalian species that form monogamous pair bonds (Kleiman 1977), beavers exhibit complex social behaviours including male parental care and shared territorial defence (Busher 2007). In fact, thus far, sex-differences have been confirmed for daily travelling time, with males allocating more time to travel (Sharpe and Rosell 2003) and scent-marking (Rosell and Thomsen 2006). Beaver territories have been found to be larger during initial settlements in an area, whereas in populations at carrying-capacity, territories of various sizes are occupied (Campbell et al. 2005; Nolet and Rosell 1994). As herbaceous central-place foragers, beavers have a preference for willows (Salix *spp.*) and poplars (*Populus* spp.) (Haarberg and Rosell 2006; Nolet et al. 1994), but also forage on aquatic plants (Parker et al. 2007). The beavers' fusiform body with short limbs, webbed hind feet and waterproof fur reflect the animals' adaption to an amphibious life (Allers and Culik 1997; Wilsson 1971). Beavers build dams to, amongst other things, raise water levels sufficiently high to keep the lodge entrance under water and hold functional winter food caches (Hartman and Axelsson 2004; Hartman and Törnlöv 2006). Bio-logging studies conducted on beavers have used radio-transmitters (implants or tail-tags) to investigate space use and movement (Herr and Rosell 2004; Nolet and Rosell 1994), as well as GPS systems to analyse resource selection (Steyaert et al. 2015).

The main goals of this thesis were to;

a) determine the general suitability of accelerometers to study beaver behaviour and advance the method (papers I, IV, V),

b) detect possible tagging effects and consequences of using bio-logging technology on animals (paper II) and

c) apply these findings when studying behavioural aspects of beavers (papers III, IV). Here, we aimed to quantify particularly costly behaviours such as spatial movement patterns linked to territorial behaviours and foraging, as well as diving behaviour.

2. Objectives and rationale

Can tri-axial accelerometers be used to study animal behaviour using beavers as a model species? (papers I, IV, V)

Today, high-resolution bio-logging data are widely used to determine the ecological function of behaviour and movement patterns of animals (Kays et al. 2015). Within this field, accelerometers provide information on body posture, movement and even movement-based energy use (e.g. ODBA, VeDBA) (Qasem et al. 2012; Wilson et al. 2008). Initial applications of the accelerometry technique mainly focused on marine species such as penguins (Yoda et al. 1999) and seals (Mitani et al. 2004), but were soon complemented by studies on free-living terrestrial species (e.g. Williams et al. 2014). Applications are multiple and range from investigations on foraging behaviour (Kokubun et al. 2011), to diving behaviour (Gallon et al. 2013), flight dynamics (Williams et al. 2015) and even welfare issues (Whitham and Miller 2016) and conservation (Wilson et al. 2015). We aimed to extend and reinforce the field of accelerometry studies by applying the method to a semi-aquatic mammalian species, the Eurasian beaver. We used acceleration data corroborated with control observations to identify a suite of behaviours in a free-living beaver population in

Norway. By using this approach on a four-leg locomoting mammal with a complex behavioural repertoire like the beaver, we aimed to attain novel perceptions on the implementation of accelerometry to explore animal behaviour.

Does capture and tagging induce changes in activity and movement patterns in beavers? (paper II)

The application of bio-logging technology to study remotely animal behaviour and movement patterns has increased significantly over the last decade (Evans et al. 2013; Wilmers et al. 2015). Increased miniaturization of bio-logging units is important for lowering the impact on tagged animals in general (e.g. Ropert-Coudert et al. 2009) and allows for applications on even 'small' animals such as neonate loggerhead turtles (*Caretta caretta*) (Mansfield et al. 2014) or songbirds (e.g. the Ovenbird *Seiurus aurocapilla*) (Hallworth and Marra 2015). Animal welfare is an integral issue in bio-logging studies and this stresses the need for determining the impact of the tagging event (Hawkins 2004; Kays et al. 2015). We tagged beavers both with tri-axial accelerometers and GPS units (or a combination) to determine whether the process affected behaviour. This is particularly important for avoiding biased research results, as we used the gathered bio-logging data in further analyses for papers III and IV. We used acceleration and GPS data to analyse tagging effects in terms of activity (mean ODBA, principal activity periods) and movement patterns (distances moved and lodge displacement rate LDR) during the first week after the tagging event. Sharpe and Rosell (2003) and Ranheim et al. (2004) implanted beavers with intraperitoneal radio transmitters and found that the animals spent more time inside their lodges during the first few days after release. We thus hypothesised that there would be a shift in activity and movement patterns and predicted that beavers would reduce their activity (i.e. lower mean ODBA and shorter principal activity periods), cover shorter distances and stay closer to the lodge in the first nights after the tagging event.

The trade-off between foraging and patrolling: Which factors explain terrestrial and aquatic movement patterns of beavers? (paper III)

Territorial behaviours such as boundary patrols and scent-marking are essential for advertising territory occupation (Sillero-Zubiri and Macdonald 1998) and are, besides foraging, an important driver of movement decisions in animals (Fagan et al. 2013). Animals need to decide on the most appropriate behaviour at any one time since simultaneous multiple behaviours are usually impossible (Mangel and Clark 1986); in territorial species such as beavers, this creates a trade-off between foraging and territorial defence. In general, territory size is suggested to be optimised by time constraints between resource defence and exploitation, resulting in a ‘minimum economically defensible area’ (MEDA) (Gill and Wolf 1975; Pyke et al. 1977). However, in dense populations close to or at carrying capacity, other factors, such as interactions among neighbours and interactions between established residents and new settlers, may influence territory size (Adams 2001). Thus, territories smaller or larger than the MEDA can be found in such populations, while larger areas are generally more costly to defend (Righton et al. 1998; Schoener 1983). In line with this, we found territories of various sizes (determined by GPS locations) for beavers in our study population, which is at carrying capacity. We thus aimed to investigate movement patterns of beavers in the context of foraging and patrolling to identify strategies that pay off according to different territory sizes. We used GPS data to analyse terrestrial and aquatic movement patterns in relation to environmental and demographic factors. These factors included territory size, resource availability, season, intruder pressure (number of neighbours) and age. We predicted that beavers owning larger territories would cover larger distances in water, but could trade this off through foraging closer to the shoreline (more space for food plants). We also predicted a higher patrolling effort both during spring, when subadult beavers are dispersing, and when facing a higher intruder pressure (more neighbours). Lastly, we predicted an age-dependent change in movement patterns linked to increased dominance and experience.

How is diving behaviour manifest in beavers and which behavioural mechanisms increase diving efficiency? (paper IV)

Semi-aquatic mammals have evolved on land and possess adaptions for moving in aquatic and terrestrial environments but are generally considered to be imperfectly adapted to both media (Fish 2000; Williams 1999). Air and water are media with distinct physical features, with water being denser and having a higher thermal conductivity than air. This implies physical constraints to semi-aquatic species, which, as a result, face higher energetic costs when moving in the aquatic environment (Dunstone 1998; Williams 1999). These costs have been found to be particularly high during diving, as a result of higher heat loss (MacArthur and Krause 1989) and increased physical effort to overcome buoyancy and drag (Fish et al. 2002). Little is known about the diving behaviour of semi-aquatic freshwater species (Hays et al. 2007), and diving in beavers has been exclusively studied in North American beavers based on physiological and morphological aspects (e.g. Allers and Culik 1997; MacArthur and Dyck 1990). Thus, we used accelerometry data combined with readings from a pressure sensor to study beaver diving performance in terms of maximum diving depth, dive duration, bottom phase duration and number of dives per night. We linked these parameters to physical effort during diving (mean VeDBA and vertical velocities during descent and bottom phase), water temperature, weight and sex of individual beavers. Due to the positive buoyancy of beavers, we hypothesised that there would be higher power use in particular during the descent, which would vary with diving depth. We predicted that beavers would perform short and shallow dives, and that reduced dive durations would be associated with higher power use (mean VeDBA). Moreover, we predicted that deeper dives should be coupled with longer bottom phase durations and that colder water temperatures would reduce diving behaviour.

How can we advance the analysis of high-frequency tri-axial acceleration data? (paper V)?

A better understanding of movement and behaviour is of particular interest for biologists, not least because movement requires energy. Movement energetics in animals are being increasingly studied through the application of accelerometers (Williams et al. 2014) and accelerometry-based metrics such as ODBA and VeDBA (Qasem et al. 2012; Wilson et al. 2006). However, linking behaviour and movement to energy-use based on accelerometry data can be challenging, as data are typically recorded at high frequencies (> 20 Hz) resulting in particularly large datasets which are expanded once the static acceleration (due to animal posture) is uncoupled from the dynamic acceleration. This points to a need for a framework for combining behaviour and energy use. Because the earth's gravity is constant, tri-axial acceleration data plotted in a three-dimensional plot fundamentally builds a sphere, a 'g-sphere' (Grundy et al. 2009). Our aim was to advance the applicability of the g-sphere by developing a framework for plotting animal postures, onto which we superimposed data on energy use (or any other parameter of interest, e.g. pressure data). We used data from different animal species (see paragraph 3.2.2) and humans to test the applicability of this approach.

3. Material and Methods

3.1. Study area

The study sites are located at the lower reaches of three large rivers, the Straumen, Gvarv and Sauar, in Telemark County, southeastern Norway (59°23’ N, 09°09’ E). All three rivers lie within an average linear distance of approx. 15 km apart from each other and empty into Lake Norsjø. The river sections are generally slow flowing with stable water levels, feature similar depth structures (average depth approx. 20 m, source: Statens Kartverk Telemark) and are about 20 - 150 m wide (Campbell et al. 2012). Beavers do not build dams in the rivers as they are deep and wide enough (Hartman and Törnlöv 2006). Riverbanks are accompanied by semi-agricultural and riparian woodland structures with tree-species such as grey alder (*Alnus incana*), willow (*Salix* spp.), bird cherry (*Prunus padus*), common ash (*Fraxinus excelsior*), rowan (*Sorbus aucuparia*), birch (*Betula spp.*) and Norway spruce (*Picea abies*) (Haarberg and Rosell 2006). Wider river sections and man-made impoundments reduce ice cover in winter (Campbell et al. 2012). The climate in the area is cool continental with a mean annual temperature of 4.6 °C and a mean annual precipitation of 790 mm (Campbell et al. 2012). Both hunting pressure (only 4.6% of the known population was hunted between 2009-2014, c.f. paper III) and the presence of natural predators in the area was low (Herfindal et al. 2005).

3.2. Study animals

3.2.1. Free-living Eurasian beavers

Eurasian beavers have inhabited the area since the 1920s (Olstad 1937) and the population has been at carrying-capacity for the last 10 years (Campbell et al. 2005; Steyaert et al. 2015). Since 1997, beavers in the study area are live-trapped every year as part of an extensive capture-mark-recapture scheme (Campbell et al. 2005;

Campbell et al. 2012). Captured animals are routinely sexed (Rosell and Sun 1999), aged (Rosell et al. 2010), weighted, measured (body length, tail length and thickness), micro-chipped and marked with unique ear-tag combinations. We only used dominant individuals in this study. Dominance status was assigned by multiple capture and/or sighting events of an individual within the same territory, body weight, disappearance of the former dominant male/female, and incidences of lactation in females (Campbell et al. 2012).

3.2.2. Control observations and other study species

For paper I, control observations were conducted on four captive and two free-living beavers. We used two North American beavers *C. canadensis* (one male, one female) in the Alpenzoo Innsbruck (AT), a male Eurasian beaver in the Highland Wildlife Park (UK) and a female Eurasian beaver in Edinburgh Zoo (UK). In addition, we also observed two device-equipped free-ranging Eurasian beavers (one male, one female) in our study area. For paper V, we compared data from Eurasian beavers and several other animal species, including Argentine sea bass (*Acanthistius patachonicus*), European badgers (*Meles meles*), imperial cormorants (*Phalacrocorax atriceps*), Magellanic penguins (*Spheniscus magellanicus*) and humans (*Homo sapiens*).

3.3. Tags

We used two types of archival tags – tags which store data on-board without satellite communication – in this study: tri-axial accelerometers and GPS systems. We also deployed radio-transmitters for retracing the beavers for tag retrieval. ***Tri-axial accelerometers (3D-ACCs).*** The data logger contained a tri-axial accelerometer (3D-ACC), as well as a temperature and a pressure sensor (JUV Elektronik, DE; size 90 x 15 mm dia, mass 62 g). Acceleration in three axes was recorded with a frequency of 8 Hz, pressure with a frequency of 2 Hz and temperature with a frequency of 1 Hz. ***GPS systems.*** We deployed rechargeable micro GPS systems (model G1G 134A, Sirtrack Ltd, NZ; size 50 × 70 mm, mass 24 g), which were programmed to take a position every 15 min from 7:00 pm to 7:00 am, and were set to sleep during the day. ***VHF-transmitters*.** We attached VHF-transmitters (Reptile glue-on series R1910; Advanced Telemetry Systems, USA; size 18 × 35 mm, mass 10 g) in combination with accelerometers and GPS systems to relocate animals for recapture or for locating lost units.

3.4. Capture method and tagging

Dominant Eurasian beavers were captured between 7:00 pm – 7:00 am with a landing net from a boat after a method developed by Rosell and Hovde (2001). The animals were then transferred into a cloth bag, where they were handled and tagged without administering anaesthesia. The tags were connected with wire or glued together and integrated in a 4.5 mm half-mesh net covering. We used a quick-setting, two-component epoxy resin to glue the final tag onto the fur of the lower back along the spine, 15 cm above the scaly tail (Figure 1). The whole unit was 130 x 90 mm in size (incl. netting) and weighed 90 g in air. Beavers were released at the trapping site within their own territory and relocated and captured via VHF-telemetry after 2-6 weeks, to cut the tag out of the fur with a scalpel. This procedure predominantly affected the guard hairs but not the under-fur and the patch of clipped hair grew back within 3-4 months.

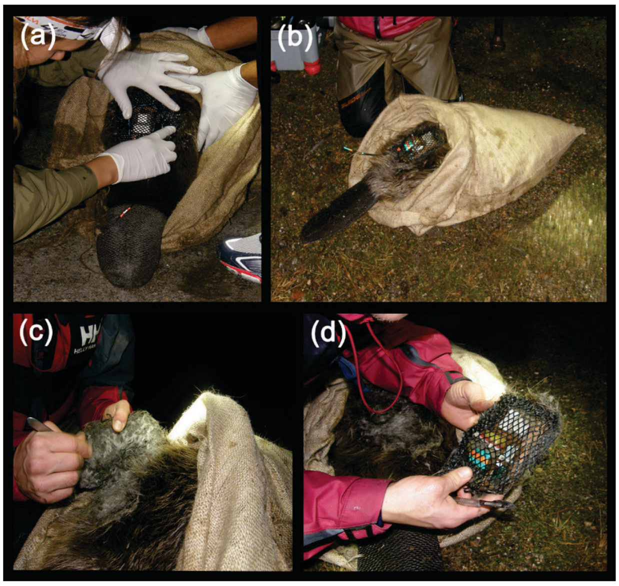

Figure 1. Tagging procedure and retrieval of tags for Eurasian beavers (*Castor fiber*) in southeastern Norway (2009 – 2014) – *reproduced from paper II*. Beavers were handled and tagged in cloth bags without the use of anaesthesia. (a) A GPS unit is glued onto the fur of the lower back (15 cm on top of the scaly tail) using two-component epoxy resin. (b) By using VHF-telemetry, a beaver tagged both with an accelerometer and a GPS unit has been recaptured. (c) The tag is cut out of the guard hair with a scalpel, leaving the underfur intact. (d) The tag is retrieved.

3.5. Data collection and preparation

All data were collected in the years 2009 to 2014. We analysed data from 10 beavers tagged with 3D-ACCs paper I, for paper II, we used data from 11 beavers tagged with 3D-ACCs and 15 beavers tagged with GPS units, for paper III, we used data from 17 beavers equipped with GPS units and in paper IV, we used data from 12 beavers tagged with 3D-ACCs. Raw acceleration data for determining beaver behaviour and activity were only used in paper I. We corroborated the raw acceleration data with control observations and then exported 10 sequences of static acceleration data for each behaviour using the software Snoop (Swansea University, UK). In addition, we calculated mean ODBA as a proxy for movement-based activity for each behaviour. In paper II, we calculated mean ODBA values over 15 min to investigate activity levels after the capture and tagging event, and paper IV mean VeDBA over 15 min to examine power use during the descent and the bottom diving phases. Accelerometry data were also used to derive principal activity periods (active time per night; time from emergence from the lodge in the evening to return to lodge in the morning) to investigate the beavers' nightly activity budgets (papers II, IV). Pressure data were used in paper IV, where we calculated maximum diving depth, dive durations, bottom phase durations and vertical velocities during the descent and bottom phases using Multitrace (Jensen Software Systems, DE).

Raw GPS data were cleaned by removing fixes with a horizontal dilution of precision (HDOP) ≥ 5 (papers II, III; Lewis et al. 2007). In paper II, we calculated distances moved (distance between two consecutive GPS locations) and the lodge displacement rate LDR (linear distance from a GPS location to the main lodge) using the adehabitatLT package in R (Calenge 2006). For this, we raised the sampling interval from 15 to 30 min to increase the number of consecutive GPS locations. In paper III, we used GPS data to determine territory sizes based on stretches of shoreline used. Moreover, we calculated average perpendicular distances from the shoreline when beavers where either in water or on land. We also counted the number of GPS locations that were in close vicinity to absolute and relative border zones (absolute: time within 75 m from the territory border, relative: time within 5% zones depending on territory length) to determine patrolling effort and territorial behaviours. All data preparation for paper III was conducted in ArcMap 10.1 (Esri, USA).

In papers I, III, IV, V, we removed the first 1-2 days of the dataset to account for possible capture effects, while we included all days in paper II as our aim was to test for such effects. In papers II and IV, we standardized the dataset to range from 5-7 nights. Data for paper V were collected from a range of different animal species (see section 3.2.2) by several different research groups. In paper V, we plotted normalised three-dimensional static acceleration vectors as points onto the surface of a sphere (the '*g*-sphere') and divided the sphere into facets. We then projected the number of points within facets as spherical histograms to quantify the time allocated to different postural states creating a 'Dubai' plot. In another representation, the '*g*-urchin' plot, dynamic body acceleration DBA was superimposed onto postures. For this, we exchanged histogram bars with spines (one spine per facet, only for facets that include data) and displayed the frequency distribution of the DBA values as stacked rings. The position on the spine corresponds to the DBA value (higher values are further away from the surface), the depth of the ring indicates the width of the DBA bin and the diameter of the ring represents the number of data points in each bin.

3.6. Statistical analyses

For classifying behaviours in paper I, we used a random forest algorithm (R package randomForest; Liaw and Wiener 2002). All behaviours, apart from sleeping (which consists of several different postures) were classified using mean values and standard deviations of the surge, sway and heave acceleration and ODBA. In paper II, we used linear mixed-effects (LME) models with the log-transformed response variables 'mean ODBA', 'distance moved' and 'LDR', the main predictor 'minutes after release' and 'individual' nested within 'year' as random effect. For the response variable 'principal activity period' we also used a LME model with 'night' as the main predictor and 'individual' as random effect. In all models, we also used the covariates 'season' (spring: April-May vs. autumn: August-November), 'sex', 'total number of times captured before' and 'tag load' (smaller and lighter vs. larger and heavier tag). In analyses based on GPS data, we also used the covariate 'territory size' (= bank length used). When necessary, we also accounted for temporal autocorrelation of the response variables by adding a first-order autoregressive term (corAR1) to our models (Pollitt et al. 2012; Zuur et al. 2009).

In paper III, we ran separate generalized linear models (GLMs) for GPS locations on land and in water. For movement patterns in water, we used the response variables 'distance moved/h', 'relative patrolling effort' and 'absolute patrolling effort'. For movement patterns on land, we used the response variables 'average distance from the shoreline', 'time spent on land' and 'average distance between GPS positions/h'. In all models, we used the predictors 'territory size' (= bank length used), 'resource availability' (area of mixed-deciduous forest in ha), 'number of neighbours', 'season' (spring vs. autumn) and 'age'. In paper IV, we used LME models for the ln-transformed response variables 'maximum diving depth' and 'dive duration' and included the predictors 'mean VeDBA during descent', 'vertical velocity during descent', 'water temperature', 'sex' and 'weight'. Moreover, we ran a separate LME without covariates to analyse the relationship between 'maximum diving depth' and 'dive duration'. We calculated a GLM for the ln-transformed response variable 'mean number of dives per night' and included the covariates 'water temperature', 'sex' and 'weight'. We ran a double-hurdle model for the response variable 'bottom phase duration' to determine whether the animals invested in a bottom phase, and if so, which factors determined the length of the bottom phase. We used the covariates 'maximum diving depth', 'water temperature' and 'mean VeDBA during the bottom phase'. In all models, we used 'individual' as random effect. Before running the models, we excluded collinearity between the predictors ($r < 0.6$ and variance inflation factor $VIF < 3$; Zuur et al. 2010).

3.6.1. Model selection

In papers II and IV, we applied a backward model selection procedure, while we selected 12 explanatory variables *a priori* in paper III. For all papers, the most parsimonious models were selected based on the Akaike information criterion corrected for small sample sizes (AIC_c) (Burnham et al. 2010; Wagenmakers and Farrell 2004). Candidate models within AIC_c differences (ΔAIC_c) between 0-2 were considered as models with strong levels of empirical support (Anderson 2008). Amongst these models, we chose the simpler model as the final model in papers II and III, while we applied a model-averaging procedure in paper IV. Model parameters including zero within their 95% confidence interval (CI) were considered as uninformative (Arnold 2010). All statistical analyses were performed using the software R (R Development Core Team 2013).

3.7. Ethical statement

The study, including all handling and tagging procedures, was approved by the Norwegian Experimental Animal Board (FOTS id 742, 2170, 2579, 4387 and 6282) and the Norwegian Directorate for Nature Management (archive code 444.5 and 446.15/3), which also granted permission to conduct fieldwork in our study area.

4. Summary of results

In paper I, we identified seven beaver behaviours including standing, walking, swimming, feeding, grooming, diving (Figure 2) and sleeping. All behaviours were identified using video-recordings from control observations and showed distinctive static acceleration sequences (Figure 2). The random forest model classified behaviours with 95% accuracy; kappa statistics were over 0.94 and the model showed high specificity and sensitivity (100% and 95.8%, respectively).

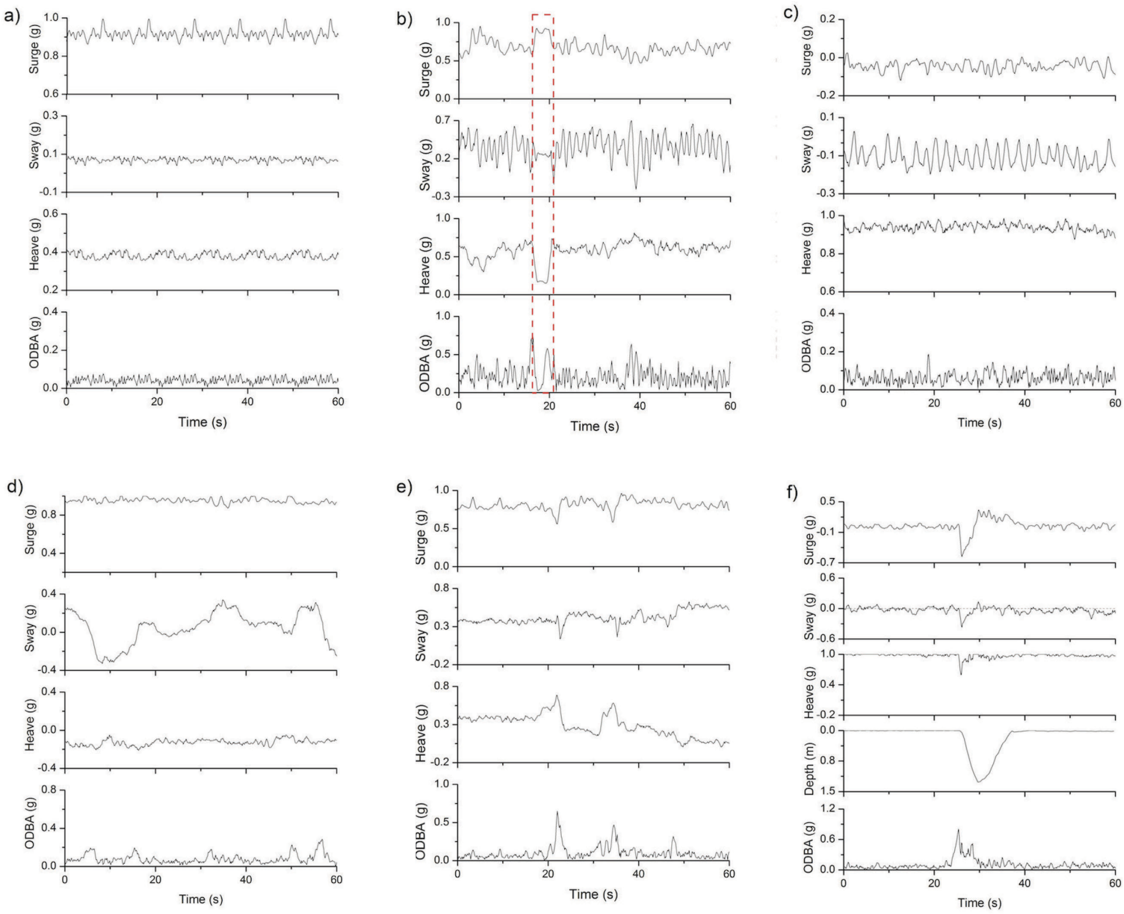

Figure 2. Changes in the static acceleration signal of Eurasian beavers (*Castor fiber*) during standing (a), walking (including a standing period within the dashed rectangle, b), swimming (c), grooming (d), feeding (e), and a v-shaped dive with short bottom phase (f) – *reproduced from paper I.*

For the classification of behaviours, mean values of the static surge, heave and sway were more important variables than standard deviations, with the mean static heave acceleration signal contributing most. While standing behaviour was characterized by largely steady acceleration signals in all three axes (Figure 2a), both walking and swimming showed oscillations in the sway axis, which stem from alternating footsteps and foot beats during swimming, respectively (Figure 2b, c). Walking static sway signals had greater amplitude ($\bar{x}_{\text{walk}} = 0.26\ g$, $\bar{x}_{\text{swim}} = 0.11\ g$) and lower cycle frequencies ($\bar{x}_{\text{walk}} = 0.82$ Hz, $\bar{x}_{\text{swim}} = 0.44$ Hz) than swimming (Figure 2b, c). Grooming was characterized by a negative mean static heave acceleration ($\bar{x} = -0.15\ g$) and cyclic patterns in the sway linked to repetitive grooming motions (Figure 2d). Feeding featured the lowest positive mean static heave acceleration ($\bar{x} = 0.19\ g$, Figure 2e). Diving was visible through changes in the depth transducer and had a mean static heave acceleration of 0.91 *g* (Figure 2f). Sleeping was characterized by stable lying postures accompanied by occasional turns, which were manifest as radical changes in the static heave acceleration.

After testing the acceleration methods' potential to study beaver behaviour, we investigated whether the capture and tagging event altered activity and movement patterns within the first week after release (paper II). Beavers showed a lower post-release activity and mean ODBA (Figure 3), respectively, although effect size measures suggested this difference was only minor ($\beta_{log} = 2.\ 15e^{-05}$, Cohen's $d = 0.17$). Principal activity periods did not change after the tagging event but were shorter during spring. Moreover, we did not detect any changes in movement patterns after the tagging event, i.e. distances moved and LDRs did not change within the first week after release. Distances moved were best explained by territory size, with beavers covering greater distances in larger territories.

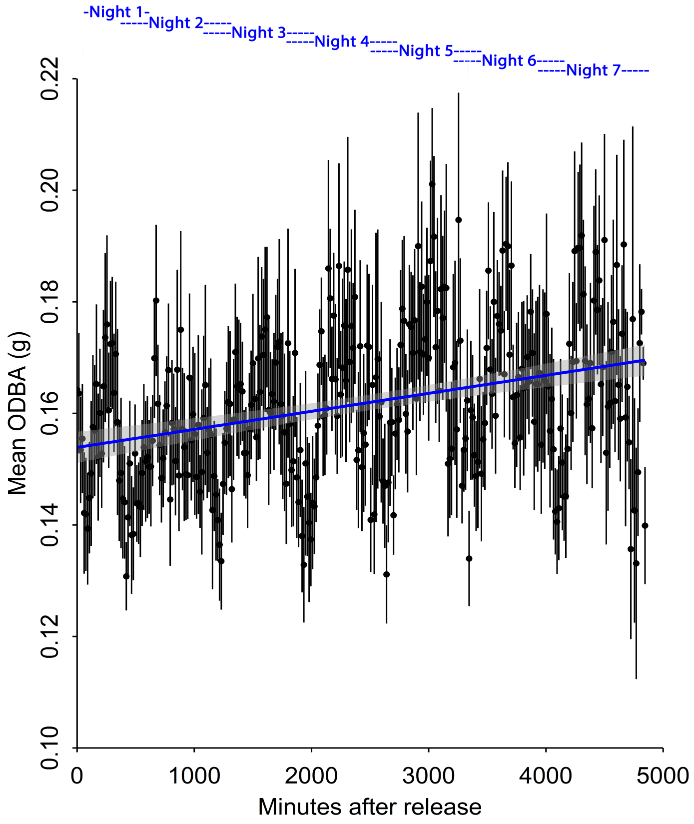

Figure 3. Linear relationship (regression line and 95% confidence interval) between mean ODBA (overall dynamic body acceleration) and minutes after release for 14 dominant Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2014). The axis on top of the graph shows the different nights after release; overlap results from the different capture times in the first night. Each point represents the overall mean (± SE) over individual mean ODBA values measured every 15 minutes after the tagging event – *reproduced from paper II*.

In papers III and IV, we used bio-logging technology (accelerometers, GPS units) to study selected behavioural aspects of beavers. In paper III, we investigated the spatial movement of beavers in water and on land and found that these movement patterns were largely linked to territory sizes and the age of an individual. Beavers in larger territories moved greater average distances per hour in water but stayed closer to the shoreline when being on land (Figure 4). Relative patrolling effort – the time beavers spent within 5% zones at the upper and the lower border – also increased with territory size. Both absolute patrolling effort (time spent within 75 m border zones) and time spent on land increased with the age of an individual (Figure 4). Average distances covered per hour on land were best explained by season, with beavers moving greater distances in spring.

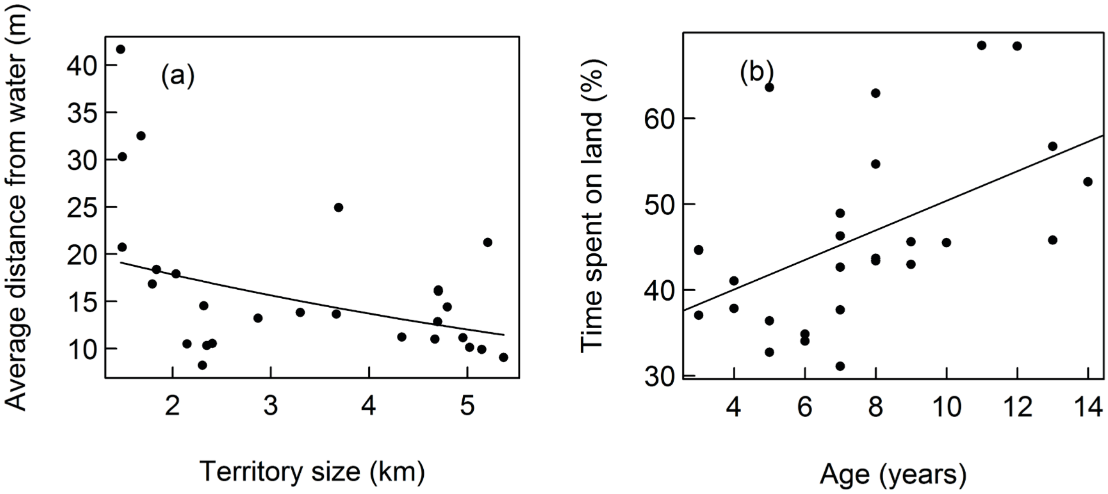

Figure 4. Back-transformed prediction (solid line) between territory size (measured as bank length) and average distance from the shoreline for all land positions (a), and predicted relationship between the age of an individual and the time spent on land (b) for 25 Eurasian beavers (*Castor fiber*) in southeast Norway – *reproduced from paper III*.

In paper IV we studied the diving performance of beavers and analysed at total of 2596 dives. Beavers generally dived in shallow water (< 1m) and for short periods (< 30 sec). Diving activity increased throughout the night and peaked between 03:00 – 07:00 am. Dive duration increased with diving depth, while only 2.8% of the beavers' principal activity periods constituted of diving. Both maximum diving depths and dive durations were best explained by mean VeDBA – which we used as a proxy for power use – and vertical velocities during the descent phase. Shallower dives were associated with higher mean VeDBA values (Figure 5a), while deeper dives featured higher vertical velocities (Figure 5b). Both higher mean VeDBA and vertical velocities resulted in shorter dive durations (Figure 5c,d). The mean number of dives per night was best explained by water temperature, but the variable was not informative and thus impeded further conclusions. The majority of the dives included a bottom phase (82%), with a higher likelihood in deeper dives. Bottom phase durations were shorter when mean VeDBA during the bottom phase was higher, but increased with diving depth (Figure 5e,f). In addition, we found that beavers also featured dives with longer bottom phase durations, which were executed at greater diving depths but were coupled higher mean VeDBA values.

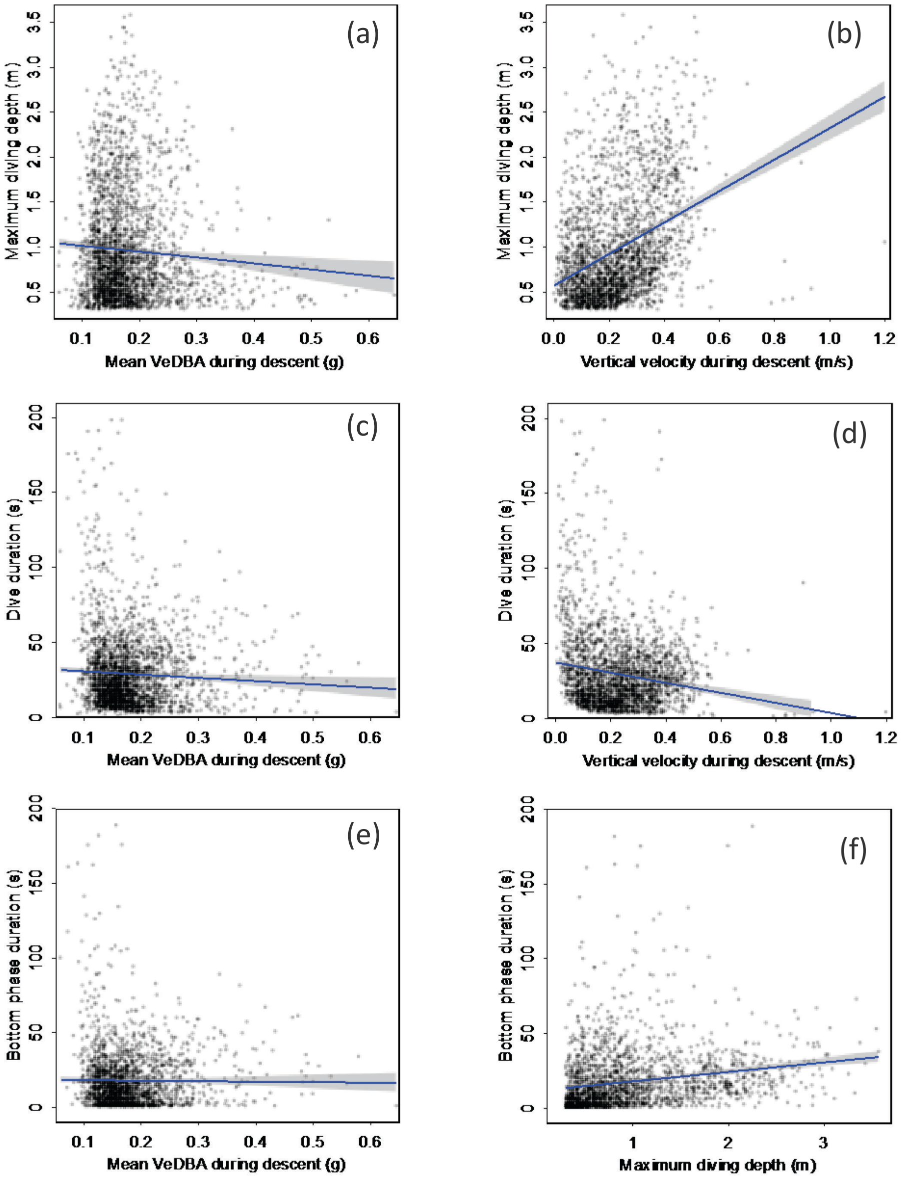

Figure 5. Predicted relationship between maximum diving depth and mean VeDBA (vectorial dynamic body acceleration) during the descent (a), maximum diving depth and vertical velocity during the descent (b), dive duration and mean VeDBA during the descent (c), dive duration and vertical velocity during the descent (d), bottom phase duration and mean VeDBA during the descent (e) and bottom phase duration and maximum diving depth (f) for 11 Eurasian beavers (*Castor fiber*) in southeast Norway – *reproduced from paper IV.*

In the last paper, we show that static acceleration data points can be clustered according to their body attitude trough plotting them on a g-sphere. Over-plotting can hamper analyses in large datasets; by dividing the sphere into facets and plotting the number of data points as spherical histograms, which reflect the time spent in each posture, we present the Dubai plot as a solution to this. Instead of plotting histograms, data points can also be plotted as spines with stacked rings, which represent, for example, DBA values during different postural states (Figure 6). Data points in the g-urchin plot can be normalised for the whole time period considered to show general time and proxy for energy (Figure 6), or be normalised per facet to fade out the time factor and just highlight energetic proxies for different behaviours. Both Dubai and g-urchin plots can be subtracted from each other to derive colour-coded differential plots, which refer to differences in posture and power use, respectively. We also present a simplified version of the g-sphere: the ‘lifestyle’ plot represents a 2-d line graph illustrating the time and/or DBA in relation to the percentage coverage on the g-sphere.

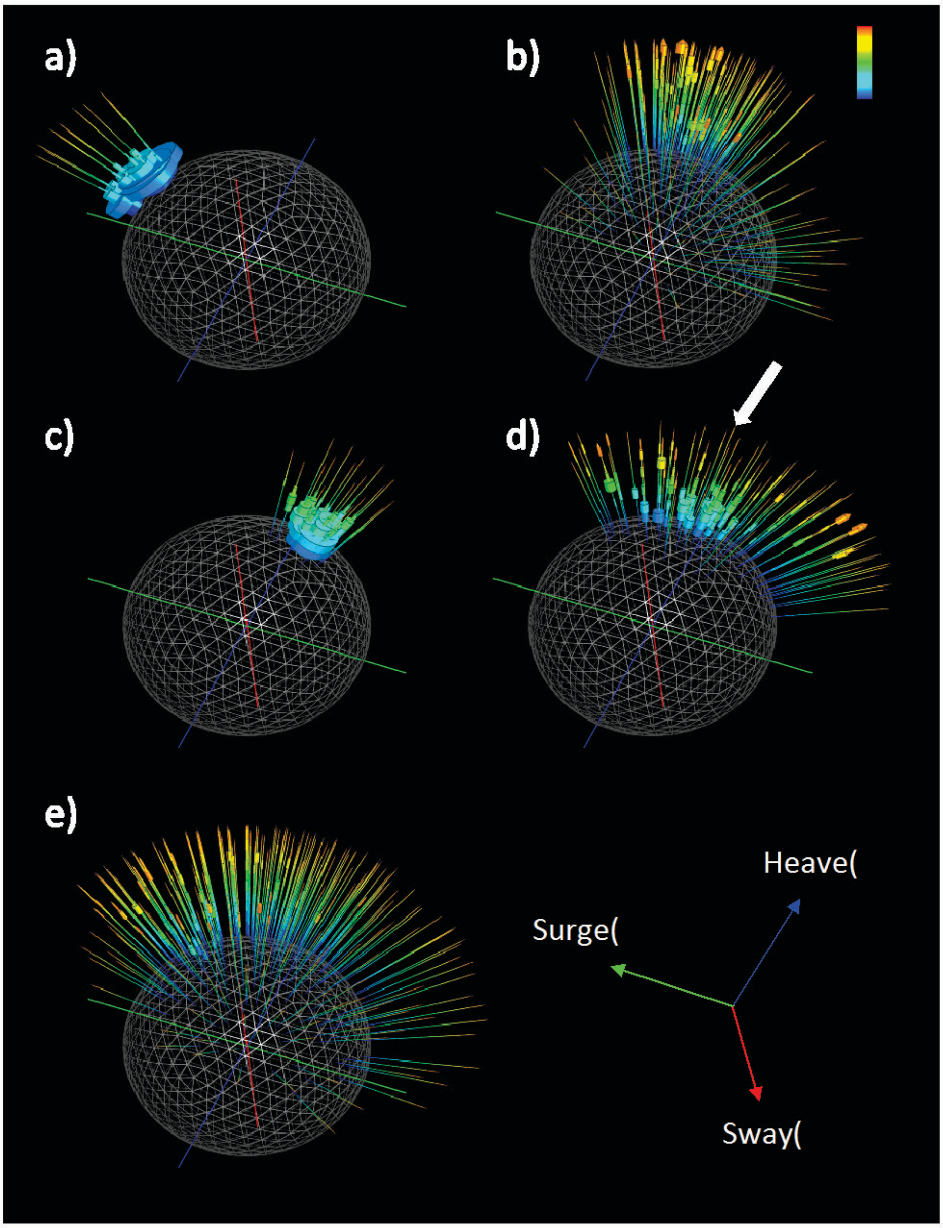

Figure 6. Example of posture and DBA (dynamic body acceleration)-linked urchin plots for five Eurasian beaver (*Castor fiber*) behaviours, including standing (a), walking (b), swimming (c), diving (d), and grooming (e). Standing and swimming include stable/less variable postures, i.e. the spines cluster in one area on the sphere; they also include relatively low DBA-levels, exemplified by the large diameter blue discs. Note the lower DBA-values associated with the bottom phase during diving (white arrow). Note also the broad scattering of spines for grooming, which represents the various postures adopted by the animals during this behaviour. The g-urchin for each behaviour was normalised for all data across the sphere and the discs are colour-coded with maximum values of 1 *g* (in red).

5. Discussion

In this thesis, we underline the accelerometry technique's high potential for studying animal activity and behaviour (papers I, II, IV) and provide researchers with a tool for visualizing acceleration data coupled with proxies for power use or any other parameter of interest (paper V). Capture and tagging may alter an animal's behaviour (Saraux et al. 2011; Wilson 2011) and we documented lower activity (via mean ODBA) of beavers within the first week after release, although this finding was linked to a small effect size (paper II). Finally, we used data from bio-logging units (accelerometers and GPS systems) to study movement patterns (paper III) and diving performance (paper IV) of beavers. We found that movement patterns of beavers in water and on land could be explained by differences in territory size and age (paper III), while much of diving behaviour was defined by the physical effort during the dive phases and the maximum depth reached (paper IV).

5.1. The accelerometry technique – implementation and advancement

Accelerometers have been used to study body motion and activity in animals and human subjects since the 1960s (Coermann et al. 1960; Morris 1973; Mundl 1966; Mundl and Malmo 1979); but only recently has the technique experienced a significant upturn and been increasingly used in animal studies (Wilson et al. 2008). Over the past five years, more and more mammalogists have recognized the potential of the method: Byrnes et al. (2011) tagged five Malayan colugos (*Galeopterus variegatus*) with accelerometers and identified climbing, foraging, gliding, other behaviours and resting. In Arctic ground squirrels (*Spermophilus parryii*), Williams et al. (2016) used ODBA to investigate sex-differences in movement-based energy expenditure during gestation and lactation. Lush et al. (2016) used the accelerometry technique on five European hares (*Lepus europaeus*) to categorize running, feeding and vigilance behaviours with high accuracy. Accelerometers combined with a GPS system were also trialed on one European badger (*Meles meles*) to determine behaviour-time budgets and habitat use (McClune et al. 2015). In wild felids, accelerometers have been used to study key behaviours and activity in cheetahs (*Acinonyx jubatus*) (Grünewälder et al. 2012), identify behavioural categories of pumas (*Puma concolor*) (Wang et al. 2015), including the energetics of instantaneous kills in relation to prey size (Williams et al. 2014). The small sample sizes in these studies (n = 1-6 individuals) illustrate the challenges researchers working on wild mammals still have to face. Not only is capturing and tagging a decent number of study animals an arduous task, but also, researchers have to anticipate a number of tag losses and/or failures (Bidder et al. 2014). We extend the field of mammalian studies by deploying accelerometers on a free-living, semi-aquatic freshwater species, the Eurasian beaver. In paper I, we analysed data from twelve individuals, and, by using a random forest classifier, were able to categorize a set of seven different behaviours including standing, walking, swimming, feeding, grooming, diving and sleeping. Body postures adopted by beavers during different behaviours were mirrored in the acceleration signal and could easily be quantified by using video-recordings of control observations. Limitations of the accelerometry method are typically related to the manner the unit is mounted and its stability, problems of detecting behaviours which occur simultaneously, and physical features such as the size, weight and battery life of the unit.

Another major issue of the accelerometry technique is that data are commonly recorded at high frequencies (today often > 20 Hz), which make interpretation and illustration of such ‘big data’ difficult. Thus, we provide researchers with a solution for visualizing behavioural data coupled with proxies for power use (e.g. ODBA, VeDBA) or any other parameter of interest. Conventional software for inspecting acceleration data typically comprises of panels with line plots for each of the acceleration axes and derivates for power use. Users usually scroll through the data manually and pinpoint behaviour-specific data sequences based on a verified library of control observations. In paper V, we advanced this approach by plotting static acceleration data on a faceted g-sphere, where behavioural patterns were clustered into groups and could thus be identified even without prior knowledge of the animal's behavioural repertoire. In addition, we show that these plots – the 'Dubai' and the 'g-urchin' plots – can also be used to merge information on the allocation of time to each posture and/or DBA metrics associated with different postures. By concatenating three lines of acceleration into one visualisation and adding time- and energy features as projections into space (histograms or spines with stacked rings), we provide researchers with a tool to get an overview over their dataset at one glance. Even changes in posture and/or energy were apparent through plotting differences between various Dubai or g-urchin plots. Interspecific comparison of these metrics was possible by displaying data in lifestyle plots, which highlighted consistent patterns within and between species. This approach for visualizing accelerometry data allows energy allocation to be linked to behaviour and time and even to detect subtle changes in this respect. The implication is that this technique will help unravel unprecedented movement-related processes, with ramifications for research areas as diverse as disease identification, lifestyle, sports practice and wild animal ecology.

5.2. Tagging effects

In the beginnings of bio-logging, effects of capture and tagging were often ignored (Godfrey and Bryant 2003), or even considered negligible (Wilson and McMahon 2006). The situation is now changing and specific research is being focused on tagging-induced effects of the study animals. We also considered this an important topic and thus determined whether tagging induced changes in activity and movement patterns in paper II. We only documented changes in the activity level (mean ODBA), with lower activity levels in the first days after the tagging event. However, the small effect size for mean ODBA alludes to only a minor difference in activity and puts the practical relevance of this finding into question (Sullivan and Feinn 2012). Still, we suggested that lower mean ODBA levels could be associated with a more vigilant and cautious behaviour after release. In line with this, reduced foraging and scent-marking activity, as well as increased stopping and sniffing has been observed in studies where beavers were presented with predator odours (Basey and Jenkins 1995; Rosell and Czech 2000; Rosell and Sanda 2006). In contrast to that, we did not detect any changes in the beavers' movement patterns (distances moved and LDR) after release. We proposed several mechanisms that could be responsible for our findings; firstly, the capture from the boat and the non-invasive tagging method – which does not require anesthesia – reduces handling time, allows for a quick release and may thus reduce stress-responses in beavers. In addition, we showed that mechanical constraints associated with hydrodynamic drag should be negligible in beavers, due to their slow swim speeds (0.6 - 0.8 m/s; Allers and Culik 1997; Nolet and Rosell 1994). The beaver's pronounced territorial behaviour, which includes patrolling and scent-marking of borders (Rosell et al. 1998), could also provoke a fast resumption of nightly routines in our study population at carrying-capacity. Moreover, all of the study individuals have a least been captured once before the tagging event, and even this could induce long-term changes in neuroendocrine and behavioural stress responses and, thus, trigger the process of habituation (Armario et al. 2008; Lynn et al. 2010). In conclusion, we found that bio-logging data were useful in examination of tagging effects and ideally should be considered in combination with physiological and life history data to gain a comprehensive understanding of an animal's response to tagging.

5.3. Territory size and age explain movement patterns of beavers

Territorial animals need to advert territory occupation through, for example, patrolling and scent-marking borders (Henschel and Skinner 1991; Johnson 1973), which makes this investment more extensive in larger territories. Herbivores also need to spend a considerable amount of time on foraging in order to sustain their energy requirements on food of relatively low nutritional value (Senft et al. 1987). In paper III, we inspected movement patterns of beavers in water and on land in relation to patrolling and foraging activities. We found that beavers in larger territories moved greater distances in water, spent more time patrolling within relative territory border zones and stayed closer to the shoreline when on land. In smaller territories, this relationship was inverted; beavers had a lower relative patrolling effort, but moved at greater distances from the shoreline, which is likely to be attributable to resource depletion along the shoreline in such territories. Higher patrolling effort in larger territories not only imposes constraints on time investment in other behaviours, it also likely increases energy requirements due to higher thermoregulatory needs in water (Nolet and Rosell 1994). Conversely, beavers in smaller territories also face costs when foraging at greater distances from the shoreline since travelling on land may also be costly (Belovsky 1984) and involve a greater predation risk (Basey and Jenkins 1995). This results in a trade-off between patrolling and foraging, with territory sizes being a counterbalancing factor for these two activities: Individuals holding larger territories have to invest more time in patrolling, but can forage closer to the shoreline. In smaller territories, beavers invest less in border patrolling, but cover greater distances when foraging on land.

Remarkably, we also found that movement patterns changed with increasing age. Older beavers spend more time on land and within absolute border zones. Still, distances moved in water were not explained by age, which suggests that older beavers spend more time per visit at a border. Changes in movement patterns have been reported with respect to sex or social status. For example, female jaguars (*Panthera onca*) had smaller home ranges and moved less than males (Sollmann et al. 2011) and differences in extraterritorial movements have been shown in adult and yearling wolves (*Canis lupus*) (Messier 1985). To our knowledge, this is the first study to show changed movement patterns with age, which may be linked to increased experience of dominant territory holders with time. Plasticity in behavioural traits is important for individual fitness (Dingemanse et al. 2010) and boldness has been shown to increase with age (Magnhagen and Borcherding 2008; Wilson et al. 1994) and/or body mass (Mayer et al. 2016). Beavers reach their maximum body mass at an age of seven (Mayer et al., unpubl. results), and this could also partly explain our finding. In general, we found that beavers covered greater distances on land during the spring season, which may represent a more selective foraging strategy during the spring green-up when food quality is higher. Due to the beavers' 'busy' behavioural ecology, which includes scent-marking territory borders, travelling in water and foraging on land, we were able to draw interferences on foraging and patrolling tactics by using GPS units. We show that owning both larger and smaller territories can be advantageous, and that patrolling tactics changed with age.

5.4. Diving performance of beavers

Diving in semi-aquatic species is costly, as these animals possess less efficient physical (e.g. body appendices, fur) and physiological (e.g. thermoregulation) adaptions to life in water compared to fully aquatic species (Fish 2000; Williams 1999). Thus, diving behaviour constitutes a particularly interesting feature of semi-aquatic species, but has been difficult to quantify under natural conditions (with a few notable exceptions; e.g. Kruuk and Hewson 1978; Nolet et al. 1993). By using accelerometers combined with depth transducers, we were able to quantify the diving performance of free-living beavers in paper IV. We found that dives were generally short and shallow and, thus, are likely to be aerobic. Dives of this type can also be found in a range of other freely diving mammals and birds (Snyder 1983; Thompson and Fedak 2001), and it is suggested that animals may maximize bottom phase durations through conducting a series of shallow, aerobic dives as opposed to single, longer dives (Boyd 1997). Beavers typically travel along the shoreline (paper IV) and this alone may predispose them to shallow diving, although these sections also feature the highest water plant densities (Moss 2009). In our study area, beavers dived during only 2.8% of their nightly activity budget, which is considerably less than found in many other semi-aquatic species (Kooyman and Ponganis 1998; Tremblay et al. 2005). For example, sea otters (*Enhydra lutris*) have been found to dive for 48% of their 24-hr cycle (Bodkin et al. 2007) while

Australian sea lions (*Neophoca cinerea*) for 58% of their at sea time (Costa and Gales 2003). In contrast to beavers, these species rely entirely on diving for food acquisition. As generalist herbivores, beavers forage on a broad range of different plant species (Jenkins 1975), both on land and in water.

Dive durations generally increased with diving depth, which is a typical feature of many semi-aquatic divers (Cook et al. 2010). Both maximum diving depth and dive durations (total and bottom phase) were defined by the physical effort (mean VeDBA, vertical velocities) during the descent and bottom phases in tandem with the maximum depth reached. According to Boyle's Law, which describes the nature of air compression with depth, air volumes associated with fur or plumage should decrease by 10% within the first meter of the water column. It is thus not surprising, that descent mean VeDBA in beavers was highest near the surface, alluding to increased power use and upthrust due to higher volumes of fur- and lung-associated air (Fish et al. 2002; McKean and Carlton 1977). Similarly, diving birds have been found to use most power near the water's surface during the descent phase of a dive (Wilson et al. 1992; Wilson et al. 2010). In addition, increased power use can also be attributed to the acceleration in vertical speed (from 0 m/sec at the surface to normal descent speed) and forces used to counteract surface drag (Williams 2001; Wilson et al. 1992). Vertical velocities increased with diving depth, which is likely to be attributed to steeper dive angles in deeper dives (Ropert-Coudert et al. 2002), which lead to increased rates of change in depth. Longer bottom phase durations were generally accompanied by lower power use (mean VeDBA), which is expected because VeDBA equates with power and higher power depletes oxygen reserves faster. However, in some deeper dives, extended bottom phase durations were coupled with higher mean VeDBA values. We suggest that this phenomenon could be linked to a specific dive type, such as foraging on aquatic plants or acquiring building material from the riverbed with the animals perhaps respiring anaerobically at this time. Water temperature and associated thermoregulatory needs are reputed to affect diving costs in homeotherms (Bevan and Butler 1992; Ciancio et al. 2016). In beavers, a decrease in body temperature has been found during swimming and, in particular, in winter (Nolet and Rosell 1994; Smith et al. 1991). However, we found no effect of water temperature on any of the dive parameters analysed in this study. This finding suggests that beavers have evolved specialized adaptions to life in cold water, which are of morphological (e.g. thick pelage, adipose tissue), physiological (e.g. local heterothermy) and behavioural nature (e.g. partitioning of time in water/on shore or inside lodge). By implementing bio-logging technology, we were able to gain detailed insights into the diving performance of beavers and shed light on their adaptions to counterbalance diving costs related to buoyancy, drag, heat loss and limitations in oxygen supply.

6. Conclusions and future perspectives

Animals have colonised a broad range of terrestrial, aquatic and aerial ecosystems and have evolved specialised adaptions and sensory organs to operate in their preferred habitats. Clearly, it is impossible for the human observer to follow animals on all their paths, and even when observable, animals may behave in ways that cannot be perceived visually. Bio-logging technology has provided us with the unique opportunity to overcome this ‘visual barrier’ and has allowed us to plunge into a new world of behavioural studies: It is now possible to follow animals in the dark (Zavalaga et al. 2011), underground (Markham et al. 2010), over long distances and time periods (Flack et al. 2016), below the water’s surface (Jouma'a et al. 2016) and even record subtle body motions which may be related to internal states (Wilson et al. 2014) (Figure 7). In this thesis, we capitalised on the power of accelerometers and GPS systems to study activity, behaviour and movement patterns of a nocturnal, semi-aquatic species, the Eurasian beaver. The accelerometry technique proved to be a useful tool for determining beaver behaviours, ranging from the construction of ethograms, to evaluating tagging effects, to gaining detailed insights into the beavers’ diving performance. We also unravelled spatial movement of beavers with respect to

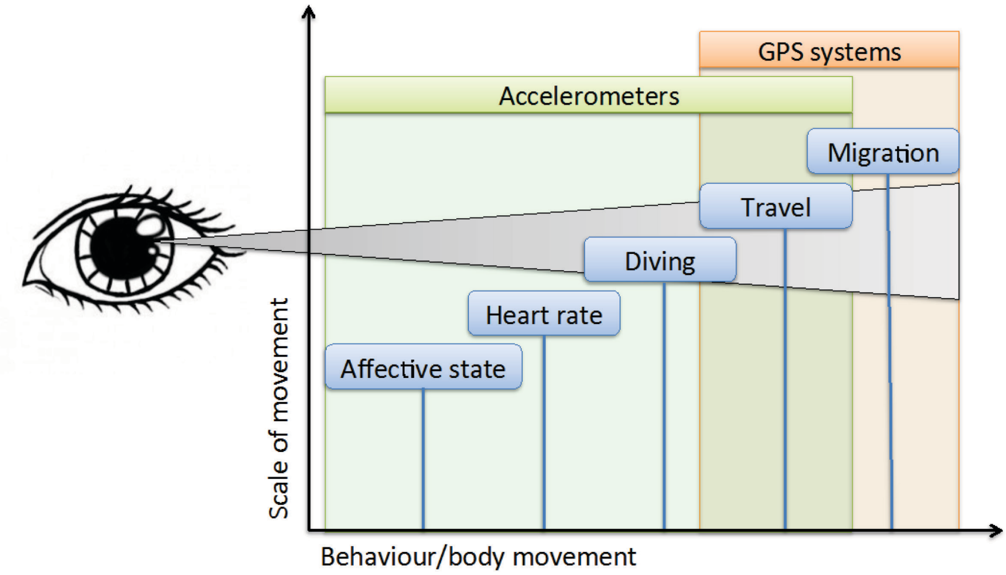

Figure 7. The power of bio-logging. The human visual system has clear limitations in perceiving animal behaviour and movement. Bio-logging units such as accelerometers and GPS systems are today used to unravel a broad range of aspects of animal behaviour, ranging from the detection of subtle body movement linked to affective states (Wilson et al. 2014), to large scale spatial movements such as migration (Flack et al. 2016).

differences in territory sizes and investigated changes in movement patterns in response to tagging by using GPS systems. Comparative, fine-scaled insights into animal behaviour are rarely attainable outside of the laboratory setting and without the influence of an observer’s presence (Brown et al. 2013). There are challenges though. Accelerometers, in particular, typically produce large amounts of data and the development of software with the capacities for visualising and analysing accelerometry data is a major issue. Our contribution to this provides researchers with software for visualising accelerometry data in tandem with other metrics (e.g. DBA), which does not require prior knowledge on the animals’ behaviour. Through this, we facilitate the identification of patterns that are not obvious using current approaches and highlight movement-related processes, subtle differences in movement and associated energetics.

Understanding animal behaviour is key to a holistic study of animal ecology and authors have suggested that the ‘golden age’ of bio-logging technology has just begun (Kays et al. 2015; Wilmers et al. 2015). Technological advances promise the development of affordable, smaller and lightweight tags with increased memory capacities, which can be used to collect data on a greater variety of animal species, while at the same time minimizing tagging effects (Ropert-Coudert and Wilson 2005; Wilson et al. 2008). This will pave the way for multi-individual monitoring programs for drawing conclusions useful for examining population-level trends and specifically helping identify the factors driving population increases or declines (Kays et al. 2015). A new generation of tags will also render long-term tag deployments – from months to years – possible and allow the identification of complex behavioural traits such as social interactions, parental care, mating and courtship behaviours. This may also be promoted by combining accelerometers with other sensors such as GPS systems (Kays et al. 2015), proximity loggers (Ossi et al. 2016), magnetometers (Bidder et al. 2015), temperature (McCafferty et al. 2015) and pressure transducers (Hussey et al. 2015).

Indeed, the possibility of collecting large amounts of data with high spatio-temporal resolution may change the common scientific approach. In the past, carefully considered data collection was based on hypotheses based on previous ‘observations’. Today, by using multi-channel data loggers, researchers have the possibility to collect data from a multitude of sensors collecting information that is not visually apparent (Figure 7), ostensibly collecting more information than actually ‘needed’. In fact, such data can, and perhaps should, be used to formulate hypotheses before rigorous scientific hypothesis testing is implemented. This implies, perhaps, that we should collect as much data as possible ‘blind’, using the suite of capable sensors used in bio-logging before we embark on theory. Certainly, inspection of such data can show unexpected (serendipitous) patterns, which may lead to new hypotheses that may not be entertained based on visual information alone. If this became a new paradigm, it would be a significant departure from the conventional hypothesis-driven approach in science, which advocates careful consideration before embarking on any data collection (Popper 2005).

In the case of accelerometry data, in order to gain a more complete picture of the proximate causes underlying a specific behaviour, accelerometry data could be linked to physiological (e.g. body temperature, heart rate) and/or environmental data (e.g. weather, temperature, light or satellite-derived environmental data). Such a multidisciplinary approach may also be used to determine the critical needs of animals and highlight key ecological processes, which, ultimately, enable better conservation and management (Wilmers et al. 2015; Wilson et al. 2015). Today, we are living in a time where human actions inflate extinction rates massively, – currently at about 1000 times the background rate of extinction (Pimm et al. 2014) – so this is a critically important matter. Finally, as bio-logging technology becomes more ubiquitous and deployed on species over years, we may expect it to inform us about how animals respond to environmental change because sensors will not only describe the animals' behaviours, they will also track environmental changes in, for example, temperature or vegetation cover (van Wijk et al. 2012). This will be particularly useful in environments that are difficult to access (e.g. war-torn countries; Kays et al. 2015) but will be, above all, another important tool in the armoury that we must develop if we are to understand and mitigate the huge changes man is imposing on this planet.

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Paper I

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RESEARCH ARTICLE

The Use of Acceleration to Code for Animal Behaviours; A Case Study in Free-Ranging Eurasian Beavers *Castor fiber*

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Abstract

Recent technological innovations have led to the development of miniature, accelerometer-containing electronic loggers which can be attached to free-living animals. Accelerometers provide information on both body posture and dynamism which can be used as descriptors to define behaviour. We deployed tri-axial accelerometer loggers on 12 free-ranging Eurasian beavers *Castor fiber* in the county of Telemark, Norway, and on four captive beavers (two Eurasian beavers and two North American beavers *C*. *canadensis*) to corroborate acceleration signals with observed behaviours. By using random forests for classifying behavioural patterns of beavers from accelerometry data, we were able to distinguish seven behaviours; standing, walking, swimming, feeding, grooming, diving and sleeping. We show how to apply the use of acceleration to determine behaviour, and emphasise the ease with which this non-invasive method can be implemented. Furthermore, we discuss the strengths and weaknesses of this, and the implementation of accelerometry on animals, illustrating limitations, suggestions and solutions. Ultimately, this approach may also serve as a template facilitating studies on other animals with similar locomotor modes and deliver new insights into hitherto unknown aspects of behavioural ecology.

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Introduction

Understanding animal behaviour is fundamental to biology, and an important precondition for other fields of research [1]. Indeed, the behaviours that animals adopt have profound consequences for lifetime reproductive success [2, 3], reason enough to study them and their consequences. Ethologists have used different approaches to document animal behaviour, of which direct observation and radio-tracking are probably the most common [4]. However, these methods have limitations, particularly with regard to shy or elusive species, or those that live in inaccessible habitats. Recently, scientists have recognized the potential of accelerometers in animal-attached loggers to identify animal behaviour [5–7]. Acceleration forces produce a signal that depends on the orientation of the device (and when fixed to a subject, therefore, the posture of that subject), often called the 'static' acceleration, onto which is superimposed a 'dynamic' signal derived from the subject motion [8].

Initial applications using animal-borne accelerometers have mainly focused on marine species, where researchers had none or only limited access to investigate their study species' behaviour in their natural habitats [9]. A vast majority of these studies were conducted on birds including penguins [5, 10, 11], other seabirds such as cormorants [12, 13], boobies and gannets [14, 15], but also marine mammals such as seals [16, 17] and cold-blooded animals such as turtles [18, 19] and a range of fish species [20–22]. In land-based studies, accelerometers have been used on domestic animals [23, 24], livestock [25, 26] and other animal species in captivity [27, 28]. Moreover, there is a range of studies on terrestrial birds both in captivity and in the wild including many raptor species [29–31]. The field is rapidly growing and in the last years, accelerometers have also been increasingly used on free-living terrestrial mammalian species [32–34].

Specific applications vary from investigations of body movements to elucidate foraging behaviour [35, 36], particularly as relates to diving behaviour [5, 37], to travel speed [38, 39], to flight dynamics [30, 40, 41], to animal welfare issues [42, 43], to construction of activity-budgets [44, 45] and even time/energy activity budgets [46–48]. The latter can be derived from both overall- or vectorial dynamic body acceleration (ODBA or VeDBA, respectively). Both ODBA and VeDBA produce, calibrated by means of one of the common methods for determining energy expenditure in animals [49, 50], a powerful predictor of movement-based energy expenditure [12, 51].

In this study, we deployed tri-axial acceleration loggers on free-ranging and captive beavers *Castor spp*. to examine how acceleration coded for behaviour. Beavers are large, territorial rodents that feature a monogamous mating system [52]. They live in family groups and defend their territories aggressively against intruders [53]. As strict herbivores, they feed on tree bark and other herbaceous plants including aquatic plants [54]. Beavers are semi-aquatic and combine four-legged locomotion on land with aquatic locomotion (swimming, diving) in water. Moreover, beavers are nocturnal and exhibit a hidden lifestyle that is difficult to trace with conventional methods (see above). Due to this and their complex behavioural repertoire, beavers form a perfect study system for our approach.

To reinforce and complete the field of accelerometry studies, we present a framework for identifying a suite of behaviours in beavers. By using this approach, we aim to shed light onto several aspects of beaver behaviour and present an innovative, non-invasive method that can be used to remotely quatifiy the behaviour of free-living animals. We suggest that our study should provide researchers with a starting point for constructing behaviour-, time-, or even energy budgets and thus provide an important cornerstone to understanding animal behavioural ecology.

Materials and Methods

Free-ranging animals

The study was carried out between April-November 2009–2011, and September-October 2011 on a population of free-ranging Eurasian beavers *C. fiber* in south-eastern Norway (59°23' N, 09°09' E, Telemark). The study sites were the three rivers Gvarv, Saua and Straumen, which flow through a semi-agricultural and mixed woodland landscape. Beavers have inhabited the study area since the 1920s [55]. Since 1997, the animals have been part of a live-trapping program with an extensive capture-mark-recapture scheme [56]. Captured animals are routinely sexed [57], weighted, micro-chipped (ID-100A Microtransponder, Trovan Electronic Identification Devices LTD., Hull, UK) and marked with unique colour-plastic (Ovine Rototags or Research Minitags, Dalton Continental BV, Lichtenvoorde, The Netherlands) or metal (1005–3 Self piercing monel ear tag, National Band and Tag Co., Kentucky, USA) ear-tag combinations [56].

Live-trapping and attachment of acceleration loggers

We caught 12 known adult Eurasian beavers (8 males—mean mass 21.7 ± 1.5 kg and 4 females–mean mass 23.1 ± 2.6 kg) from 10 different territories. Beavers were located during the night (usually from 9:00 pm – 6:00 am) using a hand-held spotlight, approached by boat, identified by their ear-tags and caught by jumping into the water with a landing net, following the method established by Rosell and Hovde [58]. The animals were then transported onto the shore, and transferred into a cloth bag where handling and tagging procedures were undertaken without the use of anaesthesia. Tags, consisting of an eight-channel acceleration logger (JUV Elektronik, Schleswig-Hollstein, Germany, size 90 x 15 mm dia—mass 62 g) and a VHF-transmitter (Reptile Glue-On R1910, Advanced Telemetry Systems, Minnesota, USA, size 35 x 18 x 8 mm—mass 10 g), were attached on the fur of the lower back using two-component epoxy resin. Before attachment, the tags were connected with wire and integrated in 4.5 mm half-mesh net covering (Mørenot Fishery AS, Møre og Romsdal, Norway). The whole unit was 130 x 90 mm in size (incl. netting) and weighed 90 g in air, which accounts for 0.69% of the body weight of the lightest beaver (weighing 13 kg, see below) used in this study. We attached all units identically at precisely 15 cm above the tail along the spine because device orientation was critical for this study. Overall handling time was no more than 20 minutes and beavers were released at the trapping site where they swam calmly away. Pictures were taken of all animals to ascertain tag orientation. After one to three weeks the animals were recaught and the units removed from the fur, using a scalpel to cut the guard hair, leaving the underfur unaffected.

Tri-axial acceleration loggers

The tri-axial acceleration loggers used in this study included orthogonally placed sensors for tri-axial acceleration (-4 to +4 *g*) and pressure transducers (range 950 to 10,000 mB). The three acceleration channels were so placed within the logger and the logger so placed on the animal, that they represented the animal's dorso-ventral axis (heave), the anterior-posterior axis (surge) and the lateral axis (sway) [7]. Data (22 bit resolution) were recorded at 8 Hz and 2 Hz for acceleration and pressure, respectively, and stored on a 1 GB memory card. The loggers were programed using a simple serial port (COM) terminal emulation program (Terminal by Bray pp).

Control animals

We conducted control observations to determine how accelerometer signal related to behaviour in three zoos. Tri-axial acceleration loggers were deployed on; (i) two North American beavers *C*. *canadensis* (one male, mass 22 kg and one female mass 19 kg) in the Alpenzoo Innsbruck, Austria during June 2009, (ii) a male Eurasian beaver (mass 13 kg) in the Highland Wildlife Park in Kincraig, United Kingdom and (iii) on a female Eurasian beaver (mass 19 kg) in Edinburgh Zoo, United Kingdom, both in February 2010. In September 2011, we also observed two device-equipped free-ranging Eurasian beavers (one male, one female) in our study area. We observed and/or filmed both captive and free-living animals with a hand-held video camera (NVGS-180, Panasonic Corporation, Osaka, Japan) for three to four hours a day over a week. The clock times on the video-camera and the acceleration logger were synchronised to allow us to compare the recorded beaver behaviours with the acceleration data. In captivity, we observed the animals from outside their enclosure and used a small head-mounted torch during dark periods. Elevated paths, observer platforms and glazed windows guaranteed good visibility of the focal animals. All enclosures contained at least one water basin that enabled the animals to swim and was deep enough to dive. One of the basins in the Alpenzoo had a ground-level glazed front, which allowed for detailed observations of body postures during diving. In addition, the two animals from Alpenzoo had a glazed window into their sleeping chamber so we were able to observe them as they slept or moved within this space. Rocks, soil, grass and concrete stretches were available in all enclosures and promoted land-based activities such as standing, walking, feeding and grooming. Furthermore, the animals were provided with branches and twigs of woody plants, vegetables and fruit to stimulate feeding behaviour on different food items. In the wild, all observations were conducted from a boat, using binoculars and a spotlight when needed. Data collected during observation periods were excluded from analysis and no other tagged beavers were present in the respective territories. Neither the presence of the observer nor the use of light had any detectable influence on the subject (see e.g. [59]).

Data analysis

Downloaded data were inspected using custom-made software (Snoop, Swansea University, UK) and compared to video tapes from zoos and notes from direct observations to identify behaviours and associated data sequences. Analyses on free-ranging animals were started on day two after capture to avoid possible effects of the handling process. Data from both sexes and different seasons was pooled since beavers are sexually monomorphic and we did not intend to compare time budgets but rather focused on the implementation of physical movements. We exported 10 examples for each behaviour, using 10 seconds of walking and standing (more transient behaviours) and one minute of swimming, grooming and feeding behaviours (behaviours which occur over long periods). Sleeping consists of a whole sequence of lying postures, thus sleeping sessions were inspected visually only and ODBA values (see below) were recorded. After ensuring that our transducers were properly calibrated, we derived the static acceleration signal from each axial sensor by using a running mean over 2 seconds [7]. In this study, the overall dynamic body acceleration (ODBA) was used to relate to the animals' movement and activity [7, 60], respectively. ODBA was calculated by subtracting the derived static acceleration from each acceleration channel (see above) and calculating the absolute product from consequent dynamic acceleration values for each behaviour (see [12]).

Statistical analyses were conducted in R 2.14.1 (R Foundation for Statistical Computing, Austria) and OriginPro 8.5.1 (OriginLab Corporation, USA). Accelerometry data have been analysed by a range of machine learning algorithms [31, 61] and we used random forests (R package randomForest, n = 500 trees, mtry = 2, Liaw & Wiener 2002) to classify our data. Random forests are a powerful statistical classifier for acceleration data [31] that include variable importance measures for each predictor variable [62, 63]. All behaviours, apart from sleeping (see above for rationale), were categorized using mean values and standard deviations of surge, sway, heave acceleration and ODBA.

Ethics statement

The study, including all handling and tagging procedures (for details see above), was approved by the Norwegian Experimental Animal Board (id 742, id 2170) and the Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID), which also granted permission to conduct fieldwork in our study area. Subsequent observations of individuals with acceleration loggers indicated no obvious differences in behavioural patterns of tagged and untagged individuals. The patch of clipped guard hair grew back within three to four months.

Results

Overall, we identified seven different behaviours including standing, walking, swimming, feeding, grooming, diving and sleeping. All behaviours could be clearly differentiated by the static acceleration signal from the beavers during captive studies, and all of which were recorded by the free-living animals. During individual observations, we captured at least 10 video sequences for each of the seven behaviours, lasting for a minimum of 10 seconds. The unit's positioning on the lower back facilitated, in particular, distinguishing postures in water (flat, stretched out) from postures on shore, as illustrated for standing, walking and swimming in Fig 1. Our random forests model classified behaviours with 95% accuracy (see Table 1 for all goodness-of-fit metrics). Kappa statistics were over 0.94 and the model showed high specificity (100%) and sensitivity values (95.8%), indicating substantial predictions with low cross-classification error.

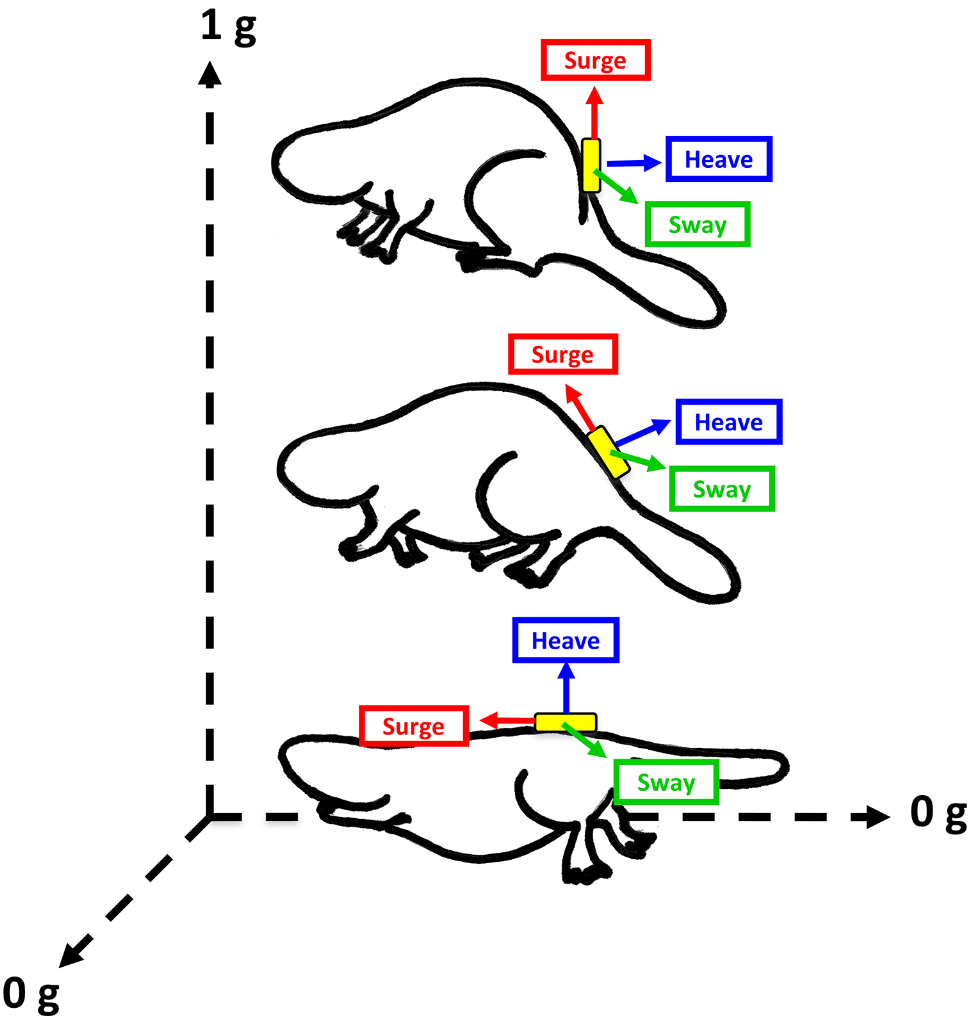

Fig 1. Changes in Eurasian beaver posture. Changes in orientation of the surge, sway and heave acceleration axes are illustrated during standing, walking and swimming (top to bottom).

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Table 1. Accuracy measures for the random forests model predicting class affiliation to six different Eurasian beaver behaviours.

Metric		Value (%)
	Out-of-bag error rate	4.84
Cross-validated	Accuracy	94.99
	Specificity	100.00
	Sensitivity	95.79
	Error rate	5.01
	Cohen's Kappa	93.90

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All data points clustered out according to their class affiliation, with only minor overlap between standing and feeding (with cross-tabulated class errors of 0.08% and 0.10%, respectively; Fig 2). The class center for feeding (the prototype) indicated that feeding involves

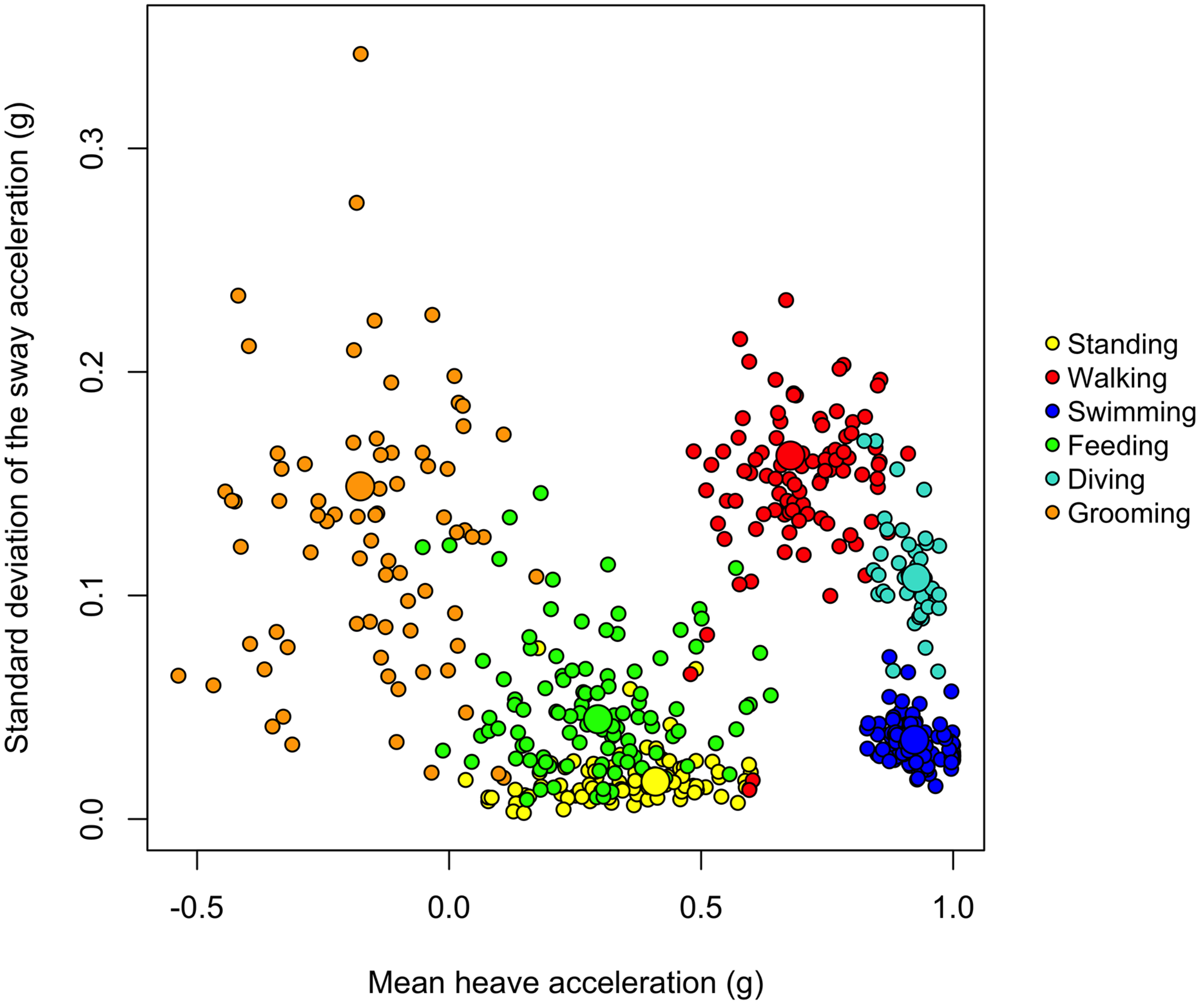

Fig 2. Class center plot for Eurasian beaver behaviours. The plot contains prototypes (big dots) for the six behavioural classes modelled by random forests. Prototypes are median values of samples with the largest number of k-nearest neighbours of the same class. In this way, they mark the center of each class and indicate how the variables relate to the classification.

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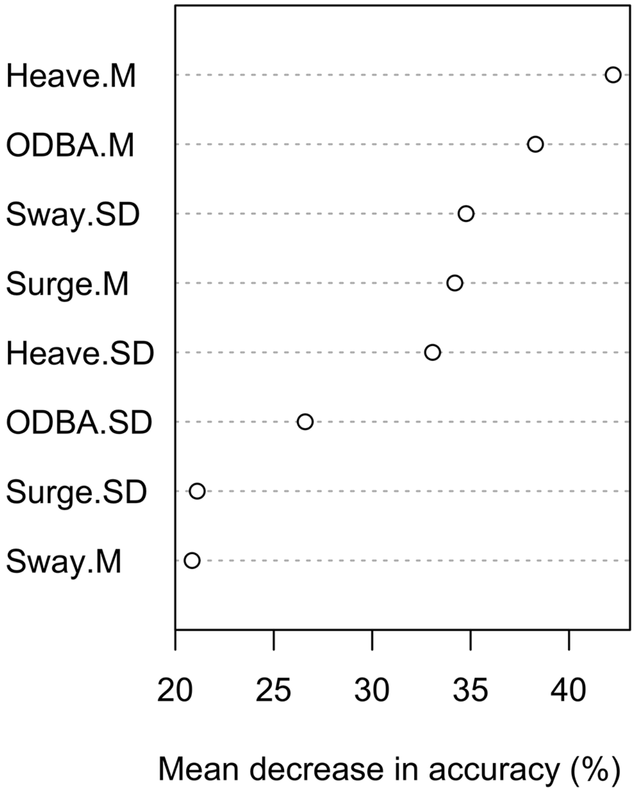

Fig 3. Variable importance plot for Eurasian beaver behaviours. A relative ranking of significant predictors, the permutation-based variable importance measure of the random forest model, is shown as the mean decrease in accuracy in percent. Higher values of mean decrease in accuracy indicate variables that contribute more to the accuracy of the classification.

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animals leaning more backwards than with simply standing (with mean heave values closer to 0) because the front part of the body is more upright during processing of food items (Fig 2). The greater spreading of grooming values along the y-axis in Fig 2 shows the variability of this behaviour, in particular with regard to lateral movement. This is largely owing to variable time periods spent on grooming either the right or the left side of the body (Fig 2).

In general, mean values were more important for classification than standard deviations, with the exception of the sway acceleration, where this relationship was inverted (Fig 3). As sway-heavy lateral movements (e.g. walking, swimming) are performed rhythmically, they result in a mean sway acceleration of about 0 g, a value that is common for all the behaviours observed in this study. Thus, the upper and lower peaks of the sway acceleration, as measured by the standard deviation, are more important for classification than the mean sway acceleration, which is least important (Fig 3). The mean heave acceleration proved to be most variable between behaviours and is therefore particularly important for classification (Fig 3).

A partial dependence plot of the mean heave acceleration shows the trend of this predictor after averaging out the effects of the other predictor variables in the model. The linear, horizontal trend at the beginning of each curve can be attributed to the sparseness of values in this range (see large decile). For grooming, feeding and standing, values between -0.5–0.5 *g* were good predictors, while values around 1 *g* indicate that it is unlikely the animal is performing one of these behaviours. Grooming shows the sharpest decline and thus mean heave acceleration values around 1 *g* are highly unlikely to be grooming. For walking, there was an upwards

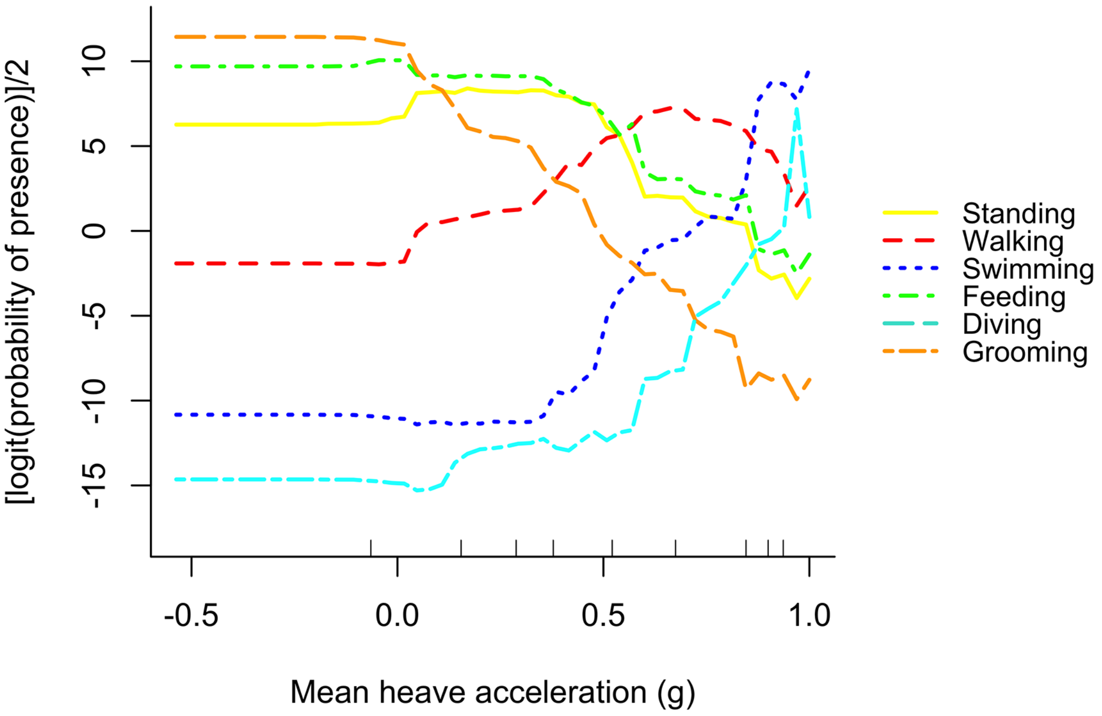

Fig 4. Partial dependence plot for the most important predictor variable, the mean heave acceleration. The partial dependence function plots a grid of values over the range of the mean heave acceleration on the x-axis, with decile rugs at the bottom of the plot representing the distribution of the total mean heave acceleration. The y-axis is on the logit scale and is centred to have zero mean over the data distribution.

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trend from 0 *g* with values between 0.6–0.9 *g* having the greatest predictive power. Swimming and diving show a sharp increase from 0.5 *g* on, indicating that values around 1 g are good predictors for these behaviours (Fig 4). In terms of postural changes, the upwards trend for walking, swimming and diving reflects the more bent-forward or stretched-out posture during these behaviours, while the downwards trend for standing, grooming and feeding indicates a more upright and leaned-back posture. In the following section, we refer primarily to mean heave acceleration values and illustrate the other axes when appropriate.

Classification of behaviours

Standing behaviour showed no appreciable temporal variation in any axis (Fig 5A, Table 2), while both walking and swimming were characterized by oscillations in the sway axis (Fig 5B and 5C, Table 2). Sway oscillations during walking showed greater amplitudes ($\bar{x}$ = 0.26 *g*, σ = 0.05 *g*) and lower cycle frequencies ($\bar{x}$ = 0.82 Hz, σ = 0.14 Hz) than during swimming (amplitude $\bar{x}$ = 0.11 *g*, σ = 0.07 *g*; cycle frequency $\bar{x}$ = 0.44 Hz, σ = 0.08 Hz). The wave pattern in the sway acceleration signal during walking originates from the beavers' rolling gait, while oscillations in the sway acceleration during swimming represent propulsive, alternating leg strokes with the hind legs. Aside from having a negative mean heave static acceleration ($\bar{x}$ = -0.15 *g*, σ = 0.18 *g*), grooming also showed cyclic patterns in sway acceleration as the animals systematically undertook repetitive grooming motions, although amplitude over time was much more variable than in swimming or walking and the frequency much lower (Fig 5D, Table 2). Feeding was characterised by the lowest positive mean static heave acceleration ($\bar{x}$ = 0.19 *g*, σ = 0.13 *g*; Fig 5E). During diving, mean static heave acceleration was 0.91 *g* (σ = 0.08 *g*) and with different dive types being readily defined by data from the depth transducer (Fig 5F, Table 2). Sleeping

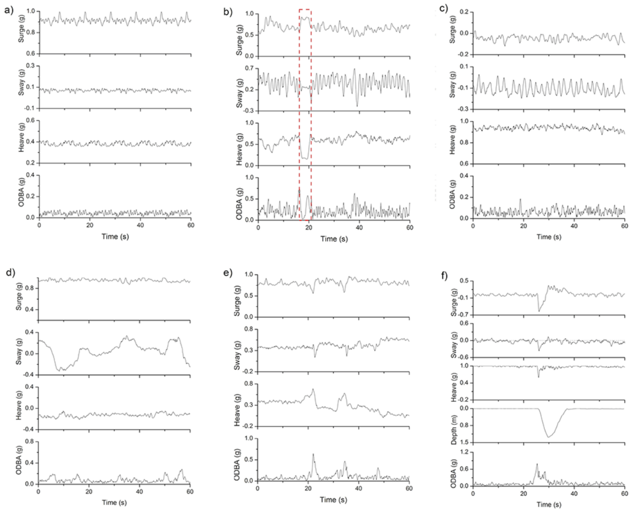

Fig 5. Changes in the acceleration signal during different Eurasian beaver behaviours. Examples of the static surge, sway and heave acceleration signals for Eurasian beavers during (a) standing, (b) walking (incl. a standing period within the dashed rectangle), (c) swimming, (d) grooming, (e) feeding and (f) a v-shaped dive with short bottom phase.

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behaviour was typified by very stable lying postures for long periods (normally minutes to hours) accompanied by occasional turns exemplified by radical changes in heave acceleration. Lying on the belly, on the sides, or on the back are illustrated in Fig 6. Gross mean ODBA values for various behaviours ranged from 0.056 *g* (σ = 0.013 *g*) for standing, to 0.233 *g* (σ = 0.046 *g*) and 0.265 *g* (σ = 0.029 *g*) during diving and walking, respectively (Table 2).

Discussion

Accelerometry is a powerful tool for remotely studying animal ecology and by using this approach on beavers, we were able to categorize a set of seven different behaviours. Studies using accelerometers for identifying such a detailed suite of behaviours are rare, and this study is the one of the few to investigate a series of behaviours in a free-living mammal. A notable exception here is a study by Byrnes et al. [34], who were able to detect 5 locomotor behaviours in free-ranging Malayan colugos *Galeopterus variegatus*; including climbing, foraging, gliding, other behaviours and resting. Besides this, recent accelerometry studies have focused on wild felids, where researches used accelerometers integrated in GPS-collars to investigate behaviour and energetics of their study species. In cheetahs *Acinonyx jubatus*, Grünewälder et al. [32] were able to classify 5-min activity scores into a set of three key behaviours such as feeding, mobile and stationary. Similarly, Wang et al. [64] identified three behavioural categories in pumas *Puma concolor*, including low (walking) and high acceleration movement behaviours (trotting, running), and non-movement behaviours (resting, eating, grooming). On the same study species, Williams et al. [33] combined information from both GPS and acceleration sensors to investigate the energetics of instantaneous puma kills during three characteristic periods: pre-kill activity, pounce and kill and post-kill prey handling/eating. Apart from that, behavioural research using accelerometers on mammals has mainly focused on pets [23, 24, 65] or livestock [66, 67].

Research of this type on other animal classes includes a study by Tsuda et al. [20], who investigated the spawning behaviour of chum salmon *Oncorhynchus keta* and classified swimming, nosing, exploratory digging, nest digging, probing, oviposition, covering and post-

Table 2. Statistics of the static surge, sway and heave acceleration signal and overall dynamic body acceleration for the seven identified Eurasian beaver behaviours.

		Surge (*g*)		Sway (*g*)		Heave (*g*)		ODBA (*g*)			
Behaviour	**n**	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	**Additional information**	**Fig**
Standing	12	0.853	0.066	-0.004	0.097	0.360	0.136	0.056	0.013	No movement visible, thus the acceleration signal in all three axes is a straight line. Small variation in the heave acceleration channel due to different body angles, which are likely to represent different terrain slopes.	5A
Walking	12	0.624	0.131	-0.005	0.208	0.691	0.110	0.265	0.029	During walking, the beaver's posture is leaned forward ($\bar{x}$ surge and heave ≈ 0.6–0.7 *g*). The beaver's rolling gait is manifested as high, cyclic peaks in the sway acceleration (and therefore higher σ) where each peak represents a footstep.	5B
Swimming	12	0.128	0.104	-0.123	0.106	0.905	0.034	0.060	0.005	Due to the attachment on the lower back, swimming resulted in a mean heave acceleration close to 1 *g*, with a mean surge and sway acceleration around 0 *g*. Swimming beavers paddle with their hind legs, which results in low, cyclic peaks in the sway acceleration (see Fig 5C).	5C
Grooming	12	0.909	0.066	0.133	0.185	-0.149	0.185	0.075	0.020	When grooming, beavers usually sit on their hind legs and groom belly, and the left and right side of their back alternatively. This results in an undulated pattern in the sway acceleration channel (see Fig 5D), accompanied by an often negative heave acceleration due to leaned back posture.	5D
Feeding	12	0.919	0.048	-0.012	0.140	0.188	0.126	0.086	0.030	Feeding beavers adopt a more leaned back posture as in standing ($\bar{x}$ surge and heave ≈ 0.9 *g* and 0.2 *g*, resp.). The acceleration signal shows a steady sequence in all three channels, with betimes variation in the heave acceleration.	5E
Diving[a]	8	0.100	0.210	0.120	0.100	0.910	0.080	0.233	0.046	A dive is initiated by a v-shaped peak in the heave and surge acceleration channel, but also clearly visible due to changes in the depth transducer (see Fig 5F).	5F
Sleeping[b]	12	-	-	-	-	-	-	0.057	0.007	Sleeping consists of a series of steady sequences in all three channels, including occasional turning rates (see Fig 6).	6

[a] Similar-shaped, comparable dive types were only found in 8 individuals.

[b] Sleeping consists of a series of different postures (e.g. lying on the belly, on the sides, or on the back), thereby impeding the specification of mean values.

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spawning digging. Similarly, Whitney et al. [21] investigated mating behaviour of free-living nurse sharks *Ginglymostoma cirratum*, something that is, like the salmon study, facilitated by a sequence of highly conserved behaviours. Moreover, Lagarde et al. [45] used accelerometers on Greek tortoises *Testudo graeca* and distinguished five behavioural categories including immobility, feeding behaviours, digging, walking and sexual behaviours. Notwithstanding the pioneering work by Yoda et al. [5], Gómez Laich et al. [13] were the first to identify an independent series of behaviours in a free-living seabird species, the Imperial cormorant *Phalacrocorax atriceps*, where six behaviours including standing, sitting, floating on water, flying, walking and diving were identified. Together with the other studies cited above, we show the potential that accelerometers have for identifying the behaviour of free-living animals that cannot easily be observed (cf. [35]).

Linking behaviour with acceleration signal

The static acceleration signals produced by the accelerometers are explicable in the light of the postural changes defining the different behaviours and the way this affects the orientation of

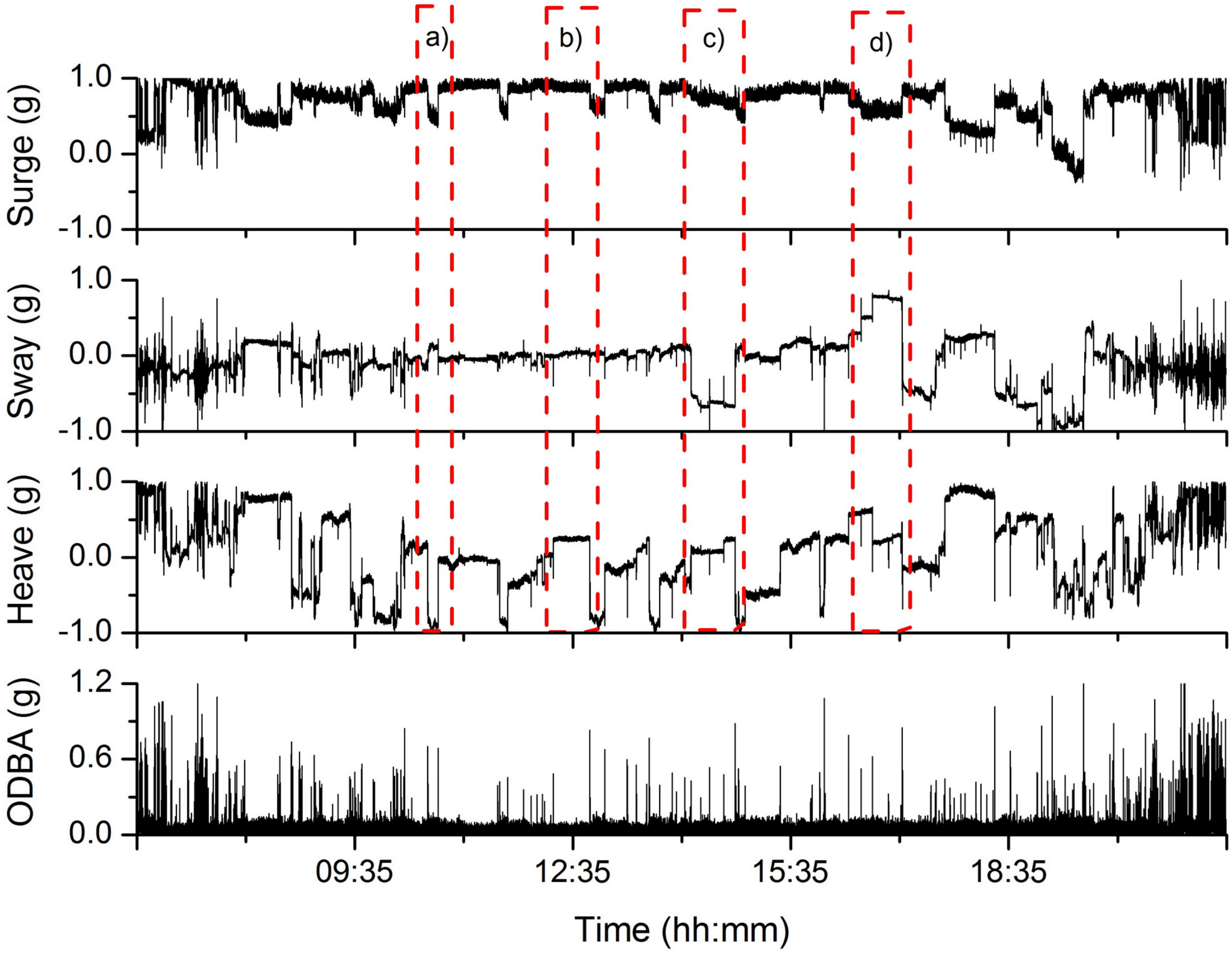

Fig 6. Changes in the acceleration signal of Eurasian beavers during a whole sleeping session. Example of the static surge, sway and heave acceleration of Eurasian beavers during a whole sleeping session. (a) Static heave acceleration values towards -1 *g* indicate lying on the back. (b) Static surge acceleration values towards +1 *g* and static sway acceleration values towards 0 *g* imply that the animal is sleeping in a sitting posture on its belly. (c) Static sway acceleration values towards -1 *g* indicate that the animal is lying on the left side, while (d) static sway acceleration values towards +1 *g* indicate lying on the right side.

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the animal-attached logger. Firstly, the overall static values of the heave during standing, walking and swimming represent values that are, respectively, progressively angled to reflect the angle of the lower back. The beaver's short-legged, plump body causes its rolling gait and sideways oscillations during walking; while during swimming leg-propulsion with the hind legs are responsible for sway oscillations. Grooming the belly and the back invariably involves the animal leaning back, which explains the mean negative static heave acceleration values. While using their forelegs to comb the water out of their pelage [18, 68], beavers typically start grooming their belly, then turn left and right, respectively, to groom their backs. These motions elicit the wave pattern in the sway acceleration, where individual differences in terms of time spent grooming each body part presumably cause the variation in the acceleration signal. Thus, the slightly positive mean sway acceleration indicates a higher grooming activity on the right side of the back which may reflect a tendency towards preferential use of the right paw, as found in other rodents such as mice [69] and rats [70, 71]. Feeding beavers adopt a seated posture while processing food items with their forelegs, often accompanied by occasional changes in position to facilitate another bite. These postural changes are apparent in the static heave acceleration. Finally, although diving behaviour can be identified definitively by changes in pressure, the systematic changes in body angle associated with the descent, bottom phase and ascent are definitive and are not characteristic of any other behaviour.

Limitations in ability to deduce behaviour

The value of animal-attached accelerometers for determining behaviour depends on methodological issues and the hardware, or are related to the behaviour itself. Methodological issues are primarily related to the manner which the unit is mounted [72]. As pointed out by Gleiss et al. [73], accelerometers mounted on different sites on the body will give very different signals in response to both movement and posture, affecting the capacity of the researchers to determine behaviour. Similarly, the precise attachment mechanism should be identical between individuals, and preferably as stable as possible so that the unit records proper body movement rather than some concatenation of the body movement modulated by an unstable base. Practicalities may preclude the use of glue as used in this study, which creates a steady, stable support for the device. Despite the instability issue though, we note that collars have successfully been used for attaching accelerometers to animals [33, 65, 74].

Sampling frequency also plays a critical role in the ability of the tag to code for behaviours. Although the sampling frequency of 8 Hz allowed us to distinguish seven behaviours, any cyclical patterns in acceleration (analogous, for example, to the wave patterns produced in the sway acceleration during walking) will not be resolvable as such unless described by at least the Nyquist rate (at least twice of it's naturally occurring frequency) [75]. Thus, a sampling frequency of 8 Hz will normally not allow resolution of any wave pattern with a frequency of greater than about 1.6 Hz, something that would, for example, make it impossible to determine the paw movements in grooming or the bites in gnawing. Similarly, highly transient behaviours may not be resolvable and simply contribute to the noise of the signal. We note that highly transient behaviours may not be resolvable even if the sampling frequency is high enough because not enough time is allocated to the activity for the pattern to be obvious. Thus, the binning duration is likely to play a role in determining the ability of dynamic body acceleration to help differentiate between transient behaviours with higher confidence with increasing time span over which the behaviour occurs.

Outside influences such as terrain, waves or wind can alter posture and induce variation in the manifestation of a behaviour via accelerometry. In our study area, there was great diversity in river bank types, ranging from steep, rocky slopes to grassy, flat banks. The consequence of this was that walking, in particular, sometimes involved heave acceleration values at considerable variance than would normally be exhibited, albeit for short periods. Even though waves can influence posture in water, this seemed to occur little in our study. Similarly, wind speed may alter flying behaviour in birds and should be taken into account where relevant [41, 76].

In addition, there are two other main issues that limit the use of accelerometry to identify animal behaviour. The first one relates to animals performing multiple behaviours at the same time, such as walking and eating. In this case, it is likely that behaviour with the higher amplitude overshadows the other behaviour and is dominant in the acceleration signal. The second issue is related to behaviours exhibiting little movement such as resting and sleeping. In this study, we were able to differentiate those two behaviours by picking resting periods when the animal was outside the lodge. Still, both cases may hamper the correct assignment of acceleration data to behavioural classes.

Conclusions and Perspectives

Our study demonstrates that acceleration data loggers can be used to elucidate the behaviour of free-living animals with only minor disturbance. Model outputs, such as the random forests classification applied in this study, can be used to inform computer programs to search automatically for behaviours, although it is unclear how well such systems will deal with problems such as transience between behaviours. There are obvious current limitations on software, particularly software that has the flexibility to work for multiple species with differing acceleration signatures. Ultimately, it may be possible to treat animals according to type, such as tetrapods versus birds, but this will require an extensive multi-species database to inform development. Other avenues such as spectral analysis [77] and machine learning approaches (cf. [78]) will also be useful as well as powerful visualization techniques such as spherical plots [79]. Developments in the solid state industry fuelled by, for example, mobile phones, will inevitably lead to the development of smaller acceleration units with increased battery longevity and storage capacity that operate with higher sampling frequencies. The new generation of tags, coupled with appropriate software, will lead to systems that can be deployed for months or years and allow identification of highly complex behavioural traits such as social interactions or behaviours with highly varying appearance. Ultimately, it seems likely that this approach will be implemented on pest [80] and endangered wildlife [81, 82] alike to help inform management and conservation actions [83, 84].

Supporting Information

S1 File. Dataset. Static acceleration values (*g*) and overall dynamic body acceleration (ODBA) (*g*) during six Eurasian beaver behaviours. Means and standard deviations of the static surge, sway and heave acceleration signal and ODBA for beavers during standing, walking, swimming, grooming, feeding and diving.
(CSV)

S2 File. Ethics statement documents.
(ZIP)

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Author Contributions

Conceived and designed the experiments: PG RPW KH FR. Performed the experiments: PG FR. Analyzed the data: PG LQ. Contributed reagents/materials/analysis tools: FR RPW. Wrote the paper: PG RPW LQ KH FR.

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Paper II

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ORIGINAL ARTICLE

Short-term effects of tagging on activity and movement patterns of Eurasian beavers (*Castor fiber*)

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Abstract Bio-logging is becoming increasingly popular amongst wildlife researchers, providing a remote way of monitoring free-ranging animals in their natural habitats. However, capturing and tagging can be stressful and may alter animal behaviour. In this study, we investigated whether tagging altered activity and movement patterns of Eurasian beavers (*Castor fiber*) during the first week after release, predicting that beavers would be less active, travel shorter distances and stay closer to the lodge in the first nights after the tagging event. We captured 29 dominant free-ranging beavers (12 females, 17 males) in Telemark county, Norway, and tagged them with GPS units ($n = 23$; 12 males, 11 females) and tri-axial acceleration data loggers ($n = 14$; 9 males, 5 females). Accelerometer data was used to investigate activity levels (using mean overall dynamic body acceleration ODBA and principal activity periods), while GPS data was used to determine movement patterns (using distance moved and lodge displacement rate). Tagging effects were apparent only in activity levels of beavers, where we found lower mean ODBA values after release although the small effect size (Cohen's $d = 0.17$) indicates only a minimal difference in activity. Neither principal activity periods nor distances moved or lodge displacement rate changed within the first week after release, which indicates that beavers were active and post-release space use within the territory was not affected by the tagging event in this respect.

Keywords Accelerometer · Activity · *Castor fiber* · GPS · Movement · Tagging effects

Introduction

The tagging of wild animals with miniaturized electronic devices has proved pivotal to many wildlife studies and has now become a commonplace within the field of animal ecology (Cagnacci et al. 2010; Rutz and Hays 2009). In particular, bio-logging technology, which specifically deals with logging sensor-derived parameters from animal-attached tags, now includes systems such as implants, anchors, glue-on tags and collar or harness-mounted units (i.e. Cooke et al. 2011; Kays et al. 2015). These tags can be equipped with a suite of sensors related to animal state, such as heart beat frequency and/or body temperature (Butler et al. 2004; Evans et al. 2016; Friebe et al. 2014), but may also document movement patterns (Rhodes et al. 2005; Zimmermann et al. 2007), general activity, behaviour and proxies for energy expenditure (Shepard et al. 2008; Wilson et al. 2006). Such tags can be used under challenging environmental conditions, including aquatic (Gleiss et al. 2011; Thorrold et al. 2014) and terrestrial habitats (Steyaert et al. 2014; Williams et al. 2014), as well as on species that spend a considerable amount of their time in air (Nathan et al. 2012; Spiegel et al. 2015). The general premise is that such tags allow free-living animals to be studied with

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only minor disturbance (Boyd et al. 2004; Ropert-Coudert and Wilson 2005) and minimal observer effects (Cagnacci et al. 2010) while delivering insights into animal behaviour and ecology (Shillinger et al. 2012; Weimerskirch 2007) with potential implications for conservation and management actions (Schofield et al. 2007; Wilson et al. 2015).

Increased focus on miniaturization has led to reduced size and weight of bio-loggers, extending the application range to even smaller animals (i.e. Kissling et al. 2014; O'Mara et al. 2014) and reduced perceived impact on tagged animals in general (Golabek et al. 2008; Ropert-Coudert et al. 2009). Yet, the capture and tagging procedure can be stressful for the animal (Fletcher and Boonstra 2006; Lapointe et al. 2015) and trigger physical and psychological effects, which can alter the animals' behaviour (Saraux et al. 2011; Wilson 2011). Until recently, many researchers have considered such effects to be negligible (Wilson and McMahon 2006) with, for example, a review on radio transmitter studies by Godfrey and Bryant (2003) reporting that, of 836 published papers, 83.3 % ignored the impact of marking with tracking devices on their study species. Fortunately, since the early 2000s, awareness of capture and tagging-related effects on animals has grown with researchers using various approaches to tackle potential problems (McMahon et al. 2011; Vandenabeele et al. 2015; White et al. 2013). While some studies found no evidence for such effects (McMahon et al. 2008; Ropert-Coudert et al. 2009), others showed tagging-related impacts ranging from physiological effects, such as changes in cortisol levels (Cattet et al. 2014) or capture myopathy (Höfle et al. 2004; Ponjoan et al. 2008), to behavioural effects including changes in movement and space use (Morellet et al. 2009; Rachlow et al. 2014) or generally reduced activity (Broell et al. 2016; Dennis and Shah 2012). Tagging effects may accumulate over time and can have detrimental influence on life history parameters such as reproductive success or survival rate (Barron et al. 2010; Blanchet et al. 2014; Casas et al. 2015), or may only be short-termed and diminish over time (Dennis and Shah 2012; Morellet et al. 2009).

Awareness of tagging-induced effects is not only important for the sake of animal welfare but should also be considered to prevent biased research results (Dechen Quinn et al. 2012; Ropert-Coudert and Wilson 2005). In particular, determination of effects which occur immediately after releasing the animal is important for researchers working with relatively short-term datasets. Such tagging effects can be assessed via direct observations of tagged individuals (Gendron et al. 2014) and/or a control group (Authier et al. 2013; Ropert-Coudert et al. 2007), by measuring physiological parameters such as blood sampling (Montané et al. 2002; St. Aubin et al. 2013) or by using the logged data itself (Broell et al. 2016; Rachlow et al. 2014). A particular value of bio-logged data for examining tagging effects is that it is effectively seamless and has high temporal resolution.

In this study, we investigated the short-term effects of capture, handling and tagging (hereafter "tagging") on a semi-aquatic, nocturnal rodent, the Eurasian beaver (*Castor fiber*). Both beaver species (*C. fiber* and the North American beaver *Castor canadensis*) are socially monogamous and live in colonies consisting of a dominant pair and their non-dominant offspring including kits, yearlings and individuals of 2 years or older (Campbell et al. 2005; Novak 1987). They are highly territorial and deposit scent mounds at territory boarders in order to advertise occupation (Rosell et al. 1998; Schulte 1998; Sun and Müller-Schwarze 1999). Beavers are herbivores with a preference for softwood such as poplars (*Populus* sp.) and willows (*Salix* sp.), terrestrial herbs and forbs, ferns and aquatic vegetation (Bergman and Bump 2015; Haarberg and Rosell 2006; Wilsson 1971). As central-place foragers, they typically return to the shoreline to consume their food (Haarberg and Rosell 2006; Jenkins 1980). The beaver's principal activity period (time the animals start/end their activity) is approximately from 07:00 pm to 07:00 am (Sharpe and Rosell 2003). This nocturnal activity means that beavers cannot easily be observed and makes them ideal candidates for logging technology.

By examining acceleration and GPS data, we aimed to determine acute tagging effects on Eurasian beaver activity and movement patterns during the first week after the tagging event. Two studies have reported such effects for Eurasian beavers who were implanted with intraperitoneal radio transmitters and found that the animals spent more time inside their lodges within the first few days after release (Ranheim et al. 2004; Sharpe and Rosell 2003, respectively). However, post-release differences in movement and/or activity patterns were not investigated in detail in these studies, nor did the authors report the significance of their findings. We hypothesized that beavers would alter their activity and movement patterns in response to the tagging procedure. We predicted that beavers show reduced activity both in terms of body movement-based activity level (measured as mean overall dynamic body acceleration, ODBA) and principal activity period, travel shorter distances and stay closer to the lodge in the first nights after tagging. Finally, we predicted that such effects would decrease during the observed period, due to habituation and recovery.

Methods

Study area and animals

The data for the study was collected between 2009 and 2014 in Telemark County, southeastern Norway (59°23′ N, 09°09′ E). The study site consists of the rivers Gvarv, Straumen and Sauar, all three rivers empty into Lake Norsjø. The rivers flow through a landscape dominated by semi-agricultural and riparian woodland structures; the latter are formed by species such as grey alder (*Alnus incana*), willow (*Salix* spp.), bird cherry (*Prunus padus*) and birch (*Betula* spp.) (Haarberg and Rosell 2006). Eurasian beavers have inhabited the area since the 1920s (Olstad 1937) and the population has been at carrying capacity for the last 10 years (Campbell et al. 2005; Steyaert et al. 2015). Beavers in the study area are monitored every year between March and November as part of a long-term capture-mark-recapture study (since 1998) for individual identification (micro-chip and ear-tags) and data acquisition (i.e. Campbell et al. 2013; Cross et al. 2014; Tinnesand et al. 2013). Since 1999, beavers have also been tagged with tracking devices such as VHF transmitters (Herr and Rosell 2004; Ranheim et al. 2004), GPS systems (Steyaert et al. 2015) and tri-axial accelerometers (Graf et al. 2015). Consequently, information on age, sex, social status (dominant, subordinate; see Campbell et al. 2012 for details), territory sizes, group sizes, reproduction and morphometric parameters (e.g. weight, body size, tail length and thickness) was available for beavers in the study area (Campbell et al. 2012, 2013).

Tagging procedure

Dominant Eurasian beavers were captured during the night (between 7:00 pm and 7:00 am) with a landing net from a boat (Rosell and Hovde 2001). For handling, the animals were transferred into a cloth bag, thereby dispensing with the need for anaesthesia (Fig. 1). We attached tags consisting of a VHF-transmitter (18 × 35 mm, 10 g; Reptile glue-on series R1910; Advanced Telemetry Systems, Isanti, MN, USA) in combination with an archival tri-axial accelerometer (15 × 90 mm, 62 g; JUV Elektronik, Schleswig-Hollstein, GER), or a rechargeable, archival μGPS unit (50 × 70 mm, 24 g; model G1G 134A; Sirtrack, Havelock North, NZ), or both units (Fig. 1). The units were connected with wire, integrated in 4.5 mm half-mesh net covering (Mørenot Fishery AS, Møre og Romsdal, NO) and fixed on the lower back, exactly 15 cm above the scaly tail along the spine using two-component epoxy resin (Fig. 1). The complete attachment, including all units, had a size of 130 × 90 mm and weighted approx. 250 g, which accounts for 1.3 % of the body weight of the lightest beaver (19 kg) used in the study. Additionally, we took measurements (body length, tail length and width) and samples (hair, castoreum and anal gland secretion) from the captured animals, resulting in an average handling time of 44 ± 25 min. Beavers were then released at the trapping site within in their own territory. GPS systems were programmed to take a position every 15 min from 7:00 pm to 7:00 am to cover the beavers' principle active period (Sharpe and Rosell 2003). Acceleration data (22 bit resolution) was recorded 24 h a day at a frequency of 8 Hz. After 2–3 weeks, beavers were located and re-captured via VHF-telemetry and the tags were cut out of the fur with a scalpel (Fig. 1). This procedure only affected the guard hairs, with the under-fur remaining unaffected (Graf et al. 2015).

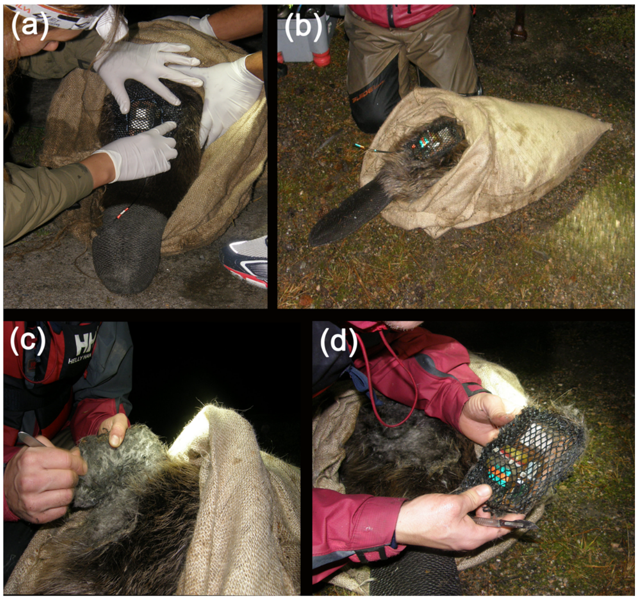

Fig. 1 Tagging procedure and retrieval of tags for Eurasian beavers (*C. fiber*) in southeastern Norway (2009–2014). Beavers were handled and tagged in cloth bags without the use of anaesthesia. **a** A GPS unit is glued onto the fur of the lower back (15 cm on top of the scaly tail) using two-component epoxy resin. **b** By using VHF-telemetry, a beaver tagged both with an accelerometer and a GPS unit has been recaptured. **c** The tag is cut out of the guard hair with a scalpel, leaving the under-fur intact. **d** The tag is retrieved

Ethical statement

The study, including all handling and tagging procedures (for details see above), was approved by the Norwegian Experimental Animal Board (FOTS id 742, 2170, 2579, 4387, 6282) and the Norwegian Directorate for Nature Management (archive code 444.5, 446.15/3), which also granted permission to conduct fieldwork in our study area. The patch of clipped guard hair grew back within 3 to 4 months.

Data analysis

All data analyses were performed with R version 3.0.3 (R Development Core Team 2013). Accelerometer and GPS data were analysed separately, as we only had combined accelerometer and GPS data for five individuals (Table 1). We used the xts package version 0.9-7 (Ryan and Ulrich 2014) for the accelerometer data and the adehabitatLT package (Calenge 2006) for the GPS data. The accelerometer dataset was cut to time periods between 7:00 pm and 7:00 am (to coincide with previously reported principal activity period for beavers) and shortened to seven nights per individual for standardization. Accelerometer data was used to derive two activity response variables: 'mean overall dynamic body acceleration'

Table 1 Meta-data of 29 dominant Eurasian beavers (*C. fiber*) and tagging devices used in this study in Telemark, southeastern Norway (2009–2014)

Beaver	Tag[a]	Territory[b]	Sex[c]	N_{night}[d]	Season[e]	Year[f]	N_{pos}[g]	N_{capt}[h]
Chris	ACC	L5b	M	6	S (Apr)	2009	ACC only	22
Demi	ACC	E	F	8	A (Oct)	2009	ACC only	2
Easy	ACC	L5a	M	7	S (Apr)	2009	ACC only	19
Frode	ACC	L2b	M	7	S (May)	2009	ACC only	10
Jan-Marc	ACC	P0	M	17	A (Oct)	2011	ACC only	5
Kathrin	ACC	H	F	13	A (Sept)	2011	ACC only	2
Klumpen	ACC	GM	M	8	A (Oct)	2009	ACC only	6
Lasse	ACC	L2	M	7	S (May)	2009	ACC only	6
Oddi	ACC	H	M	7	A (Oct)	2009	ACC only	4
Apple	GPS	P2a	F	17	A (Oct)	2013	147	1
Åse	GPS	P5	F	11	S (Apr)	2014	134	1
Christina	GPS	P3a	F	19	A (Aug)	2010	105	3
Hanne-Synnove	GPS	P0	F	11	A (Aug)	2010	96	5
Hazel	GPS	G	F	23	S (Apr)	2010	122	5
Horst	GPS	P4	M	7	A (Oct)	2010	107	2
Jan-Marc	GPS	P0	M	17	A (Aug)	2014	109	7
Jodie	GPS	N1	F	12	S (Apr)	2012	122	12
Kjartan	GPS	LP	M	9	A (Aug)	2010	105	2
Klumpen	GPS	GM	M	12	S (Apr)	2014	126	8
Lasse	GPS	L2	M	10	S (May)	2011	121	6
Loran	GPS	L4a	M	11	A (Sept)	2009	135	15
Malena	GPS	L4a	F	9	S (May)	2014	108	2
Manuel	GPS	P1	M	9	A (Sept)	2013	121	1
Moritz	GPS	B2	M	7	A (Aug)	2010	99	3
Moses	GPS	P2b	M	15	A (Aug)	2010	77	7
Paddy	GPS	GL	M	12	S (Apr)	2012	142	3
Thomas	GPS	P4	M	9	S (Apr)	2014	128	1
Andreas	GPS+ACC	B1	M	8 (G), 19 (A)	S (Apr)	2010	123	8
Erlend	GPS+ACC	P3b	M	13 (G), 15 (A)	S (Apr)	2010	141	6
Ida	GPS+ACC	LP	F	14 (G), 19 (A)	A (Sept)	2010	147	6
Leslie	GPS+ACC	B1	F	18 (G), 9 (A)	S (Apr)	2010	151	8
Maud	GPS+ACC	L6a	F	11 (G), 9 (A)	A (Nov)	2009	126	1

[a] Tag, GPS or ACC (accelerometer) or both

[b] Territory, territory identifier

[c] Sex (M = male, F = female)

[d] N_{night}, number of nights in original dataset

[e] Season (S = spring: April–May, A = autumn: August–November)

[f] Year, year of monitoring

[g] Npos, number of valid GPS positions per individual for seven nights

[h] Ncapt, number of times the animals have been captured before

(ODBA, in units of gravity *g*) and 'principal activity periods' (in minutes). Mean ODBA at 8 Hz was calculated by summing up the dynamic acceleration logged in all three axes (Wilson et al. 2006) and averaged over 15 min to investigate movement-based activity levels for each individual. The beavers' principal activity periods were determined visually by identifying movement patterns indicating when the beavers left their lodges (indicated by the first dive in the evening) and returned to the lodges again (the last dive in the morning followed by a grooming session; for information on behavioural identification using accelerometry, see Graf et al. (2015)). The first night was excluded from this analysis since we captured beavers that night and thus did not have a full principal activity period.

We also standardized the GPS dataset for all individuals to seven nights. For improving spatial accuracy, we cleaned the raw GPS data by removing all fixes with horizontal dilution of precision (HDOP) values ≥5 or with only two dimensions (2D) (Lewis et al. 2007). Further, the GPS fix rate was raised from 15 to 30 min to increase the amount of consecutive GPS fixes (necessary for calculating distances) and to reduce the number of missing values. The final dataset used for analyses had an overall fix rate performance (potential GPS fixes vs. actual GPS fixes of cleaned dataset) of 75 %. Based on the GPS data, we created two movement response variables: 'distance moved' (m)—the distance between two consecutive GPS fixes in 30-min intervals—and 'lodge displacement rate (LDR)'—the distance (m) of each GPS position (taken every 30 min) to the individual's main lodge. For calculating displacement rates from lodges, we identified active lodges within each territory by visually screening the GPS positions in ArcMap10 (ESRI, Redlands, CA, USA), in particular the first and last positions for each night (the time of emerging and returning to the lodge). A map containing both active and old lodges which were used by beavers over the years was then used to localize the coordinates for the relevant main lodges.

We created linear mixed-effects (LME) models using the nlme package (Pinheiro et al. 2016) including the time-variable 'minutes after release' as the main predictor for 'mean ODBA', 'distance moved' and 'LDR', and the main predictor 'night' for 'principal activity period' (since we just had one data point per night). In all models, we used the covariates 'season' (spring: April–May, autumn: August–November), 'sex', 'total number of times captured before' (typically between 0 and three times within a year; F. Rosell, unpublished results; total $\tilde{x}$ = 5.0, IQR = 2–7) and 'tag load' (1 = either GPS or accelerometer, a lighter and smaller tag, 2 = both GPS and accelerometer, a heavier and larger tag). In addition, we included 'territory size' (calculated as bank length, $\bar{x}$ = 3650.8 ± 1524.6 m) as a covariate in analyses based on GPS data. For the response variables 'mean ODBA', 'distance moved' and 'LDR', we included 'individual' nested within 'year' as random effect. For the response variable 'principal activity period', we only included 'individual' as random effect, due to the smaller sample size. However, mean principal activity periods were similar between years (Kruskal-Wallis test, $\chi^2 = 5.534$, $df = 2$, $p = 0.063$).

The three response variables 'mean ODBA', 'distance moved' and 'LDR' were log-transformed to meet the LME model's assumptions for normally distributed residuals. When necessary, we also accounted for non-independence of errors due to temporal autocorrelation of the response variables by adding a first-order autoregressive term (corAR1) to our models (Pollitt et al. 2012; Zuur et al. 2009). No collinearity between independent variables were detected ($r < 0.6$ in all cases) and variance inflation factors (vif) for all models were <3 (see Zuur et al. 2010). We used a backward model selection procedure and selected the most parsimonious model based on the Akaike information criterion corrected for small sample sizes (AIC$_c$) and AIC$_c$ differences (ΔAIC$_{c)}$ (Burnham et al. 2010; Wagenmakers and Farrell 2004). We selected the final models from a subset of top models with strong levels of empirical support (ΔAIC$_c$ = 0–2) (Anderson 2008). Model parameters that included zero within their 95 % confidence interval (CI) were considered as uninformative (Arnold 2010). Cohen's d scores (Cohen 1988), β estimates and coefficients of determination (R^2) were used as a measure of effect size (Nakagawa and Cuthill 2007). Bootstrapped CIs for tagging-related informative responses were reported using the bootES package (Kirby and Gerlanc 2013).

Results

We analysed data from 29 individual dominant beavers (12 females, 17 males), 3 of these beavers were captured a second time (Table 1). As the period of time between subsequent captures was at least 2 years (2, 3 and 5 years) and a different tag type (GPS vs. accelerometer) was deployed on the second capture, we included both datasets in our analysis. The accelerometer dataset consisted of 14 beavers (5 females, 9 males) and GPS dataset of 23 beavers (11 females, 12 males); five individuals were represented in both datasets as they were tagged with a combination of GPS unit and accelerometer (Table 1). Accelerometer data was collected in 11 different territories and included in total 7–19 nights; GPS data was collected in 15 different territories and included 7–23 nights per individual (Table 1). We analysed only six nights of acceleration data for one beaver (Chris, Table 1), since the unit ran out of battery. For the same reason, analyses of principal activity period for the last night (night 8; analyses started on night 2) included acceleration data for only 8 out of 14 individuals. For four individuals, we got only one GPS location in the first night (indicating that the beavers went into their lodges) and could thus calculate distances moved only for nights 2–7. We removed one individual (Loran, Table 1) from our LDR analysis since we were unable to identify the main lodge and calculate corresponding displacement rates (he used two lodges at distances that could be covered within the sampling interval of the GPS units). As the first night after release was shorter than the following six nights, we also ran all models without night 1, but found that the results were unchanged for all response variables. Initially, we also included the predictor 'handling time' in all models; however, since there were several missing values, this lowered sample sizes considerably (GPS data: $n = 12$, acceleration data: $n = 11$). As handling time was uninformative, and in order to maintain the original sample size, we did not include this predictor in the final models. The predictors included in the most parsimonious models for the four response variables are presented in

Table 2 (for full model selection, see Additional Tables S1–S4 given in Online Resource 1); informative predictors and according model outcomes are shown in Table 3.

Mean ODBA

The grand median for mean ODBA values for seven nights was 0.15 *g* with an IQR of 0.13–0.19 *g*. Mean ODBA was best explained by the main predictor 'minutes after release' (Table 2), with beavers showing a lower activity level after release (Table 3, Fig. 2). The standardized effect size (Cohen's *d*) for differences in mean ODBA values in the first and the seventh night was 0.17 (LL = 0.04, UL = 0.30). This small effect size (Cohen 1988), in combination with the low power of the other model effect statistics β and R^2 (Table 3), suggests only a minimal difference in activity level within the first week after release. Plotting mean ODBA values over time also revealed a periodicity in the activity level, with lower activity levels at the beginning and at the end of the night (Fig. 2).

Principal activity period

Mean principal activity period in the first week was 10.95 ± 1.19 h. Beavers started their principal activity periods on average at 20:19 h ± 58 min in the evening and went back into their lodges in the morning on average at 07:16 h ± 57 min. The best model included the main predictor 'night' and the covariates 'season', 'tag load', 'number of times captured before' and 'sex' (Table 2). By investigating the CI's for the dependent variables, we found only season to be informative, with beavers being active for shorter periods in spring (Table 3).

Distance moved

Median distance moved in 30 min was 158.52 m for the seven nights with an IQR of 56.63–316.70 m. Distance moved was best explained by territory size (Table 2), with beavers in larger territories covering greater distances (Table 3).

Lodge displacement rate (LDR)

Median LDR for the seven nights was 359.56 m with an IQR of 179.69–634.36 m. LDR was best explained by season (Table 2); however, CI's for β estimates incorporated 0 ($\beta = 0.18$, LL = −0.09, UL = 0.45) and we thus considered season as an uninformative variable.

Discussion

Short-term tagging effects on Eurasian beavers included only changes in their activity level, with beavers having a lower mean ODBA after release. However, the small effect size for mean ODBA calls the practical relevance of this finding into question (Sullivan and Feinn 2012). Four individuals went back into their lodges after release and stayed there until the next day (night 2). This finding indicates that individual beavers may alter their behaviour in response to the tagging event in the capture night. Contrary to our predictions, principal activity periods, distances moved and LDR were not altered by the tagging event. In a study on North American beavers, Smith et al. (2016) found no effects of transmitters (both tail-tags and implants) on the animals' short- and long-term survival (monthly and annual over 8 years) when compared to ear-tagged beavers only. While body condition was similar for the two groups, beavers with transmitters had higher winter weight loss, which could have been trigged by tail-tagging and transmitters tearing out of the tail, respectively, since the beaver tail serves as a fat storage depot (Aleksiuk 1970). Non-tagging related, but informative effects included longer principal activity periods in autumn and greater distances covered by beavers living in larger territories. The latter result is intuitive and accords with Graf et al. (2016), who showed that beavers exhibit different movement strategies in relation to territory sizes and describe the same relationship for a different subset of beavers from the same study area. In contrast to two studies that found no seasonal differences in principal

Table 2 Most parsimonious models based on Akaike's information criterion corrected for small sample sizes (AIC_c) for the four response variables for 29 dominant Eurasian beavers (*C. fiber*) in Telemark, southeastern Norway (2009–2014)

Response variable	Most parsimonious model	AIC_c[a]	w_i[b]	K[c]
Mean ODBA	MIN	−1039.89	0.76	6
Principal activity period	NIGHT + SEASON + TAG_LD + TIMES_CAPT + SEX	906.04	0.96	9
Distance moved	TERR_SIZE	7746.97	1	4
Lodge displacement rate	SEASON	6627.08	1	6

MIN minutes after release, *TAG_LD* tag load, *TIMES_CAPT* times captured before, *TERR_SIZE* territory size measured as bank length (m)

[a] Akaike information criterion adjusted for small sample sizes

[b] Akaike weight

[c] Number of parameters

Table 3 Model outcomes for the three response variables with informative predictors for 29 dominant Eurasian beavers (*C. fiber*) in Telemark, southeastern Norway (2009–2014)

Response variable	Informative model term	β^a	σ^b	LL^c	UL^d	R^{2e}
Mean ODBA^f	Minutes after release	$2.15e^{-05}$	$4.20e^{-06}$	$1.33e^{-05}$	$2.98e^{-05}$	0.29
Principal activity period	Season spring	−100.464	42.815	−197.318	−3.610	0.58
Distance moved^f	Territory size	$7.85e^{-05}$	$3.61e^{-05}$	$2.01e^{-06}$	$1.55e^{-04}$	0.08

[a] Estimated regression coefficient

[b] Standard error,

[c] Lower 95 % confidence levels around the estimated coefficient ($\beta \pm 1.96 \times \sigma$)

[d] Upper 95 % confidence levels around the estimated coefficient ($\beta \pm 1.96 \times \sigma$)

[e] Coefficient of determination

[f] Log-transformed model outcomes

activity periods (Sharpe and Rosell 2003; Swinnen et al. 2015), we suggest that longer principal activity periods in autumn could be coupled with winter preparations such as food-caching behaviour (Busher 1996; Hartman and Axelsson 2004) and lodge repair work (Żurowski 1992).

Reduced activity level (mean ODBA)

We found a time-dependent increase in beaver activity (manifest by mean ODBA) after the tagging event. However, the small effect size ($d = 0.17$) likely equates to a small difference in terms of activity and thus implies only minor biological relevance. Besides these effect size issues, a more vigilant and cautious behaviour after release may be responsible for the observed lower mean ODBA levels. In their study on anti-predator behaviour of North American beavers, Basey and Jenkins (1995) showed that the animals would stop periodically between their activities and appeared to look and smell for predators in risky situations (e.g. when presented with predator odour). In agreement with this observation, both Rosell and Czech (2000) and Rosell and Sanda (2006) found a reduced foraging and scent marking behaviour in beavers when confronted with a predator odour.

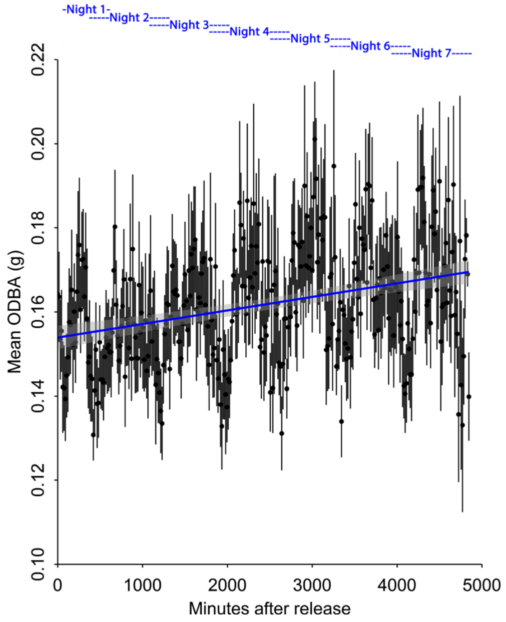

Fig. 2 Linear relationship (regression line and 95 % confidence interval) between mean ODBA and minutes after release for 14 dominant Eurasian beavers (*C. fiber*) in Telemark, southeastern Norway (2009–2014). The *axis on top of the graph* shows the different nights after release; overlap results from the different capture times in the first night. Each point represents the overall mean (±SE) over individual mean ODBA values measured every 15 min after the tagging event. Periodic oscillations of ODBA means for each night suggest similar activity patterns of all individuals, with an activity peak in the middle of their active period (~7 pm to 7 am)

Periodic oscillations in activity levels of our study animals suggest that beavers seem to follow a similar activity pattern each night, with peaks during the mid-part of the beavers' principal activity periods. Similar oscillations in activity levels were found in all study animals during the seven nights. Higher mean ODBA levels in the middle of the night suggest that this is the peak activity time for beavers. The mean ODBA value for standing (or being inactive) is 0.06 *g* ($\sigma = 0.02$ g) (Graf et al. 2015) and none of our mean ODBA values was below 0.1 *g*, which suggests that the animals were active during all seven nights after the tagging event.

No short-term effects on principal activity period, distances moved and LDR

We found no evidence for short-term tagging effects on principal activity periods, distances moved and LDR. This contrasts a study by Ranheim et al. (2004), who implanted radio transmitters in 22 adult beavers from the same study area and found that beavers spent more time inside their lodges within the first few days after release. Similarly, Sharpe and Rosell (2003), who worked with a subset of 12 adult beavers with implanted radio transmitters, report that beavers spent more time inside their lodges in the first two days post-release.

However, capture effects were not the main focus of these studies and were thus just reported anecdotal. In addition, both Ranheim et al. (2004) and Sharpe and Rosell (2003) used anaesthesia and surgery (in the latter study in 10 out of 12 beavers), which is likely to have a greater impact than our quick, non-invasive tagging-method. An advantage of our net-capture method from the boat (Rosell and Hovde 2001) is that there is only a short time lag between the capture and handling event, which substantially reduces the overall time used for the handling and tagging procedure. Certainly, shortened handling periods appear to help mitigate stress (e.g. Bosson et al. 2012; Ponjoan et al. 2008). Even though some studies claim that using chemical immobilization reduces capture and handling stress (Montané et al. 2002; Read et al. 2000), we argue that not using anaesthesia can be an advantage: Our procedure meant that beavers were released immediately back into their familiar surroundings (including lodges and burrows for refuge) without adverse affects from anaesthesia and/or surgery. Tagged beavers were quite often observed swimming or foraging shortly after release (F. Rosell, personal communication), which confirms our assumption.

Territoriality against all odds

We found no effect of the tagging procedure on the beavers' spatial movement within their territories and suggest that principal activity periods and movement patterns of territorial animals may be constrained by the need for territorial defence. Kukalová et al. (2013) found that edible dormice (*Glis glis*) switched their den site after being handled, but returned on average after 4 days. The authors suggest that the level of territoriality may play a role in a species' response to handling and tagging with animals returning to the same place because of a defended resource in the area. Similarly, daily patrolling and scent marking is an important constituent of the beaver's nightly routine (Rosell et al. 1998), particularly for the dominant individuals as they are the main contributors of territory defence (Rosell and Thomsen 2006). In beaver populations at carrying capacity, such as in our study area (Campbell et al. 2005; Steyaert et al. 2015), the risks of intrusion following insufficient territory maintenance might be high (Steyaert et al. 2015). Due to this, there is likely strong selection pressure for beavers to resume their nightly routines even shortly after the tagging event.

The effect of habituation

The number of times a beaver had been captured before did not affect movement and activity within the first week after tagging. Beavers in our study area are typically captured and handled for the first time when they are still kits and all animals in this study have been captured at least once before. It has been shown that a single exposure to a stressor can induce long-term changes in neuroendocrine and behavioural stress responses (Armario et al. 2008). Lynn et al. (2010) measured plasma corticosterone levels in free-living Eastern bluebirds (*Sialia sialis*) and found a reduced stress response 7 weeks after a single first exposure to capture and handling. However, most studies on this topic have been conducted in captivity and have measured subsequent stress responses within just a few days or weeks (for review, see Wiedenmayer 2004). Other studies have found no such effects and argue that habituation needs repeated handling at relatively short intervals (several times per week) (Hämäläinen et al. 2014). In addition, the interval between two subsequent captures for individual beavers in this study can range up to several years and it is not clear whether beavers possess a long-term memory that can relate to past events in this order. Consequently, for determining whether habituation in beavers can occur after just a single exposure to a stressor and last over extended time periods, further research on neuroendocrine stress responses is needed.

Drag

A major issue invoked by researchers working with external tags on aquatic animals is that of drag (e.g. Bannasch et al. 1994; Culik et al. 1994; Jones et al. 2011), which is not expected to change over wearing time since it is a purely physical constraint. The power required to overcome drag (P) is given by $P = 0.5\,A\,Cd\,v^3\,\rho$, where A is the cross-sectional area of the animal, Cd is the drag coefficient, ρ is the density of the fluid medium and v is the velocity. Thus, although our attached device would increase the drag by increasing the cross-sectional area marginally, it is the swim speed that is going to be a prime modulator of increased energy expenditure (Vandenabeele et al. 2015). Importantly, work by Vandenabeele et al. (2015) showed that up to speeds of 1.5 m/s, the energy consumption of a tag-fitted great cormorant *Phalacrocorax carbo* was unlikely to differ much from the untagged conspecific, but that differences between them accelerated quickly thereafter. Thus, since beavers generally swim between 0.8 m/s on the surface (Nolet and Rosell 1994) and 0.6 m/s when submerged (Allers and Culik 1997), we would not expect drag-based power to compromise the animals greatly. This does not, however, apply to fast swimming manoeuvres, such as during escape responses (e.g. tail-slap dives; see Hodgdon and Larson 1973; Wilsson 1971), and this warrants further consideration.

Future perspectives

Ideally, tagging effects should be analysed by combining both behavioural and physiological data (e.g. blood parameters and/or faeces; Bosson et al. 2012; Harcourt et al. 2010; Rehnus et al. 2009; Sheriff et al. 2011). Indeed, capture effects might only be physiological (Kock et al. 1987; Meyer et al. 2008) and do not necessarily imply visible behavioural changes. Likely, these effects do not lead to a bias of results in behavioural studies, but do still have implications regarding animal welfare. Moreover, a period of 7 days might be too short to detect alterations in behavioural patterns, and perhaps may not cover the whole habituation period. The technical constraints we experienced in our study, which were mainly related to battery life and the size of the unit, meant we were not able to investigate longer time periods for all individuals. Other studies have described habituation periods to last for 4 days in the common brushtail possum (*Trichosurus vulpecula*) (Dennis and Shah 2012), 10 days in European roe deer (*Capreolus capreolus*) (Morellet et al. 2009), or even 2 and up to 4 weeks in white-tailed deer (*Odocoileus virginianus*) and pygmy rabbits (*Brachylagus idahoensis*), respectively (Dechen Quinn et al. 2012; Rachlow et al. 2014). However, these differences in habituation periods may be related to the study species' ecology, as well as the different capture and handling procedures and are thus hard to put into perspective here. Another difficulty in investigating tagging effects by using logged data is that 'measurement may affect performance'—i.e. the simple act of having a tag on an animal means there is no control for when it has no tag at all (cf. Wilson et al. 1986). Only long-term studies on lifetime reproductive success or survival and/or control observations of untagged individuals (see Authier et al. 2013) may deliver answers to that indirectly (Bro et al. 1999; Côté et al. 1998). Indeed, the issue of proper control in studies such as these is likely to be perennial.

Conclusion

In this study, we emphasize the potential of bio-logged data to investigate tagging effects on study animals and highlight awareness of such effects. This is important for animal welfare and for the development of methods that mitigate tagging effects, but also for avoiding biased research results. We found short-term tagging effects only related to activity levels, which were of low practical relevance due to the small effect size. The discovery that there were no changes in principal activity periods, distances moved and LDR indicates that beavers were active and did not change space use within the territory following tagging. Based on these results, we suggest excluding data from the capture night from analyses. Ultimately, combined bio-logging with physiological data, as well as long-term data on life history parameters such as fitness and survival, should be examined for getting deeper insights into an animal's response to tagging events.

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Table S1. Model selection using Akaike's information criterion corrected for small sample sizes (AIC_c) for mean ODBA in relation to the five predictor variables for 14 dominant Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2014).

Mean ODBA

Model[a]	AIC_c	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
MIN	-1051.38	0.00	0.76	6	531.70
MIN + TAG_LD	-1048.08	3.30	0.15	7	531.05
MIN + TAG_LD + TIMES_CAPT	-1038.76	12.62	0.00	8	527.40
MIN + TAG_LD + TIMES_CAPT + SEASON	-1034.88	16.50	0.00	9	526.46
MIN + TAG_LD + TIMES_CAPT + SEASON + SEX	-1030.31	21.08	0.00	10	525.18

[a]MIN = minutes after release, TAG_LD = tag load, TIMES_CAPT = times captured before; [b]Difference in AIC_c relative to min. AIC_c; [c]Akaike weight; [d]Number of parameters

Table S2. Model selection using Akaike's information criterion corrected for small sample sizes (AIC_c) for principal activity period in relation to the five predictor variables for 14 dominant Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2014).

Principal activity period

Model[a]	AIC_c	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
NIGHT + SEASON + TAG_LD + TIMES_CAPT + SEX	903.54	0.00	0.97	8	-442.82
NIGHT + SEASON + TAG_LD + TIMES_CAPT	910.56	7.02	0.03	7	-447.55
NIGHT + SEASON + TAG_LD	913.92	10.38	0.01	6	-450.42
NIGHT + SEASON	922.11	18.58	0.00	5	-455.68
SEASON	926.83	23.29	0.00	4	-459.17
NIGHT	931.48	27.94	0.00	4	-461.49

[a]TAG_LD = tag load, TIMES_CAPT = times captured before; [b]Difference in AIC_c relative to min. AIC_c; [c]Akaike weight; [d]Number of parameters

Table S3. Model selection using Akaike's information criterion corrected for small sample sizes (AICc) for distance moved in relation to the six predictor variables for 23 dominant Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2014).

Distance moved

Model[a]	AIC$_c$	ΔAIC$_c$[b]	w_i[c]	K[d]	Deviance
TERR_SIZE	7716.40	0.00	0.77	6	-3852.18
TERR_SIZE + TAG_LD	7719.37	2.96	0.17	7	-3852.66
TERR_SIZE + SEASON + TAG_LD	7721.55	5.15	0.06	8	-3852.75
TERR_SIZE + SEASON + TAG_LD + TIMES_CAPT	7728.00	11.60	0.00	9	-3854.97
MIN + TERR_SIZE + SEASON + TAG_LD + TIMES_CAPT	7748.11	31.70	0.00	10	-3864.01
MIN + TERR_SIZE + SEASON + TAG_LD + TIMES_CAPT + SEX	7752.14	35.73	0.00	11	-3865.01

[a] TERR_SIZE = territory size measured as bank length (m), TAG_LD = tag load, MIN = minutes after release, TIMES_CAPT = times captured before; [b]Difference in AIC$_c$ relative to min. AIC$_c$; [c]Akaike weight; [d]Number of parameters

Table S4. Model selection using Akaike's information criterion corrected for small sample sizes (AICc) for lodge displacement rate (LDR) in relation to the six predictor variables for 23 dominant Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2014).

Lodge displacement rate (LDR)

Model[a]	AIC$_c$	ΔAIC$_c$[b]	w_i[c]	K[d]	Deviance
SEASON	6627.08	0.00	1.00	6	-3307.52
TERR_SIZE + SEASON	6646.16	19.07	0.00	7	-3316.06
MIN + TERR_SIZE + SEASON	6665.78	38.70	0.00	8	-3324.86
MIN + TERR_SIZE + SEASON + TIMES_CAPT	6673.42	46.34	0.00	9	-3327.68
MIN + TERR_SIZE + SEASON + TIMES_CAPT + SEX	6677.84	50.76	0.00	10	-3328.88
MIN + TERR_SIZE + SEASON + TIMES_CAPT + SEX + TAG_LD	6681.67	54.59	0.00	11	-3329.79

[a] TIMES_CAPT = times captured before, MIN = minutes after release, TAG_LD = tag load, TERR_SIZE = territory size measured as bank length (m); [b]Difference in AIC$_c$ relative to min. AIC$_c$; [c]Akaike weight; [d]Number of parameters

Paper III

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Original investigation

Territory size and age explain movement patterns in the Eurasian beaver

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ABSTRACT

Territoriality is only profitable when the benefits gained from territory exploitation exceed the costs of defence, and territory sizes are usually optimized by time constraints related to resource defence (e.g. patrolling) and exploitation. In this study, we equipped 25 dominant Eurasian beavers (*Castor fiber*) with GPS units to study spatial movement patterns both on land and in water in relation to territory size, resource availability, the number of neighbours, season, and the beavers' age. We show a territory size-dependent trade-off between territorial behaviours and foraging distances: Beavers in larger territories moved greater distances each night, thereby spending more time patrolling, and stayed closer to the shoreline when being on land (i.e. when foraging). Inversely, in smaller territories beavers patrolled less and foraged further away from the shoreline. These results suggest that individuals trade-off the costs of patrolling larger territories against the benefits of foraging closer towards the shoreline. Smaller territories might be more prone to resource depletion, thus, making foraging further from the shoreline a strategy to ensure sustainable resource use. Further, older beavers spent more time on land and close to territory borders compared to younger ones, suggesting a behavioural change with age possibly due to increased experience and boldness.

Introduction

Territoriality is linked to the defence of a fixed area by an individual or a group of mutually tolerant individuals (Maher and Lott, 1995). Animals typically occupy territories when resources, such as food, cover, shelter, and mating partners, are scarce (Brown, 1969; Davies and Houston, 1984; Maher and Lott, 1995). Territorial behaviour is expected to evolve when the benefits gained from the exclusive use of essential and restricted resources exceed the costs of defence (Brown, 1964; Stamps, 1994). Defence mechanisms are diverse and may include aggressive, physical disputes with intruders, which generally impose significant metabolic costs (Parker, 1974; Viera et al., 2011), and advertisement of territory ownership by chemical (e.g. scent-marking) (Gosling and Roberts, 2001; Roberts and Dunbar, 2000), acoustic (Bee et al., 2000; McGregor, 1993), or visual signals (Burst and Pelton, 1983; Penteriani and del Mar Delgado, 2008). Patrolling territory borders is essential for effectively advertising territory occupation (Sillero-Zubiri and Macdonald, 1998) and is, besides foraging, an important driver of spatial movement behaviour in territorial species (Fagan et al., 2013; Ims, 1995).

Animals are continually subject to multiple decisions regarding energy investment and thus need to trade-off which activity to adopt at any time (Mangel and Clark, 1986). Such trade-offs may impact an animal's fitness and survival (Ohgushi, 1996; Stearns, 1989) and have been a research area of interest for decades. The literature in this field is extensive, however, most studies focus on the trade-offs between offspring size and offspring number (e.g. Charnov and Ernest, 2006; Fleming and Gross, 1990), foraging and predation risk (e.g. Lima et al., 1985; Sih, 1980; Verdolin, 2006), or growth and reproduction (e.g. Kozłowski, 1992; Roff, 1983). Studies investigating the trade-off between foraging and territorial behaviours are comparatively rare. For example, great tits (*Parus major*) traded off food intake for territory defence in the presence of an intruder (Kacelnik et al., 1981; Ydenberg and Krebs,

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1987). Jaeger et al. (1983) found that red-backed salamanders (*Plethodon cinereus*) decreased foraging time and devoted more time to territory defence when potential competitors intruded. Wild chimpanzees (*Pan troglodytes*) reduced their feeding time by at least 50% when on patrolling trips (Amsler, 2010).

Generally, the costs of territoriality are positively correlated with territory size, because larger areas are more costly to defend (Righton et al., 1998; Schoener, 1983). Determining the costs and benefits of different territory sizes in a species is difficult (Jaeger et al., 1983) and has been subject to a range of modelling approaches (e.g. Adams, 2001; Dill, 1978; Schoener, 1983). The optimization criterion for territory size is usually related to time constraints between resource defence and exploitation (Adams, 2001; Kacelnik et al., 1981), and has been described as the minimum economically defensible area (Gill and Wolf, 1975; Pyke et al., 1977). Adams (2001) suggested two additional factors that may influence territory sizes, i.e. interactions among neighbours and interactions between established residents and potential settlers. Such interactions may be especially important in high-density populations with contiguous territory borders (Adams, 2001), and may result in territory sizes smaller or larger than the minimum economically defensible area. Further, individual differences in movement patterns might be related to age: e.g. Cederlund and Sand (1994) found that older male moose (*Alces alces*) had larger home ranges than younger ones, which may be caused by differences in nutritional demands and social activities like rutting behaviour. Similarly, in tailed frogs (*Ascaphus truei*) (Daugherty and Sheldon, 1982) and pinnipeds (Baker et al., 1995; Cameron et al., 2007), older individuals exhibited greater site fidelity than younger ones, which was suggested to be related to sexual maturation, age-specific variation in ecological requirements and accumulated knowledge on breeding site characteristics.

We used the Eurasian beaver (*Castor fiber*) to investigate factors affecting spatial movement patterns in a long-lived, territorial animal. Beavers (both the Eurasian and the North American beaver (*Castor canadensis*)) are semi-aquatic, nocturnal rodents that are socially monogamous and live in family groups consisting of the dominant pair, the young of the year, yearlings, and subadults, i.e., non-dominant individuals of two years or older (Campbell et al., 2005; Wilsson, 1971). The two beaver species are in the small percentage of mammals (3–5%) that form monogamous pair bonds (Kleiman, 1977) with complex social behaviours including male parental care and shared territorial defence (Busher, 2007). Beavers build lodges or bank dens and are central-place foragers with a preference for poplars (*Populus* sp.) and willows (*Salix* sp.) (Haarberg and Rosell, 2006; Vorel et al., 2015). They move relatively close to the shoreline and feed within approx. 40 m from the water's edge (Barnes and Dibble, 1988; Parker et al., 2001). The beavers' fusiform body with short limbs and webbed hind-feet make them good, enduring swimmers, but constrain their agility in terrestrial environments (Allers and Culik, 1997). Beavers hold larger territories during initial settlement, whereas in populations at carrying-capacity territories of various sizes are occupied (Campbell et al., 2005). To advertise territory occupation, both sexes deposit scent-marks within their territories, especially along up- and downstream borders (Hodgdon, 1978; Rosell et al., 1998; Sun and Müller-Schwarze, 1999). Scent-marking activity increases during spring when subadults disperse from their natal colony (Rosell et al., 1998). Territorial behaviour by both sexes is suggested to have evolved from a mate-guarding strategy and/or a resource defence strategy (both food and the physical family area, Busher, 2007). In autumn, beavers prepare food caches in front of their lodges to sustain the family during the cold months (Busher, 1996; Hartman and Axelsson, 2004). The dominant pair exhibits similar space use and movement behaviour, and does not reduce their patrolling activity in the presence of an increasing number of subordinate helpers in the colony (Herr and Rosell, 2004).

We deployed GPS units on dominant, territory-holding beavers to analyse terrestrial and aquatic movement patterns in relation to environmental and demographic factors. We hypothesized that terrestrial and aquatic movement patterns would depend on 1) territory size, 2) resource availability, 3) season, 4) intruder pressure (number of neighbours), and 5) age. We predicted that 1) owners of larger territories would move greater distances in water (i.e., have a higher relative patrolling effort), but 2) also have more opportunities to forage closer to the shoreline due to higher resource availability than owners of smaller territories. Third, we predicted that beavers would patrol more in spring when subadults are dispersing, and spent more time on land in autumn to prepare for winter, i.e., to build food caches and repair lodges. Fourth, we predicted that beavers would generally increase patrolling activities when facing higher intruder pressure as determined by the number of individuals in neighbouring colonies. And 5), we hypothesized that movement patterns would change with increasing age due to a shift in behavioural traits such as dominance and experience.

Material and methods

Study area, animals and capture

Our study was conducted between 2009 and 2014 in Telemark county, southeast Norway (Fig. 1). Data were collected in three connected rivers, the Straumen, Gvarv, and Saua, which flow through a semi-cultural and mixed forest landscape, and empty into Lake Norsjø. The rivers are mostly slow flowing and between 10 and 100 m wide with stable water levels, making it unnecessary for beavers to build dams. Woody vegetation along the rivers mostly consists of grey alder (*Alnus incana*), willow (*Salix* spp.), bird cherry (*Prunus padus*), common ash (*Fraxinus excelsior*), rowan (*Sorbus aucuparia*), birch (*Betula* spp.), and Norway spruce (*Picea abies*) (Haarberg and Rosell, 2006). The proportion of deciduous habitat was similar between the rivers in our study area (ANOVA: $F = 0.544$, $p = 0.586$) (Campbell et al., 2005). Hunting pressure in the area was presumably low (Rosell et al., 2000) with eight known cases of hunted beavers (4.6% of the known population) between 2009 and 2014 (unpublished results). Natural predators, predominantly Eurasian lynx (*Lynx lynx*), were present in low densities in our area (Herfindal et al., 2005). Red fox (*Vulpes vulpes*), which is known to occasionally predate on beaver kits (Kile et al., 1996), was also present.

Dominant Eurasian beavers were captured at night from a motorboat using landing nets from March to June (spring), and August to October (autumn) each year as part of a long term study (Steyaert et al., 2015). Dominance status (i.e., being the reproductive individual) had previously been assigned by multiple capture and sighting events in the same territory, body weight, lactation in females, and evidence indicating the disappearance of the previous dominant same-sex individual in that territory (Campbell et al., 2012). All individuals had been previously marked and were sex-determined based on the colour of the anal gland secretion (Rosell and Hovde, 2001; Rosell and Sun, 1999). The exact age was known for 13 individuals as they were captured as kits or yearlings; for the other 12 individuals age was determined as minimum age based on body weight (Rosell et al., 2010). There was no difference between individuals of known age and ones of uncertain age suggesting that our age determination worked reliably (8.72 ± 3.44 vs. 7.0 ± 3.19 years, $p = 0.820$). At capture, beavers were transferred into a cloth sac where they were immobilized and easier to handle (no anaesthesia was administered). We measured body mass and length, and attached a unit consisting of a VHF transmitter

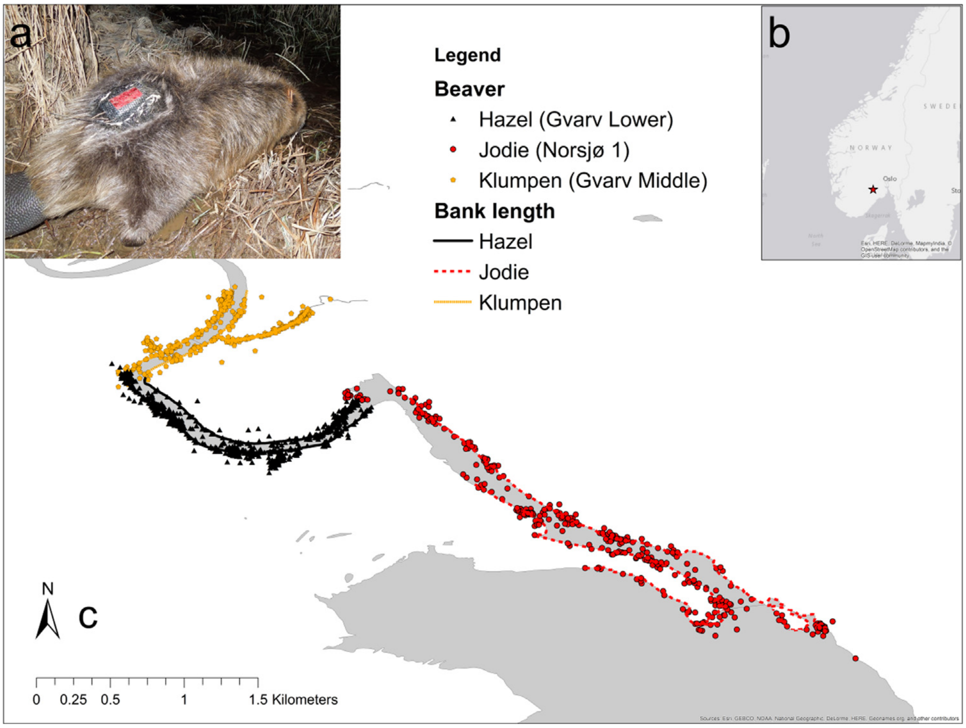

Fig. 1. A Eurasian beaver (*Castor fiber*) with a GPS unit glued onto its lower back (a) in our study area in southeast Norway (b). The main map (c) shows data examples of GPS positions and calculated territory size (measured as bank length) for three beavers in Gvarv River.

(10 g, Reptile glue-on, series R1910; Advanced Telemetry Systems, Isanti MN, USA) and a μGPS transmitter (24 g, model G1G 134A; Sirtrack, Havelock North, NZ). The unit was glued on the lower back (ca. 15 cm from the base of the tail, Fig. 1) using a two-component epoxy resin (System Three Resins, Auburn WA, USA). This position was chosen to minimize drag and potential effects on the animal, respectively, but also allowed for obtaining GPS positions while the animal was swimming as the tag was above water level. GPS transmitters were programmed to take a position every 15 min between 1900 and 0700 h and were set to sleep during the day as beavers are not active then (Sharpe and Rosell, 2003). In contrast to fully aquatic endotherms, beavers rarely dive for long periods (typically <3 min, (Graf et al., 2012)), thus, diving events were unlikely to influence the number of successful GPS fixes in water as transmitters were programmed to acquire a position for 3 min. Handling time of captured animals ranged between 20 and 50 min. The total weight of the glued-on unit did not exceed 1% of the beavers' body weight. For retrieval, animals were re-trapped after two to six weeks and the unit was cut off the fur with a scalpel. All animal handling procedures were approved by the Norwegian Directorate for Nature Management and the Norwegian Animal Research Authority.

Data preparation

Due to our long-term individual-based monitoring program, we had information on the number of individuals per colony, allowing us to estimate the number of adjacent neighbours. For adjacent colonies in which we did not obtain the number of individuals (i.e., in territories located at the edge of our study area), we used the average annual number of individuals per colony as an estimate. Kits were not included in this estimate, because they do not present an intruder threat.

The capture night and the following night were removed from the analysis to correct for possible effects of capture (Graf et al., 2016, in prep.). GPS positions with horizontal dilution of precision (HDOP) values of ≥ 5 and ≤ 4 available satellites were removed from the analysis (8.5% of the raw data), to correct for imprecise locations (Lewis et al., 2007). As a measure for distance from the shoreline (separately for land and water positions), we calculated the average perpendicular distance of GPS positions to the shoreline using the join tool in ArcMap 10.1 (Esri, Redlands, CA, USA).

We used bank length as a measure of territory size, because the beavers in our study area generally stayed close to the shoreline (on average <20 m), both when being on land and in water (see Results, Fig. 1). Other measures of territory size, such as minimum convex polygon (MCP) or kernel methods, would have resulted in an overestimation of territory size due to the inclusion of unused habitat, for example in meandering rivers. To obtain accurate estimates of bank length, we calculated the 95% MCP based on each individuals' GPS relocations in ArcMap 10.1, and then extracted bank length (from now on referred to as territory size) for each individual from the MCPs. Explorative trips (defined as a one-time movement outside the territory lasting less than 4 h) were removed when calculating territory sizes, as they were visibly outside the territorial borders (and within the neighbours' territory). Land cover data was derived from a digital topographic map (Felles KartDatabase, FKB data Geovekst, http://www.kartverket.no/). The amount of mixed and deciduous forested area within a buffer of 50 m from the shoreline was calculated to obtain a measure for resource availability (measured in ha). A buffer of 50 m was chosen because 95% of all land positions were located within this buffer (see Results).

Time spent on land was determined by the proportion of land positions. The distance between GPS positions was calculated as direct line distance between two consecutive GPS positions separately for land and water, and was averaged per hour. Beavers typically travel in water, thus, this method may have resulted in an overestimation of the average distance moved per hour on land, as it is possible that beavers swam in between two consecutive land positions. Consequently, instead of using this estimate as measure for actual movement on land, it should be interpreted as an estimate for different foraging tactics, i.e. foraging more selectively between multiple patches versus less selective foraging within the same or

Table 1
Overview of 25 Eurasian beavers (*Castor fiber*) equipped with a GPS unit between 2009 and 2014 in southeast Norway. A = autumn, S = spring.

Territory	Beaver	Sex	Year and Season	# GPS Days	# GPS Positions	Group Size	# of Kits	Banklength (km)	Time on land (%)	Absolute patrolling (%)
Bråfjorden a	Andreas	M	2010S	7	252	2	0	4.70	36.4	15.8
Bråfjorden a	Leslie	F	2010S	17	747	2	0	4.80	41.0	11.2
Bråfjorden a	Leslie	F	2014A	10	400	8	3	5.21	43.6	6.6
Bråfjorden b	Moritz	M	2010A	6	159	2	0	2.87	43.0	4.6
Gvarv_Lower	Hazel	F	2010S	22	722	8	0	2.41	46.3	15.0
Gvarv_Lower	Paddy	M	2012S	11	425	6	3	2.35	37.8	10.4
Gvarv_Middle	Klumpen	M	2014S	11	427	9	1	2.15	56.7	15.0
Lille Patmos	Ida	F	2010A	13	421	5	2	4.70	63.6	10.5
Lille Patmos	Kjartan	M	2010A	8	242	5	2	4.96	54.6	20.3
Lunde 2	Lasse	M	2011S	9	327	5	1	5.37	31.1	25.5
Lunde 4a	Loran	M	2009A	10	400	3	0	2.31	45.5	56.5
Lunde 4a	Malena	F	2014S	8	254	3	0	7.42	42.6	12.2
Lunde 6a	Bram	M	2011S	6	181	3	0	3.67	45.8	18.0
Lunde 6a	Maud	F	2009A	10	414	2	0	3.30	44.6	6.1
Norsjø 1	Jodie	F	2012S	11	407	5	1	5.02	52.6	22.1
Patmos 0	Hanne	F	2010A	10	271	4	1	4.33	34.0	8.2
Patmos 0	Jan Marc	M	2010A	14	461	4	1	4.70	32.7	14.6
Patmos 1	Live	F	2013A	18	247	5	2	2.32	34.8	9.3
Patmos 2a	Apple	F	2013A	16	709	5	0	1.80	44.7	9.1
Patmos 2b	Moses	M	2010A	14	340	5	2	1.84	48.9	48.8
Patmos 3a	Christina	F	2010A	18	539	3	0	1.68	43.4	51.4
Patmos 3b	Erlend	M	2010S	12	470	3	1	1.49	45.6	18.3
Patmos 3b	Erlend	M	2013A	15	448	3	1	1.47	68.4	36.9
Patmos 4	Horst	M	2010A	5	152	3	1	1.49	62.9	7.4
Patmos 5	Tanja	F	2014S	5	102	5	0	3.69	68.5	29.0
Patmos 6	Ase	F	2014S	10	370	4	0	4.67	37.0	14.5
Patmos 6	Edwin	M	2014S	5	182	4	0	5.15	37.7	15.6

fewer patches. Similarly, this uncertainty may have resulted in an underestimate of the average distance moved per hour in water since beavers could have been on land in between two consecutive water positions. By choosing a GPS sampling interval of 15 min, we attempted to minimize such effects. Moreover, we assume that uncertainties were consistent among individuals, thereby not or only marginally influencing our analysis.

Relative patrolling effort was estimated as the time a beaver spent inside the border zones of its territory, defined as the proportion of GPS positions inside the upper (upstream) and lower (downstream) 5% zones (ranging from 74 to 371 m) of the overall territory size. To obtain a measure of absolute patrolling effort, i.e., how much time a beaver spent at the actual territory borders, we assumed borders as independent of territory size and defined them as the last 75 m on each side of the river on the upper and lower side of each individual territory. This 75 m buffer was chosen because Rosell et al. (1998) found that the majority of scent mounds were clumped within 150 m between bordering territories (i.e., 75 m border zone per territory). For both relative and absolute patrolling effort, we only used GPS positions inside water and within two meters from the shoreline on land, because scent marking activity is limited to close proximity to water and because positions further inland most likely were foraging sites (Rosell and Nolet, 1997).

Statistical analysis

We used generalized linear models (GLM) to investigate movement patterns separately for water and land positions, as the mode and purpose of movement differs on land in comparison to water (swimming vs. walking, and patrolling vs. foraging). Initially, we also tested generalized linear mixed models (GLMM) as two beavers were equipped with a GPS twice; however, the results were not different and thus, we chose the simpler GLMs. The dependent variables for movement patterns in water were average distance moved/h, relative patrolling effort (measured as the proportion of all positions in water and within 2 m on land within 5% border zones), and absolute patrolling effort (proportion of all positions in water and within 2 m on land within 75 m from the borders; three separate analyses). The dependent variables for movement patterns on land were average distance from the shoreline, time spent on land and average distance between GPS positions/h (three separate analyses). Average distance from shoreline was ln-transformed to normalize residuals of the statistical models and one outlier was excluded based on Cook's distance (Cook, 1977).

The independent variables used in all six analyses were territory size, resource availability (i.e., area of mixed-deciduous forest in ha), number of neighbours, season (spring vs. autumn), and the beaver's age. No correlations between the independent variables were detected ($r < 0.6$ in all cases), and variance inflation factors (VIF) were <3 (see Zuur et al., 2010). To avoid overfitting the models we initially tested for an effect of sex and group size in all analyses, but removed these variables as there was no effect. For the analysis of each dependent variable, we selected 12 explanatory models *a priori* based on biological knowledge. These models included the full model (all independent variables, no interactions due to small sample size and to avoid overfitting the model); the five independent variables in separate models; and six models with a two-way interaction: 1) number of neighbours and season; 2) resource availability and season; 3) territory size and resource availability; 4) territory size and season, 5) number of neighbours and age, and 6) season and age. Model selection was based on Akaike weights (Table S1) (Wagenmakers and Farrell, 2004), i.e., the model with the highest conditional probability was chosen, and parameters that included zero within their 95% confidence interval (CI) were considered as uninformative (Arnold, 2010) as their estimated coefficients could not be reliably interpreted. All statistical analyses were performed using the software R 3.1.1 (R Core Team, 2015).

Results

Twenty-five dominant beavers (13 males and 12 females) of 17 different territories, and ranging between 3 and 14 years of age (mean ± SD: 7.3 ± 3.2 years) were equipped with a GPS (two individuals were tagged twice, Table 1). Thirteen beavers were captured in spring and 14 in autumn. On average, the GPS units delivered 11 nights of data (range: 5–22) and 356 GPS positions (range:

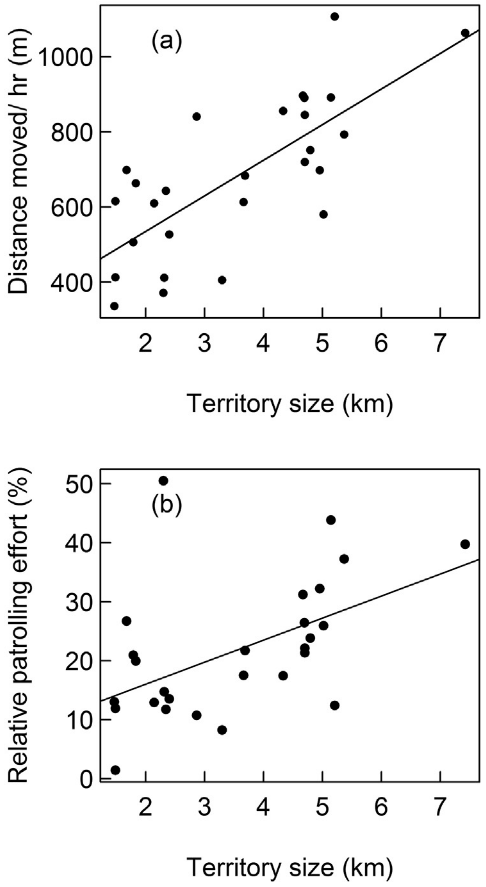

Fig. 2. Predicted relationship between territory size (given as bank length in km) and (a) average distance moved/h (in m) in water, and (b) relative patrolling effort defined as the proportion of GPS positions close to the territory borders (within the lower and upper 5% of the territory) for 25 Eurasian beavers (*Castor fiber*) in southeast Norway.

102–747) per individual. The number of neighbouring colonies varied between two (n = 13 territories) and three (n = 4 territories) with the number of neighbours varying between 4 and 16 individuals (7.1 ± 2.8). Territory sizes varied between 1472 and 7425 m bank length (3550 ± 1591 m, Table 1). Four beavers (one female and three males) made explorative trips into neighbouring territories; two individuals did three and two individuals did one explorative trip. These trips lasted on average 1.9 ± 1.1 h (range: 0.5–3.5 h).

Movement patterns in water

When in water, beavers stayed on average 14 ± 5 m (range: 0–255 m) from the shoreline, and moved on average 682 ± 204 m/h (individual range: 335–1106 m/h). The average distance moved/h was best explained by territory size (Tables 2 and S1), with beavers in larger territories moving greater distances (Fig. 2a). Relative patrolling effort varied between 1.4 and 50.5% (21.8 ± 11.5%) and was best explained by territory size (Tables 2 and S1, Fig. 2b), with beavers in larger territories spending more time patrolling. On average, beavers visited at least one territory border in 81.5 ± 20.7% of the recorded days. The absolute patrolling effort varied between 4.6 and 56.6% (19.0 ± 14.1%) and was best explained by the age of an individual (Tables 2 and S1); older beavers were spending more time at the border.

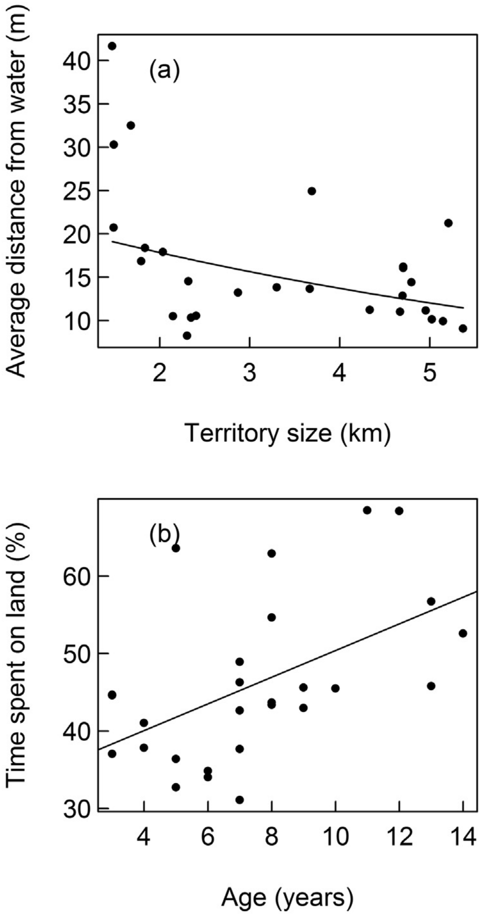

Fig. 3. Back-transformed prediction (solid line) between territory size (measured as bank length) and average distance from the shoreline for all land positions (a), and predicted relationship between the age of an individual and the time spent on land (b) for 25 Eurasian beavers (*Castor fiber*) in southeast Norway.

Movement patterns on land

When being on land, beavers stayed on average 16 ± 8 m (range: 0–201 m) from the shoreline. The average distance from the shoreline was best explained by territory size (Table 2, Fig. 3a), i.e., beavers in larger territories stayed closer to the water. Beavers spent between 31.1 and 68.5% of their active time on land (46.1 ± 10.5%). Time spent on land was best explained by the age of an individual (Tables 2, S1), with older beavers spending more time on land (Fig. 3b). The distance between GPS positions on land was on average 355 ± 121 m/h (individual range: 165–641 m/h), and was best explained by season (Table 2), i.e., beavers moved greater distances on land in spring compared to autumn.

Discussion

We found that beavers adjusted their movement patterns in water and on land in relation to territory size and age. Beavers in larger territories moved greater distances in water and spent more time within relative territory borders, thereby indicating that they patrolled more. Further, individuals in larger territories stayed closer to the shoreline when on land, i.e., when foraging. In contrast, beavers in smaller territories had a lower relative patrolling effort and foraged further away from the shoreline. Age also affected movement patterns with older beavers spending more time on land and at territory borders. In addition, we also found that beavers generally moved greater distances between land positions during spring.

Table 2
Results of the model selection showing the best model based on Akaike weight for the six dependent variables for 25 Eurasian beavers (*Castor fiber*) that were equipped with a GPS between 2009 and 2014 in southeast Norway. Number of observations = 27, β = estimated coefficient, SE = standard error, LCI = lower limit of the 95% confidence interval, UCI = upper limit of the 95% confidence interval.

Dependent variable	AICc	Akaike weight	Predictor	β	SE	LCI	UCI	R^2
Movement patterns in water								
Average distance moved/h	348.3	0.77	Territory size	94.820	17.200	61.111	128.535	0.55
Relative patrolling effort	206.3	0.55	Territory size	3.739	1.242	1.304	6.173	0.27
Absolute patrolling effort	221.4	0.34	Age	1.655	0.832	0.025	3.285	0.14
Movement patterns on land								
Average distance from shoreline	27.2	0.46	Territory size	−0.132	0.052	−0.233	−0.030	0.21
Time spent on land	201.5	0.55	Age	1.723	0.575	0.596	2.849	0.26
Average distance moved/h	327.5	0.43	Season Spring	151.390	36.590	79.664	223.113	0.41

Territory sizes found in this study are comparable with radio-tracking derived territory sizes for beavers in the same study area (Campbell et al., 2005; Herr and Rosell, 2004), as well as territory sizes of Eurasian beavers in general (Heidecke, 1986; Nolet and Rosell, 1994). Our results suggest that individuals may trade-off the costs of patrolling larger territories against the benefits of foraging closer towards the shoreline.

Changing movement patterns with age

Interestingly, we found that older beavers spent more time within the 75 m border zones than younger ones and, thus, had a greater absolute patrolling effort. However, the distance moved in water was not explained by age, suggesting that older beavers spent more time per visit at a border. Further, we found that older beavers spent more time on land. Spending more time at territory borders (patrolling via presence) may in effect allow beavers to spend more time on land instead of swimming between up- and downstream borders. Beavers can reach 20 years of age (Gorbunova et al., 2008) and only five beavers in this study were older than 10 years, suggesting that the observed pattern was rather related to a change in personality than senescence. Other studies reported changing movement patterns in relation to sex or social status, e.g. Sollmann et al. (2011) found that female jaguars (*Panthera onca*) both had smaller home ranges and moved less than males, and Messier (1985) found different amounts of extraterritorial movements between adult and yearling wolves (*Canis lupus*). However, to our knowledge we are the first to report changing movement patterns in relation to age within individuals of the same social status (dominant territory holders).

Beavers possibly gain experience over the years as a territory holder, leading to enhanced boldness and dominance. Moreover, experiencing a low abundance of natural predators coupled with a relatively low hunting pressure in the area may lead to increased boldness of older individuals explaining the higher proportion of time spent on land. Plasticity in behavioural traits related to (social) learning allows for adjusting behaviour based on environmental conditions, which is important for individual fitness (Dingemanse et al., 2010; Frost et al., 2007). An increase in boldness with age was shown in perch (*Perca fluviatilis*) (Magnhagen and Borcherding, 2008), and a shift in behavioural traits with age has also been shown in humans (Martin et al., 2002; Wilson et al., 1994). Body mass was shown to influence the boldness of fish and reptiles (Brown and Braithwaite, 2004; Mayer et al., 2016); this could also partly explain an increasing boldness with age in beavers as they reach their maximum body mass around age seven (Mayer et al., unpubl. results).

Movement in water and patrolling effort

Beavers typically disperse along watersheds; therefore intrusion by dispersers is most likely to occur at the up- or downstream borders of a territory (Herr and Rosell, 2004; Rosell et al., 1998). Thus, scent-marking activity is highest within border zones (Rosell and Thomsen, 2006), and border visits are crucial for beavers, particularly in saturated populations. Holders of larger territories showed a higher relative patrolling effort (as determined by the presence within 5% border zones) and thus swam greater distances. This suggests that beavers in larger territories generally spent more time patrolling territory borders. As beavers in larger territories have to cover greater distances to reach the borders, they face higher patrolling costs for two reasons: swimming has been shown to decrease the body temperature compared to being on land, especially during winter and early spring (Nolet and Rosell, 1994). In addition, an increased patrolling effort constrains the time that beavers can spend foraging. Similarly, wild chimpanzees (*Pan troglodytes*) reduced their feeding time from 33% to 10% during patrolling trips (Amsler, 2010), which demonstrates the trade-off between foraging and patrolling.

Foraging distance from the shoreline and distance between land positions

As central place foragers, beavers should deplete foraging patches close to the water before exploiting patches further away (Orians and Pearson, 1979). However, beavers need to forage further inland once the majority of food plants close to the shoreline are depleted. Beavers in smaller territories were found to move farther away from the shoreline when on land, which suggests resource depletion along the shoreline. However, travelling on land to forage is also considered to be costly both energetically and in time (Belovsky, 1984; Haarberg and Rosell, 2006), as terrestrial forays enhance predation risk (Basey and Jenkins, 1995). In addition, transporting food items on land is an arduous task compared to the efficient, buoyancy-supported transport in water (Novak, 1987). Several studies found beavers to be more selective (both in food item size and species) when foraging at greater distances from the shore (Fryxell and Doucet, 1991; Haarberg and Rosell, 2006; Jenkins, 1980), however, this selectivity diminished in low quality habitats (Gallant et al., 2004). Unfortunately, the resource availability in our study area was not measured on the ground, but based on land cover data. This relatively poor temporal and spatial resolution did not allow us to measure changes in resource availability over the years, and we cannot exclude the possibility that it did influence the observed movement patterns.

Contrary to our prediction, we found that beavers moved greater distances between land positions in spring, independent of territory size. This could be a strategy to compensate for winter weight loss via more selective foraging (in patches further apart from each other) during the spring green-up when food quality is higher. For example, North American beavers were shown to utilize different resources in different seasons (Milligan and Humphries, 2010; Svendsen, 1980), which may result in different movement patterns when foraging. Similarly, a study on food-caching behaviour of

North American beavers describes higher selectivity of tree species early in autumn compared to later in the caching season, suggesting that beavers appear to balance energy content and nutritional diversity of the food cache (Busher, 1996). Another semi-aquatic rodent, the capybara (*Hydrochaeris hydrochaeris*), also displayed different seasonal foraging patterns, spending more time for foraging during the dry season, but being more selective during the rainy season when food quality was higher (Barreto and Herrera, 1998).

The trade-off between patrolling and foraging distance

In general, food abundance has been shown to affect the intensity of territorial defence in animals, resulting in smaller territories (Carpenter, 1987; Simon, 1975) or even non-territorial behaviour (Davies and Houston, 1984) during high food availability. Beavers, however, show a strong, year-round territorial defence (Nolet and Rosell, 1994), which may reduce the rate of resource depletion and increases food availability during the cold months when vegetation is scarce. Because the study population is at carrying-capacity for the last ten years (Campbell et al., 2005; Steyaert et al., 2015), likely all territories in our study area are affected by resource depletion along the shoreline. Resource depletion forces beavers to forage further inland (Goryainova et al., 2014) and, in combination with male feeding territory defence, has been suggested to have triggered the evolution of social monogamy in beavers (Busher, 2007; Sun, 2003). These findings could explain the trade-off we observed in this study: In larger territories beavers have to invest more time in patrolling activities, but can forage closer to the shoreline. In smaller territories beavers moved greater distances on land, possibly as a consequence of resource depletion along the shoreline. However, the short distance between the up- and downstream border reduces patrolling costs and results in greater efficiency in territorial defence, thus, compensating for increased foraging costs in smaller territories.

Territory size seems to act as a counterbalancing factor for patrolling and foraging, making both owning larger and smaller territories a viable strategy in beaver populations at high densities. This is supported by the findings of Campbell et al. (2005), who found that beaver territories are not configured to a minimum economically defensible area: they rather seem to occupy larger territories to reduce the rate of resource depletion during initial settlements in an area, whereas in populations at or near carrying-capacity, territories that become vacant are conquered independent of size. Our findings stress the need for further investigations on whether constraints in foraging or constraints in territorial defence have greater impact on the length of territory occupation and long-term life history parameters such as life-time reproductive success.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2016.07.046.

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Supplementary material

Table S1: Model selection results showing the five best models for all six dependent variables with the AICc, delta AICc and Akaike weight values based on data from 25 Eurasian beavers (*Castor fiber*) that were equipped with a GPS between 2009 and 2014 in southeast Norway. Models were sorted after the Akaike weight from highest to lowest.

Models	AICc	delta AICc	Akaike weight	Models	AICc	delta AICc	Akaike weight
Average distance moved/hr (water)				Average distance from shoreline			
TS	348.3	0.00	0.772	TS	28.3	0.00	0.464
TS + RA + TS x RA	351.3	3.00	0.173	S	30.0	1.73	0.195
TS + S + TS x S	353.8	5.52	0.049	TS + S + TS x S	31.0	2.70	0.120
TS + NN + RA + S + A	359.2	10.92	0.003	TS + RA + TS x RA	32.6	4.27	0.055
RA	359.8	11.56	0.002	NN	33.4	5.09	0.036
Relative patrolling effort				Time spent on land			
TS	206.3	0.00	0.554	A	201.5	0.00	0.548
TS + S + TS x S	207.4	1.10	0.320	A + NN + A x NN	202.8	1.33	0.282
TS + RA + TS x RA	211.0	4.67	0.054	A + S + A x S	205.3	3.82	0.081
RA	212.6	6.25	0.024	TS	207.2	5.73	0.031
S	213.3	6.99	0.017	TS + RA + TS x RA	208.6	7.08	0.016
Absolute patrolling effort				Average distance between land positions/hr			
A	221.4	0.00	0.336	S	327.5	0.00	0.430
A + S + A x S	222.5	1.12	0.192	A + S + A x S	329.0	1.48	0.205
TS	222.6	1.19	0.186	TS + S + TS x S	329.7	2.20	0.143
RA	224.8	3.40	0.061	RA + S + RA x S	329.8	2.32	0.135

S	224.9	3.51	0.058	TS + NN + RA + S + A	331.9	4.37	0.049

The independent variables were: TS = territory size, NN = number of neighbours, RA = resource availability, S = season, and A = age.

Paper IV

Graf, P.M., Wilson, R.P., Cohen Sanchez, L.G., Hackländer, K. & Rosell, F. (*in preparation*). Diving behaviour in a free-living, semi-aquatic herbivore, the Eurasian beaver *Castor fiber*.

Diving behaviour in a free-living, semi-aquatic herbivore, the Eurasian beaver *Castor fiber*

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Short title: Diving in Eurasian beavers

Abstract

Semi-aquatic mammals have secondarily returned to the aquatic environment, although they spend a major part of their life operating in air. The aptitude for moving both on land and in water entails energetics costs, in particular during diving, as semi-aquatic species are considered to be imperfectly adapted to both environments. We deployed accelerometers combined with a depth sensor to study the diving behaviour of 12 free-living Eurasian beavers *Castor fiber* in southeast Norway in spring and autumn between 2009-2011. Dives were generally shallow (< 1 m) and of short duration (< 30 s), indicating that the majority of dives were of aerobic nature. Dive parameters such as maximum diving depth, dive duration and bottom phase duration, were related to intrinsic characteristics of the dive, particularly those linked to the effort during different dive phases and the maximum depth reached. Mean VeDBA (= vectorial dynamic body acceleration as proxy for movement power) was highest near the surface for the descending animals, alluding to increased upthrust linked to fur- and lung-associated air. Similar to other semi-aquatic homeotherms, beavers generally extended dive durations and bottom phase durations, respectively, with diving depth. Deeper dives often included a bottom phase, whose duration was shortened with higher mean VeDBA during the bottom phase. Water temperature did not affect diving behaviour. Overall, diving behaviour increased throughout the night and peaked between 03:00 – 07:00 am. However, beavers just spent 2.8% of their active time diving, which is markedly less than found in other semi-aquatic species.

Introduction

Mammals evolved on land (Kemp 1980, 2005) and were consequently under selection pressure to operate efficiently in an air-based medium. Some mammal taxa, however, secondarily returned to the water and there are now many species, notably cetaceans and sirenians, that are exclusively aquatic and others, such as pinnipeds, that are primarily aquatic (Berta et al. 2015). In comparison to air, water is dense and has a high thermal conductivity and this has profound consequences for movement and heat loss even for animals operating mainly at the surface (Butler 2000; Johansson and Norberg 2003). In addition, mammals operating at depth have to deal with a plethora of pressure-linked problems (Kooyman and Ponganis 1998). Selection pressures have operated to make these animals efficient and successful through adaptations which are some of the most extreme observed in homeotherms, including thick layers of insulation (Liwanag et al. 2012), a reduced surface area to volume ratio (Innes et al. 1990), specialised planar surfaces for propulsion (Fish 1994, 2004), highly streamlined body shape (Fish 1994) and a suite of features associated with dealing with apnea and pressure such as high myoglobin concentrations (Mirceta et al. 2013), collapsible lungs (Falke et al. 1985), and blood shunting (Kooyman and Sinnett 1982). These extreme specialisations are possible because fully, or almost fully, aquatic mammals need only to operate in water.

There are a few species that are semi-aquatic homeotherms, which spend the major part of their life operating in air but are apparently reliant on water (Dunstone 1998), in which they dive to survive (e.g. foraging: Nolet et al. 1993; escape responses: Strachan and Jefferies 1993). Living in two fundamentally different media issues profound challenges to these animals and precludes semi-aquatic mammals from being particularly well adapted for either life in the air or the water (Fish 2000; Williams 1999). Relatively little is known about the diving behaviour of small mammalian freshwater divers (Hays et al. 2007; Ropert-Coudert et al. 2009) with the majority of studies being conducted in captivity and focussing on physiological aspects of diving in species such as water voles *Arvicola amphibious* (Clausen and Ersland 1968), muskrats *Ondatra zibethica* (MacArthur 1984, 1990), American mink *Neovison vison* (Dunstone 1993; Williams 1983b) and otters *Lutra lutra* and *Lontra canadensis* (Ben-David et al. 2000; Pfeiffer and Culik 1998). A common finding of such studies is that semi-aquatic species face higher energetic costs when moving in the aquatic environment and in particular, during diving, mainly due to higher thermoregulatory needs (MacArthur and Krause 1989; MacArthur and Dyck 1990) and increased physical effort to overcome buoyancy and drag (Fish et al. 2002; Williams 1983a).

More recently though, small, high-precision bio-logging devices with integrated pressure transducers have demonstrated great potential for quantifying the diving behaviour in free-living, semi-aquatic species. Indeed, this approach has revealed insight into the behavioural strategies that such animals adopt to minimize costs (e.g. Harrington et al. 2012) and even movement-based power use during diving measured in terms of overall or vectorial dynamic body acceleration ODBA & VeDBA (c.f. Stothart et al. 2016; Wilson et al. 2006). To date, bio-logging studies on freshwater divers have exclusively focused on American mink (Bagniewska et al. 2013; Hays et al. 2007) and have shown that costs of diving, especially in cold water, may be outweighed by the energetic gains through aquatic foraging (Bagniewska et al. 2015; Harrington et al. 2012). Importantly though, this species is a carnivore and thus takes high quality food so that energetic returns are predicted to be high.

We studied the diving behaviour of a free-living, amphibious herbivore, the Eurasian beaver *Castor fiber* to define the extent to which diving constitutes part of beaver existence and to place it within the context of other homoeothermic divers, particularly those termed semi-aquatic. Both beaver species, the Eurasian and the North American beaver *C. canadensis*, are nocturnal, semi-aquatic rodents that inhabit freshwater bodies such as rivers and streams, lakes and ponds (Rosell et al. 2005). Beavers are socially monogamous (Crawford et al. 2008; Syrůčková et al. 2015), live in family groups consisting of the dominant pair and their offspring (Campbell et al. 2005; Wilsson 1971) and occupy lodges or bank dens (Barnes and Dibble 1988; Wilsson 1971). Beavers are highly territorial and announce territory occupation by scent-marking (Rosell et al. 1998; Rosell and Thomsen 2006). Both sexes participate in parental care and territory defence and sex-differences have been confirmed for travelling time (Sharpe and Rosell 2003) and scent-marking (Rosell and Thomsen 2006).

As herbaceous central-place foragers, they have a preference for willows *Salix* spp. and poplars *Populus* spp. (Haarberg and Rosell 2006; Nolet et al. 1994), but also forage on aquatic plants (Law et al. 2014; Parker et al. 2007). Beavers build dams to, amongst other things, raise water levels sufficiently high to keep the lodge entrance under water and hold functional winter food caches (Hartman and Axelsson 2004; Hartman and Törnlöv 2006).

The beavers' fusiform body with short limbs, webbed hind feet and waterproof fur reflect the animals' adaption to an amphibious life (Allers and Culik 1997; Wilsson 1971). In fact, it has been suggested that beaver streamlining is similar to those of fully aquatic animals such as phocid seals (Reynolds 1993). In beavers, physiological adaptions to diving include bradycardia and a minor post-dive tachycardia (Clausen and Ersland 1970; Swain et al. 1988). However, it has been shown that beavers have much lower myoglobin levels – the oxygen-binding blood protein that enhances the capacity to remain submerged – than fully aquatic species (Mirceta et al. 2013). To date, diving in beavers has been exclusively studied in the North American beaver with regard to physiological and morphological aspects (e.g. Allers and Culik 1997; Clausen and Ersland 1968, 1970; MacArthur and Dyck 1990; Swain et al. 1988).

We deployed data loggers consisting of a tri-axial accelerometer and a depth transducer on dominant Eurasian beavers to study their dive performance. We analysed maximum diving depth, dive duration, bottom phase duration and the mean number of dives per night and linked these parameters to physical effort during diving measured as mean VeDBA and vertical velocities during descent and bottom phases, during which the animals need to counteract buoyancy. In addition, since water temperature is predicted to have such a radical effect on heat loss, we explored differences in dive performance related to water temperature, as well as sex and weight of individual beavers. We hypothesised that beavers would rely extensively on air for insulation and so be positively buoyant and have to use more power for locomotion during the descent phase of their dives (visible in mean VeDBA and vertical velocities during descent), but that this would vary with diving depth. Specifically, we predicted that (1) beavers would primarily execute short and shallow dives, that (2) higher mean VeDBA dives would have reduced maximum depths and dive durations, while (3) deeper dives should be coupled with longer bottom phase durations. Beavers have been found to reduce swimming time in cold water (Nolet and Rosell 1994), thus, we also predicted (4) a water temperature-dependent reduction in diving with cold water temperatures. This work attempts to identify behavioural mechanisms for increasing diving efficiency and to put the diving capacities of beavers into a broader, diving endotherm-perspective.

Materials and methods

Study area and animals

The study was conducted between 2009 and 2011 in Telemark County, southeastern Norway (59°23' N, 09°09' E). The study sites are located at the lower reaches of three large rivers, the Straumen, Gvarv and Sauar, which all empty into Lake Norsjø. The river sections are mostly slow flowing with stable water levels, about 20 - 150 m wide (Campbell et al. 2012) and on average approximately 20 m deep (min. 2 m, but typically between 4-10 m; source: Statens Kartverk Telemark). The three rivers feature similar depth structures and were deep and wide enough to make damming for beavers unnecessary (Hartman and Törnlöv 2006). Riverbanks are dominated by semi-agricultural and riparian woodland structures with tree-species such as grey alder *Alnus incana*, willow *Salix spp.*, bird cherry *Prunus padus*, common ash *Fraxinus excelsior*, rowan *Sorbus aucuparia*, birch *Betula* spp. and Norway spruce *Picea abies* (Haarberg and Rosell 2006). Man-made impoundments (Straumen) and river sections that widen up to natural lakes (Gvarv and Sauar) lead to reduced ice cover in winter (Campbell et al. 2012). The climate in the area is cool continental with a mean annual temperature of 4.6 °C and a mean annual precipitation of 790 mm (Campbell et al. 2012). Water temperatures differed considerably between the seasons ($H = 2435.6$, $df = 1$, $p < 0.001$, Table 1), with colder water temperatures during spring deployments ($\bar{x} \pm SD = 3.6 \pm 0.8$ °C; Apr - May) and warmer water temperatures during autumn deployments (9.7 ± 1.4 °C; Sept - Nov). The earliest evidence for Eurasian beavers in the area is from the 1920s (Olstad 1937); today, the population is at carrying-capacity (Graf et al. 2016b; Steyaert et al. 2015). Both hunting pressure and the presence of natural predators in the area is low (Graf et al. 2016b). Since 1997, beavers in the study area are monitored every year between March and November as part of a long-term capture-mark-recapture study

(Campbell et al. 2005, 2012). Dominance status had been previously determined by multiple capture and/or sighting events of an individual within the same territory, body weight, disappearance of the former dominant male/female, and incidences of lactation in females (Campbell et al. 2012). Beavers also had been previously sexed based on the colour and viscosity of their anal gland secretion (Rosell and Sun 1999).

We captured 21 dominant Eurasian beavers from 16 different territories between 7:00 pm – 7:00 am with a landing net from a boat after the method developed by Rosell and Hovde (2001). The animals were transferred into a cloth bag, where they were handled and tagged without the need for anaesthesia. Average handling time was 30 ± 5 min. We attached tags consisting of a VHF-transmitter (18 x 35 mm, 10 g; Reptile glue-on series R1910; Advanced Telemetry Systems, Isanti MN, USA) and a data logger recording pressure and tri-axial acceleration (15 x 90 mm, 62 g; JUV Elektronik, Schleswig-Hollstein, GER) onto the fur of the lower back along the spine, 15 cm above the scaly tail. The units were connected with wire or glued together and integrated in half-mesh net covering. Once captured, we measured body length and weighted the beavers before we attached the tag onto the fur along the spine (15 cm above the scaly tail) using a quick-setting, two-component epoxy resin. The whole unit was 130 x 90 mm in size (incl. netting) and weighed 90 g in air, which accounts for 0.47% of the body weight of the lightest beaver (19.5 kg) used in this study. Beavers were released at the trapping site within their own territory. After 2-3 weeks, beavers were located and re-captured via VHF-telemetry and the tags were cut out of the fur with a scalpel. This procedure only affected the guard hairs, while leaving the under-fur unaffected (Graf et al. 2015). Data from 9 of the tags were not used in the analysis, since 3 units failed to log data (because memory cards popped out of their housing), 3 units had corrupt readings (which could be attributed to gnawing marks on the sensors) and 3 units recorded only between 1-3 nights of data (which was also accompanied by gnawing marks and water intrusion into tag housings, or early tag loss during moulting in spring).

Data preparation and dive analysis

The data logger used in this study recorded pressure (range 950 – 10000 mB) and tri-axial acceleration (± 4 g) with 22 bit resolution. Data were recorded at a frequency of 1 Hz for pressure and 8 Hz for acceleration in three orthogonal axes corresponding to the beaver's surge (longitudinal), heave (dorso-ventral) and sway (latitudinal) axes, and stored on a 1 GB memory card. Pressure data was used to identify maximum diving depth, dive duration, dive phases (descent, bottom, ascent) and, in particular, bottom phase duration via points of inflection in the dive profile. Tri-axial accelerometers recorded posture (static acceleration) and movement (dynamic acceleration) (Shepard et al. 2008) with respect to the earth's gravitational field ($1\ g = 9.81\ \mathrm{m.s^{-2}}$) and can be used for behavioural identification in animals (e.g. beavers; see Graf et al. 2015) and even humans (Leuenberger et al. 2015; Wilson et al. 2015). The accelerometers were used to derive mean vectorial dynamic body acceleration (VeDBA) according to methods described in Qasem et al. (2012). Dynamic body acceleration – both as VeDBA, the vectorial sum of the dynamic acceleration component, and ODBA, the overall (summed) dynamic body acceleration – has been shown to be a good proxy for the rate of oxygen consumption, are therefore power use (Qasem et al. 2012). Accelerometry data was also used to derive principal activity periods PAPs (active time per night; time from emergence from the lodge in the evening to return to lodge in the morning, see also Graf et al. 2016a), which were then compared to the total time spent diving per night, to determine the role of diving in the beaver's nightly activity budget.

All dive events were visually inspected and exported using Multitrace (Jensen Software Systems, Laboe, GER). Due to changes in atmospheric pressure, temperature or sensor drift, surface pressure readings had a tendency to drift with time (Hays et al. 2007). We thus used zero-offset correction (ZOC), which we adjusted manually if needed, to set the surface baseline to zero (Hagihara et al. 2011; Hays et al. 2007). We selected a dive threshold of 0.3 m to ensure pressure readings indicating dives did not result from wave action or the animal simply angling its back down (noting the posterior position of the tag) into the water when, for example, reaching for a twig. Descent, bottom and ascent phases were automatically recognised and delineated by the program based on inflection points in the dive profile and could be adjusted, as every dive was manually inspected to check that this procedure did indeed function as supposed.

We standardized all datasets to range from 5-7 full nights, excluding data from the capture night to account for possible tagging effects (Graf et al. 2016a). Water temperature data for the Gvarv and Straumen river was provided by the Norwegian Water Resources and Energy Directorate (NVE). For the Sauar river, no temperature data was available for the lower reaches of the river where we captured beavers. We thus used temperature data from the Gvarv river for the Sauar, as both rivers are in the same area (approx. 10 km linear distance apart), are of similar size and feature similar flow characteristics (*pers. comm.*, Å. Kvambekk, NVE). Daily mean water temperature for the rivers was averaged over the week of tag deployment.

Statistical analysis

We used linear mixed-effects (LME) models for the response variables ‘maximum diving depth’ and ‘dive duration’ and included the covariates ‘mean VeDBA during descent’, ‘vertical velocity during descent’, ‘water temperature’, ‘sex’ and ‘weight’ in both models. In addition, we created a separate LME without covariates to analyse the relationship between ‘maximum diving depth’ and ‘dive duration’, two variables which are known to be interrelated and which are commonly investigated in other diving homeotherms (e.g. Halsey et al. 2006; Harrington et al. 2012). We used a generalized linear model (GLM) for the response variable ‘mean number of dives per night’ and included ‘water temperature’, ‘sex’ and ‘weight’ as covariates. The covariate ‘sex’ was included to detect possible effects related to differences in nutritional needs (aquatic plants) between the sexes, while ‘weight’ was included to determine whether heavier beavers (more body fat) needed to use more power to work against buoyancy during submergence. The response variables ‘maximum diving depth’, ‘dive duration’ and ‘mean number of dives per night’ were ln-transformed to normalize residuals.

To analyse bottom phase duration we used a double-hurdle model (Cragg 1971), based on the assumption that individuals decide (i) whether to invest in a bottom phase or not, and if there is a bottom phase, (ii) how long this bottom phase should be. We used a negative binomial model for the binary response variable ‘bottom phase’ (0 = ‘no bottom phase’, 1 = ‘a bottom phase’) and a generalized linear mixed model (GLMM) with a log-link function to model the acutal continous response ‘bottom phase duration’. We included the predictor variables ‘maximum diving depth’, ‘water temperature’ and ‘mean VeDBA during the bottom phase’ in both hurdle models. In all models we used ‘individual’ as random effect to account for individual variation in diving performance. Initially, we also included ‘year’ as random effect (i.e. 'individual' nested within 'year'), but results were essentially unchanged with the same predictors being informative. For this reason, and because there is typically not enough information to accurately estimate group-level variation with only three levels (three years) (Gelman and Hill 2006), we omitted 'year' as random factor. Similarly, we also fitted all models with the predictor 'age' instead of 'weight', but did not detect any age-effects and thus used the predictors initially chosen. Before analysis, we removed three data points with extreme values – one in the response variables 'dive duration' and 'bottom phase duration', respectively; and two in the predictor 'vertical velocity during the descent' – to eliminate possible interference with the models, but report these values in the results section. For all response variables, we also included a model with an interaction of the two best predictors in the model selection process. For interactions that included non-zero centered predictors, we reran all candidate models with standardized predictors to reduce multicollinearity in interaction terms and enhance interpretability of coefficients (Afshartous and Preston 2011; Robinson and Schumacker 2009).

No collinearity between independent variables was detected ($r < 0.6$; apart from water temperature + weight, with $r = 0.8$). However, variance inflation factors (VIF) for all predictors were < 3 (see Zuur et al. 2010) and we thus included both temperature and weight as predictors in our models. We applied a backward model selection procedure and selected the most parsimonious models based on the Akaike information criterion corrected for small sample sizes (AIC_c) (Burnham et al. 2010; Wagenmakers and Farrell 2004). We considered candidate models within AIC_c differences (ΔAIC_c) between 0-2 as models with strong levels of empirical support (Anderson 2008) and derived model-averaged estimates for such models. Model parameters that did not include zero within their 95% confidence interval (CI) were considered as informative (Arnold 2010). All statistical analyses were performed using the software R 3.3.0. (R Development Core Team 2013).

Ethical statement

The study, including all handling and tagging procedures (for details see above), was approved by the Norwegian Experimental Animal Board (FOTS id 742, 2170 and 2579) and the Norwegian Directorate for Nature Management (archive code 444.5), which also granted permission to conduct fieldwork in our study area. The patch of clipped guard hair grew back within three to four months.

Results

We used data from 12 Eurasian beavers (6 females, 6 males) from 11 different territories for analysis (Table 1). In analyses including accelerometry-based variables (e.g. mean VeDBA and vertical velocities) sample size was reduced to n = 11 individuals, as the accelerometer did not work during one of the deployments. Beavers used in analyses weighed between 19.5 kg and 26.9 kg ($\bar{x}$ ± SD = 23.3 ± 2.2 kg, Table 1). Individual dataset lengths varied between 5 full nights (n = 1), 6 full nights (n = 5) and 7 full nights (n = 6).

We analysed a total of 2596 dives, with an average of 216.1 ± 139.7 dives per individual over 5 nights (n = 12). Beavers descended with an overall mean VeDBA of 0.18 ± 0.06 *g* (max. 0.64 *g*) and an average vertical velocity of 0.23 ± 0.13 m/s (max. 1.88 m/s). The majority of dives were shallow (< 1m) and short (< 30 sec) (Fig. 1, Table 1). Diving activities increased throughout the night, with beavers showing a peak diving activity between 03:00 – 07:00 am (Fig. 2). Dive duration increased significantly with maximum diving depth, with a polynomial term describing the best fit (linear model AIC_c: 5463.34, quadratic model AIC_c: 5438.98), although R^2 was 0.27 for both models ($\beta = 0.687$, 95% CI = 0.637 – 0.737, Fig. 3). When comparing nightly PAPs (654 ± 63 min) with the total time beavers were submerged each night, we found that diving accounted for only 2.8 ± 2 % of the daily activity budget of beavers. Finally, we found high individual variation in diving behaviour related to all diving parameters examined in this study (Table 1).

Maximum diving depth

Median 'maximum diving depth' for individual beavers was 0.77 m, with a range between 0.3-3.6 m (Fig. 1a). Maximum diving depth was best explained by mean VeDBA and vertical velocity during the descent phase (Table 2). Higher mean VeDBA values during the descent were associated with shallower maximum diving depths (Fig. 4a, Table 3), while higher vertical velocities and faster descents, respectively, resulted in deeper maximum diving depths (Fig. 4b, Table 3).

Dive duration

Dive duration for individual beavers varied between 1 and 400 s, with a median of 23 s (Fig. 1b). The two best candidate models for dive duration included 'vertical velocity during descent', and both the former and 'mean VeDBA during descent' (Table 2). We derived model average estimates and their 95% confidence intervals for these two models and found both predictors to be informative (Table 3). Both higher mean VeDBA and vertical velocities during the descent phase resulted in shorter dive durations (Fig. 4c,d, Table 3).

Mean number of dives per night

The overall mean number of dives per night was 42.5 ± 28.1. The mean number of dives per night was best explained by water temperature (Table 2), however the CI for β estimates incorporated 0 ($\beta = 0.065$, LL = -0.039, UL = 0.168), implying that water temperature was an uninformative variable.

Bottom phase duration

We found that 82% of all dives included a bottom phase, with a median duration of 12 s (range: 0.4-188 s). The decision whether to invest in a bottom phase or not was best explained by two models containing the predictors ‘mean VeDBA during descent’ and ‘maximum diving depth’, in one model additive, in the other as an interaction (Table 2). We derived averaged model coefficients and their 95% CI and found only maximum diving depth to be informative, stating that a bottom phase was more likely in deeper dives (Table 3). When looking at dives with bottom phase only (the GLMM), the best model included the interaction between the predictors ‘mean VeDBA during the bottom phase’ and ‘maximum diving depth’ (Table 2). By inspecting 95% CI, we found ‘mean VeDBA during the bottom phase’ and ‘maximum diving depth’, as well as the interaction between the two predictors to be informative (Table 3). Higher mean VeDBA values during the bottom phase resulted in shorter bottom phase durations, while diving in greater depths was associated with longer bottom phase durations (Fig. 4e,f, Table 3). In addition, the interaction between the two terms implies that bottom durations are also longer in deep dives coupled with high mean VeDBA values (Table 3).

Discussion

Our study shows that beavers predominantly executed shallow dives of short duration and, as such, are similar to a range of other freely diving semi-aquatic birds and mammals (Snyder 1983; Thompson and Fedak 2001). Surprisingly, we found that on average, only 2.8% of the beaver's nightly activity budget in our study area comprised diving, which is considerably less than found in many other semi-aquatic species (Bodkin et al. 2007; Kooyman and Ponganis 1998; Tremblay et al. 2005). Dive parameters such as maximum diving depth, dive duration and bottom phase duration were determined by the physical effort during the descent and bottom phases (measured as mean VeDBA and vertical velocities) and the maximum depth reached, while water temperature did not affect diving behaviour. Water temperature did not affect diving behaviour of beavers. Dive durations increased with greater dive depths, which is a common phenomenon observed in semi-aquatic divers (e.g. Chilvers et al. 2006; Cook et al. 2010) and the slope estimate ± SE of 0.69 ± 0.03 for beavers compares well with other diving birds and mammals (c.f. Halsey et al. 2006).

Beavers usually travel along the shoreline (Graf et al. 2016b) and the observed short, shallow dives presumably largely reflect the water depths available along the water's edge. Even though deeper river sections were present within all three rivers and all territories, diving deep may not be essential for beavers: In terms of foraging, shallow dives are likely to be those that provide access to the highest water plant density since macrophyte growth is encouraged by light penetration (Moss 2009; Narumalani et al. 1997). Moreover, other behaviours linked to diving in beavers, such as entering the lodge, submerged transport of sticks/building material or escaping in the water, do not necessitate particularly deep dives. Diving activity peaked late during the beaver's PAP, while general activity has been found to be highest in the middle of the beaver's PAP (~1 am, see Graf et al. 2016a). This could allude to a higher diving activity after beavers have finished patrolling their territories (Graf et al. 2016b), for example, it has been found that building behaviours – which are typically linked to diving for procuring building materials such as sticks and mud – occur in the latter part of the night (Wilsson 1971).

Time spent diving

While beavers in our study area dived during only 2.8% of their PAP, other semi-aquatic species such as tufted ducks *Aythya fuligula* dived during 25% of a 24-hr cycle (Pedroli 1982), chick-rearing Crozet shags *Phalacrocorax melanogenis* during 44% of their at sea time (Tremblay et al. 2005), sea otters *Enhydra lutris* during 48% of a 24-hr cycle (Bodkin et al. 2007) and Australian sea lions *Neophoca cinerea* during 58% of their sea time (Costa and Gales 2003). In most of these semi-aquatic species, diving is strongly linked to foraging behaviour, while beavers as generalist herbivores do not solely rely on diving for food acquisition (Severud et al. 2013; Vorel et al. 2015). Similarly, American mink, a species that uses a wide variety of terrestrial and aquatic prey, was found to dive in only 0.1% of a 24-hr cycle (Harrington et al. 2012). Diving involves high energetic costs in semi-aquatic species (Dunstone 1998; Fish 2000; Williams 1999) and may thus only play a minor role in the foraging budget of generalist species that can access food of similar nutritional quality in a range of different environments. In our study area, submergent macrophytes and rhizomes may only account for a small proportion of the beavers' diet, which is in line with other studies conducted on food preference by beavers in river habitats (Krojerová-Prokešová et al. 2010), which typically contain lesser aquatic vegetation that standing waters (Milligan and Humphries 2010). However, we did not collect data during the summer months (Jun – Aug), where beaver diets have been found to increasingly shift towards emergent vegetation (Milligan and Humphries 2010; Severud et al. 2013). In addition, we are not able to determine the role of emergent and floating-leaf species that do not necessitate diving, but can account for a substantial amount of the beavers' diet (Milligan and Humphries 2010; Parker et al. 2007). Beavers in our study area may dive less since they do not build dams, a behaviour that is connected to a substantial amount of diving as beavers typically seal their dams with mud and stones (Müller and Watling 2016; Wilsson 1971), especially during autumn. Lastly, we did not collect data during winter (Dec – Mar), were rivers are partly ice-covered in our study area and beavers may thus be forced to increase their dive time.

Dive parameters and physical effort

Much of the apparent diving behaviour in beavers was described by intrinsic characteristics of the dive, particularly those related to the effort during different dive phases (mean VeDBA, vertical velocity) in tandem with the maximum depth reached. As observed in a number of air-breathing diving homeotherms VeDBA (and ODBA, resp.), taken as a proxy for movement power (Qasem et al. 2012), was highest near the surface for the descending animals. This is presumed to be due to the fur- and lung-associated air (Fish et al. 2002; McKean and Carlton 1977), which has maximum volume closest to the surface, and therefore also has highest upthrust. As is particularly the case in diving birds, which have large amounts of plumage-entrapped air, power to overcome this upthrust for the descent must therefore also be greatest close to the surface (Wilson et al. 1992, 2010).

The nature of air compression with depth follows Boyle's Law;

$$P_1V_1 = P_2V_2$$

where P_1 and P_2 are the pressures (in Bar) at the surface and depth, respectively, while V_1 and V_2 are the volumes of air at the respective depths. Thus, in the first meter alone, the volume of any animal-associated air decreases by some 10% with an expected corresponding decrease in upthrust and therefore power required to counteract it (c.f. Wilson et al. 1992). In addition, within the first moments of a dive, extra power is expected to accelerate the animal from a vertical speed of 0 m/s (at the surface) to the normal descent speed as well as to counteract surface drag acting just below the water surface (Williams 2001; Wilson et al. 1992).

Beavers, like birds, showed an increase in descent vertical velocity with increasing diving depth (Cook et al. 2010; Noda et al. 2016; Watanuki et al. 2006). Indeed, for most diving animals, deeper dives are generally accompanied by steeper dive angles (Ropert-Coudert et al. 2001) so that even if swim speed remains constant, which it does in some penguins (Ropert-Coudert et al. 2002), the rate of change of depth is higher for deeper dives. It has been suggested that this helps animals maximize bottom duration by them consecrating less time in the transit between the surface and the foraging depth (Sato et al. 2004) but this is simplistic. It is actually power use that determines how fast body oxygen stores are used rather than time *per se*, so shorter, but higher power, descent dive phases can actually reduce oxygen available for the bottom phase (Wilson et al. 2006). Indeed, this phenomenon alone may explain the observation in this study that higher descent vertical velocities tend to be associated with shorter dive durations.

With regard to the bottom phase, which accounted for most of the dive duration due to the shallowness of dives (see above), extended durations generally accompanied lower mean VeDBA values. Given that VeDBA is a proxy for power, or oxygen use (Qasem et al. 2012), this is entirely expected. Nonetheless, there were occasional exceptions to this, with some deeper dives incurring high mean VeDBA values during the bottom phase and longer bottom phase durations. We suggest that such phenomena may be linked to a specific dive type, e.g. foraging for aquatic plants or acquiring building material at the riverbed. We note though, that since beavers do not dive serially in quick succession in the manner of many diving homeotherms, that they also may extend their dive durations by accumulating lactate (Butler 2004), using the extended post-dive surface interval to deal with the build-up (Kooyman et al. 1980; Kramer 1988). In fact, studies on putative aerobic dive limits (cf. Butler 2004) for beavers suggest that muscle oxygen stores should be depleted after 2-4 min of diving (Snyder 1983), while blood oxygen stores started to decrease at similar durations (4 min; Clausen and Ersland 1970). This suggests the marked preponderance of short dives performed by beavers in this study were aerobic, which in turn reduces the energetic and time costs of the post-dive recovery at the surface (Kooyman et al. 1980; Kramer 1988). In line with this, it is suggested that shallow dives may allow animals to maximise bottom phase durations if they conduct a series of shallow, aerobic dives as opposed to maximising the total duration of single dives (Boyd 1997; Thompson and Fedak 2001).

Water temperature

A major factor that is reputed to affect diving behaviour, via diving costs for aquatic homeotherms is water temperature (Bevan and Butler 1992; Ciancio et al. 2016) and reduced diving behaviour during winter has been confirmed for muskrats (MacArthur 1984) and star-nosed moles *Condylura cristata* (McIntyre et al. 2002).. Indeed, the body temperature of beavers has been found to drop significantly during swimming and, in particular, in winter (Nolet and Rosell 1994; Smith et al. 1991). It is therefore curious that water temperature did not influence diving behaviour. An obvious measure against colder water is for animals to have excellent insulation (Butler and Jones 1997) and in this respect, beaver fur is extraordinarily dense and fine (12.000 – 23.000 hairs/cm^2, Novak 1987), retaining a layer of air several millimetres thick when submerged (Scholander et al. 1950). In addition, beavers may mitigate the supposed metabolic effects of cold water by adopting local heterothermy through passive cooling, which is a well-established strategy for lowering metabolic costs in homeotherm divers (Boyd 1997). In fact, MacArthur and Dyck (1990) and Dyck and MacArthur (1992) observed a reduction of abdominal temperatures when immersing beavers into cold water, but suggested that this effect may be mitigated both by avoiding prolonged immersion, as well as tolerating passive cooling. Conversely, the work by Handrich et al. (1997) would suggest that the strategy is beneficial and actually enhances dive performance. Indeed, some of the longest dives ever recorded for beavers were 22.75 ± 2.78 min for free-ranging North American beavers during autumn and winter (MacArthur and Dyck 1990b), although the authors point out that beavers may have exploited air pockets beneath the ice. In beavers, other confirmed physiological dive responses for reducing energy requirements and heat loss include bradycardia and/or peripheral vasoconstriction (Müller-Schwarze and Sun 2003). Moreover, food quality and nutritional components such as polyunsaturated phatty acids (PUFAs) affect the functionality of membranes at low temperatures (Hazel 1995), and were found to comprise a major part of the adipose tissues of beavers (Razmaitė et al. 2011; Zalewski et al. 2009). Thus, beavers may also reduce thermoregulatory costs by foraging selectively on PUFA-rich food plants before winter. Lastly, behavioural adaptions such as spending more time on land or inside the lodge (Nolet and Rosell 1994; Smith et al. 1991) may mitigate heat loss during diving.

Conclusion

Beavers spend most of their time close to the shoreline (Graf et al. 2016b) and the shallow dives observed in this study may thus reflect water depths available to them at the river periphery. Dives were generally of short duration, which suggests beavers were diving within their aerobic dive limit. Beavers spent markedly less time diving than other semi-aquatic species, which may be linked to their generalist foraging strategy and the fact that they do not rely on diving for food acquisition, the river morphology in our study area (no need for dam-building) and the time of the year we recorded diving behaviour (only during spring and autumn). Physical effort during the descent and bottom phase and diving depth described dive parameters in this study and shed light on the beavers strategies to optimize diving behaviour by counterbalancing diving costs related to increased buoyancy and drag, as well as limited oxygen supply. Water temperature did not affect diving behaviour, alluding to specialised morphological (thick fur, adipose tissue), physiological (e.g. local heterothermy) and behavioural adaptations (partitioning time on shore/inside the lodge and in water) that enable beavers to dive even in cold water. Ultimately, physiological measurements including heart rate and body temperature of diving individuals should be combined with behavioural research to deepen our understanding of diving tactics and dive responses in semi-aquatic homeotherms.

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Table 1. Dive analysis metadata for 12 Eurasian beavers *Castor fiber* equipped with a data logger measuring pressure and acceleration between 2009 and 2011 in southeast Norway.

Beaver	Sex	Weight	Territory	Year	Month	Water temp	# Nights	# Dives per day ($\bar{x}$)	Max. depth ($\tilde{x}$)	Dive duration ($\tilde{x}$)	Bottom duration ($\tilde{x}$)
Andreas	M	22.5	B1	2010	Apr	3.1	7	31.3	0.8	19.5	12.8
Chris	M	20.5	L5b	2009	Apr	3.2	5	35.8	1.0	21.3	10.5
Demi	F	26.9	E	2009	Oct	9.5	7	35.0	0.7	30.0	18.5
Easy	M	19.5	L5a	2009	Apr	3.2	6	24.7	1.2	36.0	21.3
Frode	M	22	L2b	2009	May	5	6	35.5	0.7	20.6	10.0
Gyda	F	24.2	L4b	2009	May	4.9	6	102.3	0.6	20.0	8.5
Ida	F	23.9	LP	2010	Sept	10	7	94.0	0.6	17.0	12.5
Jan-Marc	M	23	P0	2011	Oct	8.7	7	35.9	0.9	21.3	18.3
Kathrin	F	25.5	H	2011	Sept	11.6	6	56.5	0.9	31.5	17.0
Klumpen	M	26	GM	2009	Oct	9.4	6	23.3	0.6	27.5	14.5
Leslie	F	22.4	B1	2010	Apr	3	7	19.3	0.7	25.3	10.8
Maud	F	23.8	L6a	2009	Nov	5.7	7	16.3	0.8	21.3	21.3

Table 2. Model selection based on Akaike information criterion corrected for small sample sizes (AICc) for 11 Eurasian beavers *Castor fiber* in southeast Norway. Model averaging was implemented on candidate models within ΔAICc < 2. w_i = Akaike weight, K = Number of parameters, *informative model terms

Response variable	Most parsimonious model	AIC_c	w_i	K
Maximum diving depth	Mean_VeDBA_des* + VV_des*	3994.75	0.79	5
Dive duration	VV_des*	6083.88	0.69	4
	Mean_VeDBA_des* + VV_des*	6085.80	0.27	5
Mean number of dives/night	Water_temp	26.88	0.88	3
Presence of a bottom phase	Max_depth : Mean_VeDBA_des	2418.64	0.45	5
	Max_depth* + Mean_VeDBA_des	2419.88	0.24	4
Bottom phase duration	Max_depth : Mean_VeDBA_bott*	16197.14	0.83	6
	Max_depth*; Mean_VeDBA_bott*	16197.14	0.83	6

Mean_VeDBA_des *Mean VeDBA during the descent phase*; VV_des *Vertical velocity during the descent phase*; Max_diving_depth *Maximum diving depth*; Mean_VeDBA_bott *Mean VeDBA during the bottom phase*

Table 3. Informative model terms for the response variables maximum diving depth, dive duration and presence/duration of a bottom phase for 11 Eurasian beavers *Castor fiber* in southeast Norway. All response variables were log-transformed and numerical predictors scaled, coefficients should thus be interpreted accordingly. β = beta coefficent, σ = standard error, LL & UL = lower and upper limit of the 95% confidence interval.

Response variable	Informative model term(s)	β	σ	LL	UL
Maximum diving depth	Mean_VeDBA_des	-0.039	0.011	-0.060	-0.018
	VV_des	0.204	0.010	0.184	0.225
Dive duration	Mean_VeDBA_des	-0.011	0.020	-0.073	-0.010
	VV_des	-0.113	0.015	-0.143	-0.082
Presence of a bottom phase	Max_depth	0.575	0.105	0.370	0.781
Bottom phase duration	Mean_VeDBA_bott	-5.807	0.885	-7.283	-4.224
	Max_depth	0.247	0.023	0.203	0.286
	Mean_VeDBA_bott : Max_depth	0.097	0.040	0.015	0.171

Mean_VeDBA_des *Mean VeDBA during the descent phase*; VV_des *Vertical velocity during the descent phase*; Max_diving_depth *Maximum diving depth*; Mean_VeDBA_bott *Mean VeDBA during the bottom phase*

Figures

Figure 1. Frequency distributions of maximum diving depth (a), dive duration (b), descent phase duration (c), bottom phase duration (d) and ascent phase duration (e) for 12 Eurasian beavers *Castor fiber* in southeast Norway (n= 2596 dives).

Figure 2. Pooled absolute number of dives per hour standardized to 5 days (n = 2544 dives;) for 12 Eurasian beavers *Castor fiber* in southeast Norway. Point size is proportional to the number of individuals diving at the given hour.

Figure 3. Polynomial regression relationship between dive duration and maximum diving depth in 12 Eurasian beavers *Castor fiber* in southeast Norway (ln dive_dur = 3.283 + 0.687 ln max_depth + -0.203 ln max_depth^2; $F_{2,2595} = 495$, R^2 (adjusted) = 0.27, $p < 0.001$).

Figure 4. Predicted relationship between maximum diving depth and mean VeDBA during the descent (a), maximum diving depth and vertical velocity during the descent (b), dive duration and mean VeDBA during the descent (c), dive duration and vertical velocity during the descent (d), bottom phase duration and mean VeDBA during the descent (e) and bottom phase duration and maximum diving depth (f) for 11 Eurasian beavers *Castor fiber* in southeast Norway.

Figure 1.

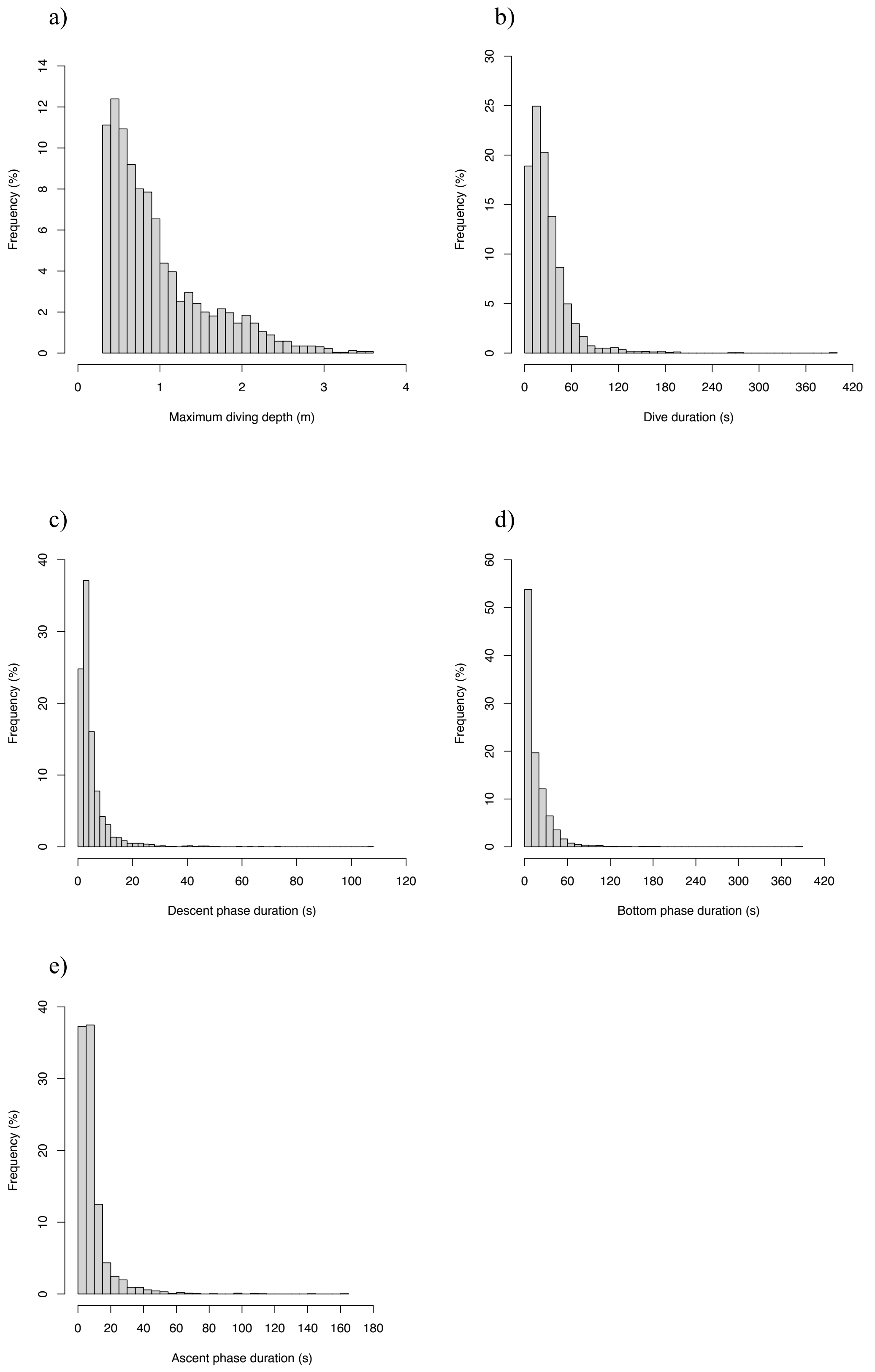
a)
Frequency (%)
0
2
4
6
8
10
12
14
0
1
2
3
4
Maximum diving depth (m)
b)
Frequency (%)
0
5
10
15
20
25
30
0
60
120
180
240
300
360
420
Dive duration (s)
c)
Frequency (%)
0
10
20
30
40
0
20
40
60
80
100
120
Descent phase duration (s)
d)
Frequency (%)
0
10
20
30
40
50
60
0
60
120
180
240
300
360
420
Bottom phase duration (s)
e)
Frequency (%)
0
10
20
30
40
0
20
40
60
80
100
120
140
160
180
Ascent phase duration (s)

Figure 2.

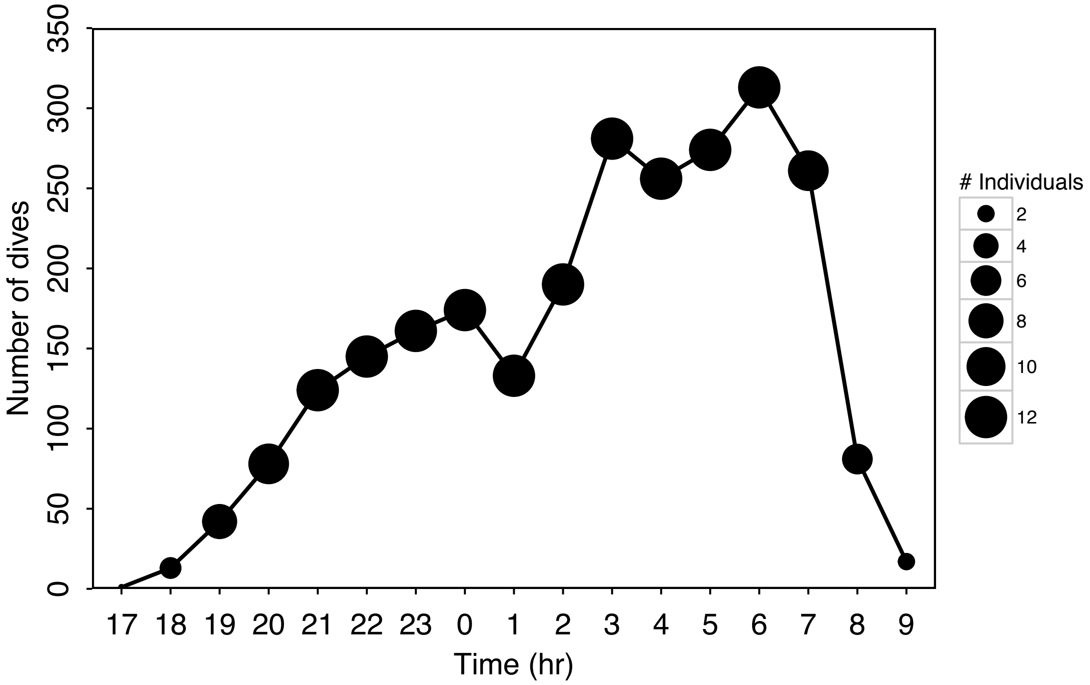
Number of dives
0
50
100
150
200
250
300
350
17
18
19
20
21
22
23
0
1
2
3
4
5
6
7
8
9
Time (hr)
Individuals
2
4
6
8
10
12

Figure 3.

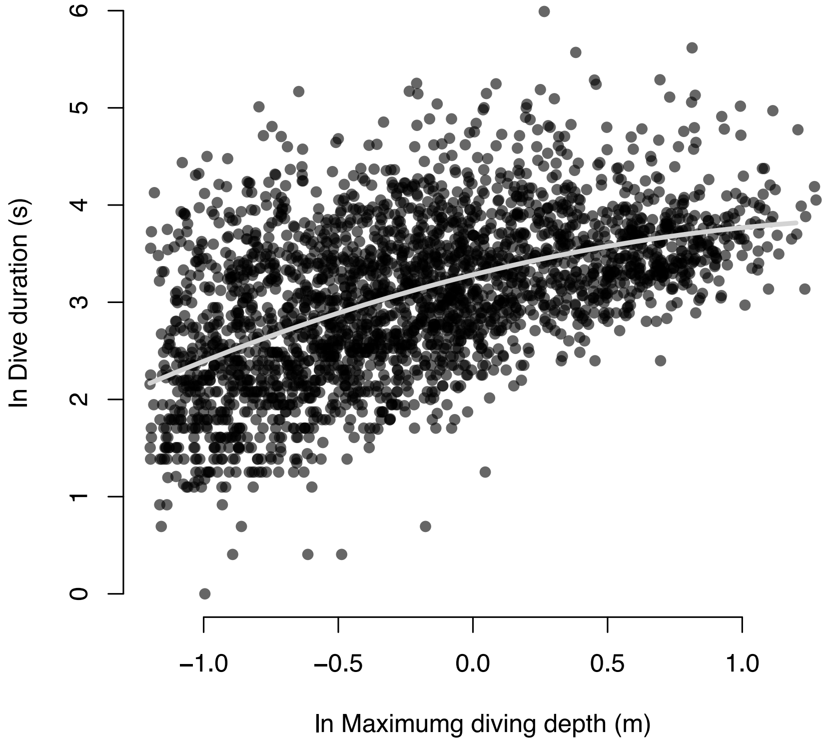
ln Dive duration (s)
0
1
2
3
4
5
6
−1.0
−0.5
0.0
0.5
1.0
ln Maximumg diving depth (m)

Figure 4.

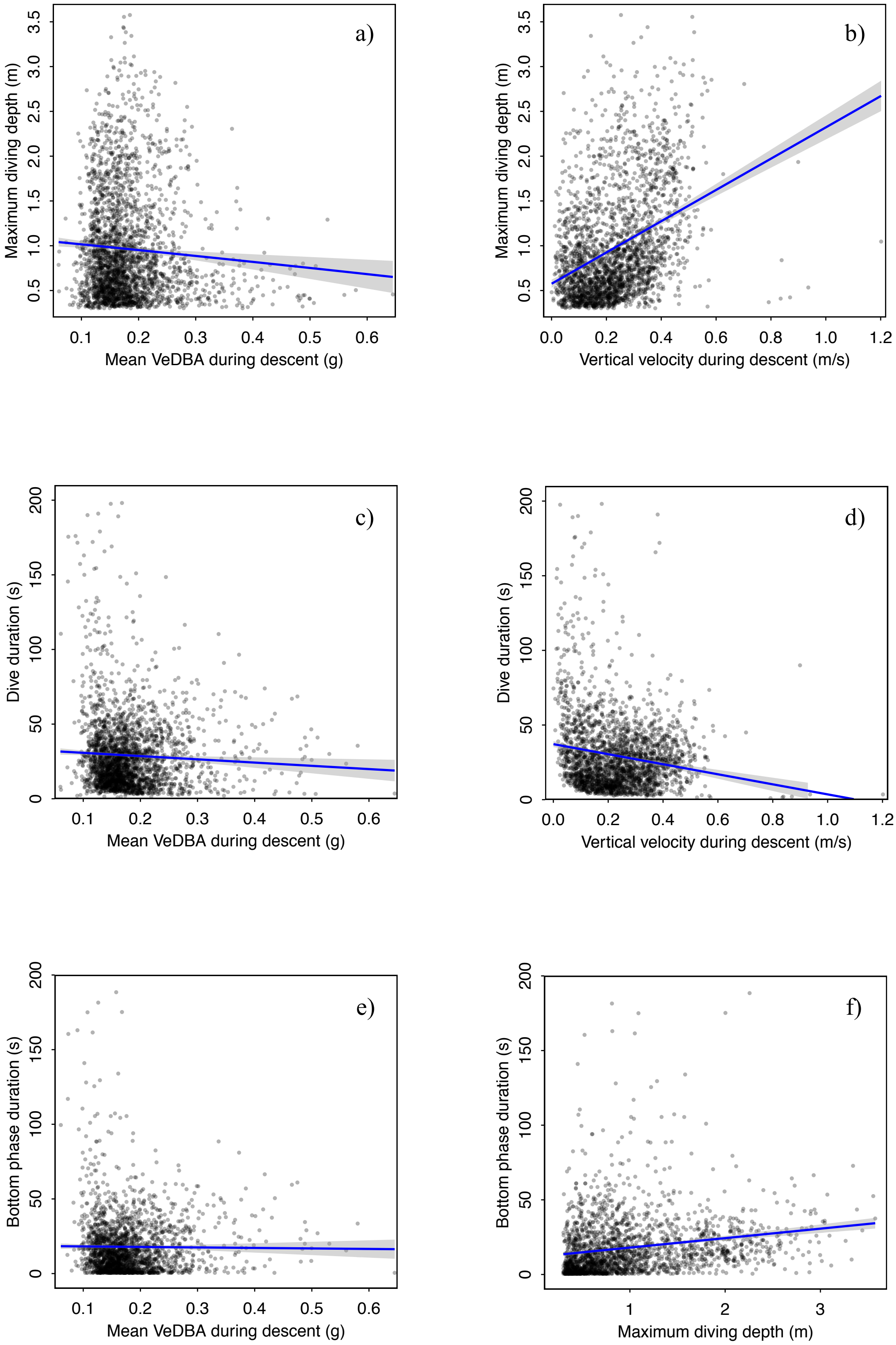
a)
Maximum diving depth (m)
0.5 1.0 1.5 2.0 2.5 3.0 3.5
0.1 0.2 0.3 0.4 0.5 0.6
Mean VeDBA during descent (g)
b)
Maximum diving depth (m)
0.5 1.0 1.5 2.0 2.5 3.0 3.5
0.0 0.2 0.4 0.6 0.8 1.0 1.2
Vertical velocity during descent (m/s)
c)
Dive duration (s)
0 50 100 150 200
0.1 0.2 0.3 0.4 0.5 0.6
Mean VeDBA during descent (g)
d)
Dive duration (s)
0 50 100 150 200
0.0 0.2 0.4 0.6 0.8 1.0 1.2
Vertical velocity during descent (m/s)
e)
Bottom phase duration (s)
0 50 100 150 200
0.1 0.2 0.3 0.4 0.5 0.6
Mean VeDBA during descent (g)
f)
Bottom phase duration (s)
0 50 100 150 200
1 2 3
Maximum diving depth (m)

Table S1. Model selection using Akaike's information criterion corrected for small sample sizes (AIC_c) for maximum diving depth in relation to the five predictor variables for 11 Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2011). Model averaging was implemented on candidate models within ΔAICc < 2 to derive averaged parameter estimates. ΔAIC_c *Difference in* AIC_c *relative to min.* AIC_c; w_i *Akaike weight*; K *Number of parameters*

Maximum diving depth

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Mean_VeDBA_des + VV_des	3994.75	0.00	0.79	5	-1992.36
VV_des	3998.37	3.62	0.13	4	-1995.18
Mean_VeDBA_des + VV_des + weight	3999.54	4.79	0.07	6	-1993.76
Mean_VeDBA_des : VV_des	4003.56	8.81	0.01	6	-1995.76
Mean_VeDBA_des + VV_des + weight + water_temp	4005.19	10.44	0.00	7	-1995.57
Mean_VeDBA_des + VV_des + weight + water_temp + sex	4010.26	15.51	0.00	8	-1997.10
Mean_VeDBA_des	4348.75	354.00	0.00	4	-2170.37

Mean_VeDBA_des *Mean VeDBA during the descent phase*; VV_des *Vertical velocity during the descent phase*; Water_temp *Water temperature*;

Table S2. Model selection using Akaike's information criterion corrected for small sample sizes (AIC_c) for dive duration in relation to the five predictor variables for 11 Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2011). Model averaging was implemented on candidate models within ΔAICc < 2 to derive averaged parameter estimates. ΔAIC_c *Difference in* AIC_c *relative to min.* AIC_c; w_i *Akaike weight*; K *Number of parameters*

Dive duration

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
VV_des	6083.88	0.00	0.69	4	-3037.93
Mean_VeDBA_des + VV_down	6085.80	1.91	0.27	5	-3037.89
Mean_VeDBA_des : VV_des	6090.13	6.24	0.03	6	-3039.05
Mean_VeDBA_des + VV_des + weight	6091.95	8.06	0.01	6	-3039.96
Mean_VeDBA_des + VV_des + weight + water_temp	6096.74	12.86	0.00	7	-3041.35
Mean_VeDBA_des + VV_des + weight + water_temp + sex	6100.79	16.91	0.00	8	-3042.37
Mean_VeDBA_des	6129.69	45.81	0.00	4	-3060.84

Mean_VeDBA_des *Mean VeDBA during the descent phase*; VV_des *Vertical velocity during the descent phase*; Water_temp *Water temperature*;

Table S3. Model selection using Akaike's information criterion corrected for small sample sizes (AIC_c) for the mean number of dives per night in relation to the three predictor variables for 12 Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2011). Model averaging was implemented on candidate models within ΔAICc < 2 to derive averaged parameter estimates. ΔAIC_c *Difference in* AIC_c *relative to min.* AIC_c; w_i *Akaike weight*; K *Number of parameters*

Number of dives per night

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Water_temp	26.88	0.00	0.88	3	-8.94
Water_temp + sex	31.07	4.18	0.11	4	-8.68
Water_temp : sex	36.03	9.14	0.01	5	-8.01
Water_temp + sex + weight	36.70	9.82	0.01	5	-8.35

Water_temp *Water temperature*;

Table S4a, b. Model selection using Akaike's information criterion corrected for small sample sizes (AIC_c) for (a) the likelihood of a bottom phase and (b) the actual bottom phase duration in relation to the three predictor variables for 11 Eurasian beavers (*Castor fiber*) in Telemark, southeastern Norway (2009 – 2011). Model averaging was implemented on candidate models within ΔAICc < 2 to derive averaged parameter estimates. ΔAIC_c *Difference in* AIC_c *relative to min.* AIC_c; w_i *Akaike weight*; K *Number of parameters*

Likelihood of a bottom phase duration (a)

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Mean_VeDBA_des : max_depth	2418.64	0.00	0.45	5	-1204.31
Mean_VeDBA_des + max_depth	2419.88	1.24	0.24	4	-1205.93
Max_depth	2420.65	2.01	0.17	3	-1207.32
Mean_VeDBA_des + max_depth + water_temp	2421.06	2.41	0.14	5	-1205.52
Mean_VeDBA_des	2451.31	32.66	0.00	3	-1222.65
~ 1	2453.36	34.72	0.00	2	-1224.68

Mean_VeDBA_des *Mean VeDBA during the descent phase*; Water_temp *Water temperature*; Max_depth *Maximum diving depth*;

Bottom phase duration (b)

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Mean_VeDBA_bott : max_depth	16197.14	0.00	0.83	6	-8092.55
Mean_VeDBA_bott + max_depth	16201.11	3.97	0.11	5	-8095.54
Mean_VeDBA_bott + max_depth + water_temp	16202.73	5.60	0.05	6	-8095.35
Max_depth	16263.21	66.07	0.00	4	-8127.59
Mean_VeDBA_bott	16323.17	126.03	0.00	4	-8157.57
~ 1	16378.08	180.95	0.00	3	-8186.04

Mean_VeDBA_bott *Mean VeDBA during the bottom phase*; Water_temp *Water temperature*; Max_depth *Maximum diving depth*;

Paper V

Wilson, R. P., Holton, M.D., Walker, J. S., Shepard, E. L. C., Scantlebury, D. M., Wilson, V. L., Wilson, G. I., Tysse, B., Gravenor, M., Ciancio, J., McNarry, M. A., Mackintosh, K. A., Qasem, L., Rosell, F., Graf, P. M., Quintana, F., Gomez-Laich, A., Sala, J.-E., Mulvenna, C. C., Marks, N. J. & Jones, M. W. (2016). A spherical-plot solution to linking acceleration metrics with animal performance, state, behaviour and lifestyle. Movement Ecology 4: 1-11. doi: 10.1186/s40462-016-0088-3

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Movement Ecology

METHODOLOGY ARTICLE Open Access

A spherical-plot solution to linking acceleration metrics with animal performance, state, behaviour and lifestyle

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Abstract

Background: We are increasingly using recording devices with multiple sensors operating at high frequencies to produce large volumes of data which are problematic to interpret. A particularly challenging example comes from studies on animals and humans where researchers use animal-attached accelerometers on moving subjects to attempt to quantify behaviour, energy expenditure and condition.

Results: The approach taken effectively concatinated three complex lines of acceleration into one visualization that highlighted patterns that were otherwise not obvious. The summation of data points within sphere facets and presentation into histograms on the sphere surface effectively dealt with data occlusion. Further frequency binning of data within facets and representation of these bins as discs on spines radiating from the sphere allowed patterns in dynamic body accelerations (DBA) associated with different postures to become obvious.

Method: We examine the extent to which novel, gravity-based spherical plots can produce revealing visualizations to incorporate the complexity of such multidimensional acceleration data using a suite of different acceleration-derived metrics with a view to highlighting patterns that are not obvious using current approaches. The basis for the visualisation involved three-dimensional plots of the smoothed acceleration values, which then occupied points on the surface of a sphere. This sphere was divided into facets and point density within each facet expressed as a histogram. Within each facet-dependent histogram, data were also grouped into frequency bins of any desirable parameters, most particularly dynamic body acceleration (DBA), which were then presented as discs on a central spine radiating from the facet. Greater radial distances from the sphere surface indicated greater DBA values while greater disc diameter indicated larger numbers of data points with that particular value.

Conclusions: We indicate how this approach links behaviour and proxies for energetics and can inform our identification and understanding of movement-related processes, highlighting subtle differences in movement and its associated energetics. This approach has ramifications that should expand to areas as disparate as disease identification, lifestyle, sports practice and wild animal ecology.
UCT Science Faculty Animal Ethics 2014/V10/PR (valid until 2017).

Keywords: Spherical plots, Tri-axial acceleration, G-sphere, Visualisation

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Background

Quantification of animal movement is a hugely complex topic. In its broadest sense, it operates over wide (3-dimensional) space-scales and highly variable time periods. For example, it encompasses everything from a single limb motion describing a simple arc lasting less than a second, through co-ordination of repetitive limb motion in a whole animal during travel, which may last hours, to the diversity in the complex movement describing the various behaviours exhibited over the lifetime of an animal. Understanding animal movement is important for a suite of reasons but particularly because voluntary animal movement requires energy. Quantification of the allocation of chemical energy for mechanical output and how this relates to movement is relevant in understanding the costs, efficiencies and values of behaviour, lifestyle and exercise physiology. Judicious use of energy is a major element of optimization studies that seek to define best strategies, which have a broad remit ranging from examining most enhanced performance by elite athletes [1, 2] to animals adopting behaviours that maximize survival [3].

Unsurprisingly, therefore, the energetics of movement is well studied e.g. [4], but it has been polarised into essentially two main branches defined by differing methodologies - One branch examines power use [5], which typically requires measurement across extended periods [6–8] but is limited by the difficulties in attributing instantaneous power to performance [9]. The other seeks to quantify behaviour, relying variously on approaches such as high-speed cameras [10], point light displays [11] and force platforms [12] for work on humans and, primarily, on observation-based methodologies for wild animals [13].

Increasingly though, both the power use and the behaviour of humans [14] and animals [15] are being studied using accelerometers in animal/human-attached tags because these sensors quantify change in speed, a fundamental property of motion, precisely [16]. Thus, in the field of energetics, workers have derived indices, such as those based on dynamic body acceleration (DBA) metrics [17], that correlate tightly with oxygen consumption [18], while behavioural studies have used various methods such as random forests, vector machines and artificial neural networks on acceleration data to identify behaviours [19, 20]. However, both groups recognise the problem inherent in the complexity of acceleration data. These provide most value when recorded at high rates (typically >20 Hz) across each of the three axes defining orientation in space, producing effectively 6 channels of data, 3 relating to the gravity-based component of the acceleration and 3 relating to the animal-based movement [21]. Indeed, it is perhaps this complexity that still represents an appreciable challenge for the animal (and human) behaviour community in binding energy use and behaviour within one framework (cf. [22]), even though they are fundamentally interdependent. Indeed, any framework that enhances consideration of animal movement, behaviour and power use simultaneously should facilitate the identification and understanding of processes and patterns across and between them.

One solution to this is to recognise that, because the earth's gravity is constant, a tri-axial plot of tri-axial, orthogonally placed, acceleration data fundamentally builds a sphere, a 'g-sphere' [23]. Acceleration data derived from animal movement change the form of this sphere. We capitalise on this to create a new visualization paradigm for animal/human-attached acceleration data whereby we generate the g-sphere and then place animal movement data on it, including those that seek to exemplify power use, over any temporal scale. The approach marries behaviour to estimated energetics and highlights some patterns that are not intuitively obvious. We show that g-sphere visualizations should have the capacity to highlight changes in movement patterns associated with e.g. human emotional state, injury and best practice in single sports manoeuvres but extend through to highlighting proxies for energy-based behavioural ecology in wild animals over time periods ranging from seconds to years.

Results

The basic g-sphere

An animal-attached tag mounted in the centre of an animal's back with orthogonal, tri-axial accelerometers (aligned with the major axes of the body) produces a 'static' g signal with a vectorial sum of $1.0\,g$ due to gravity when the animal is stationary. Plots of such tri-axial data in a 3-d graph therefore tend to populate the outer surface of the g-sphere which becomes most apparent as the animal adopts body orientations with multiple combinations of body pitch and roll (Fig. 1a). When animals move, points may leave the g-sphere surface as acceleration values reflect g-forces derived from the animal's acceleration (Fig. 1a). This has been termed 'dynamic acceleration' and can be dealt with in a number of different ways, one of which is to remove it by selective smoothing [21] and normalising (see methods) to leave the postural data. Thus, body attitude, which is a major step in elucidating behaviour [16], is defined by the position of the data points on the sphere.

Dealing with over-plotting - the Dubai plot

Increasing time periods viewed within the basic g-sphere tend to result in increasing occlusion and over-plotting of the data, making visualizations more confusing and less useful as the number of data points increases (Fig. 1a). A representation of the time allocated to various postures can, however, be obtained by tessellating the surface of the *g*-sphere into facets, summing the data points within each facet, and presenting the number of points within each

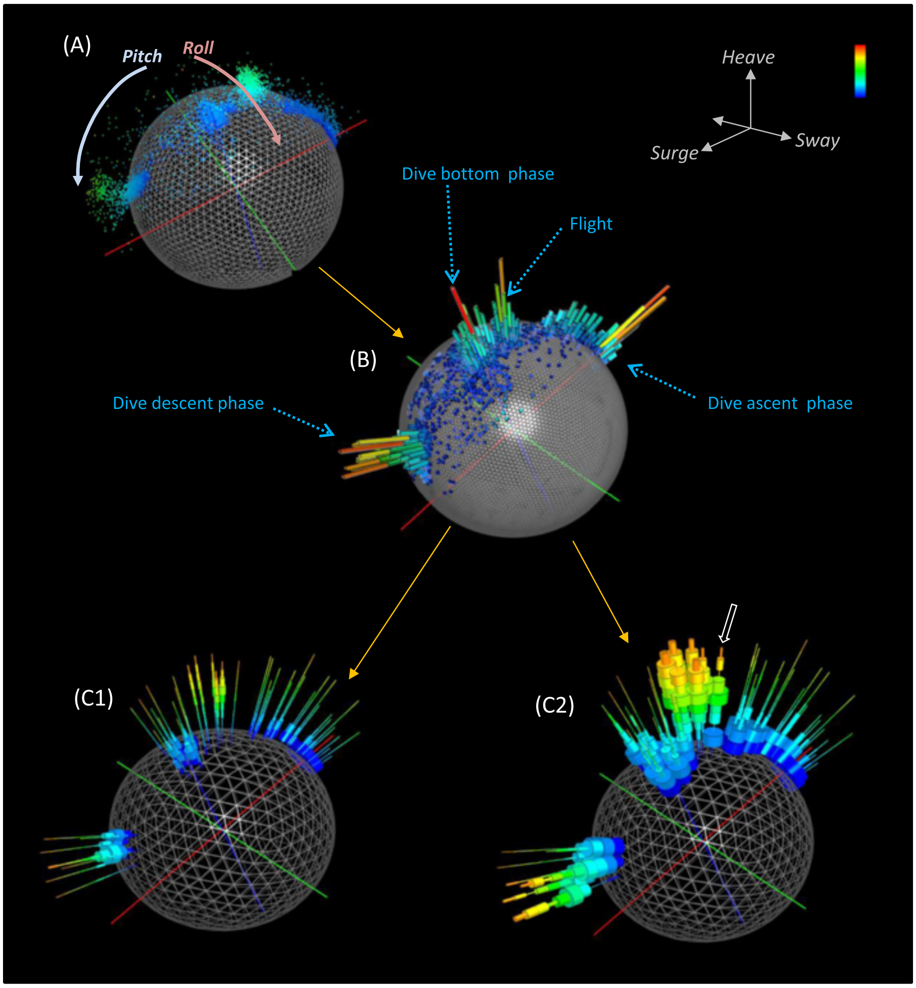

Fig. 1 Example behavioural data from a cormorant. Six dives and a short period of flight are visualised by (**a**) a point- based g-sphere [with point colour equating with DBA]. **b** shows the same data as (**a**) but as a Dubai plot. Both (**c**) images depict urchin plots of (**b**); *C1* shows percentages of DBA allocation taken across the whole g-sphere while *C2* shows percentages amounting to 100 % per facet. Note the higher values of DBA attributed to flight and descent of the water column, particularly emphasized by the 100 % facet percentage. Note also how certain spines show multi-modes (e.g. *white arrow*) which can be indicative of different behaviours at one body attitude

facet by a projection into space away from the g-sphere, producing a spherical histogram or 'Dubai plot' (Fig. 1b). Such plots typically show modes representing different type of behaviour with the higher peaks representing the more common behaviours (Figs. 1b and 2a).

Allocating putative power use to the g-sphere - the g-urchin

While basic g-spheres and Dubai plots quantify the time allocated to different postural states, they impart no information on power use. This information can be incorporated into the g-sphere by calculating the dynamic body acceleration (DBA) (see methods), which correlates linearly with power [18], for each of the postural data points within each facet on the sphere. In this, we note that although one study has shown that a strong relationship between DBA and energy expenditure holds for a (seabird) species operating in three media and multiple different body angles [22], confirmation that this is also the case for more species will need further work (but see [24]). To visualize this, the sphere facets can be populated with thin spines, one spine per facet, radiating into space, like a sea urchin (facets without data have no spine). Spines acquire stacked rings representing the frequency distribution of the DBA values associated with that posture/facet. The position of each ring on the spine indicates the DBA value (lower values are closer to the g-sphere surface), the depth of the ring indicates the width of the DBA bin, and the diameter of the ring is proportional to the number of data points within that bin (Figs. 1c and 2b). This 'g-urchin' can be represented so that it is normalised for all data across the sphere, which highlights the processes that dominate in terms of

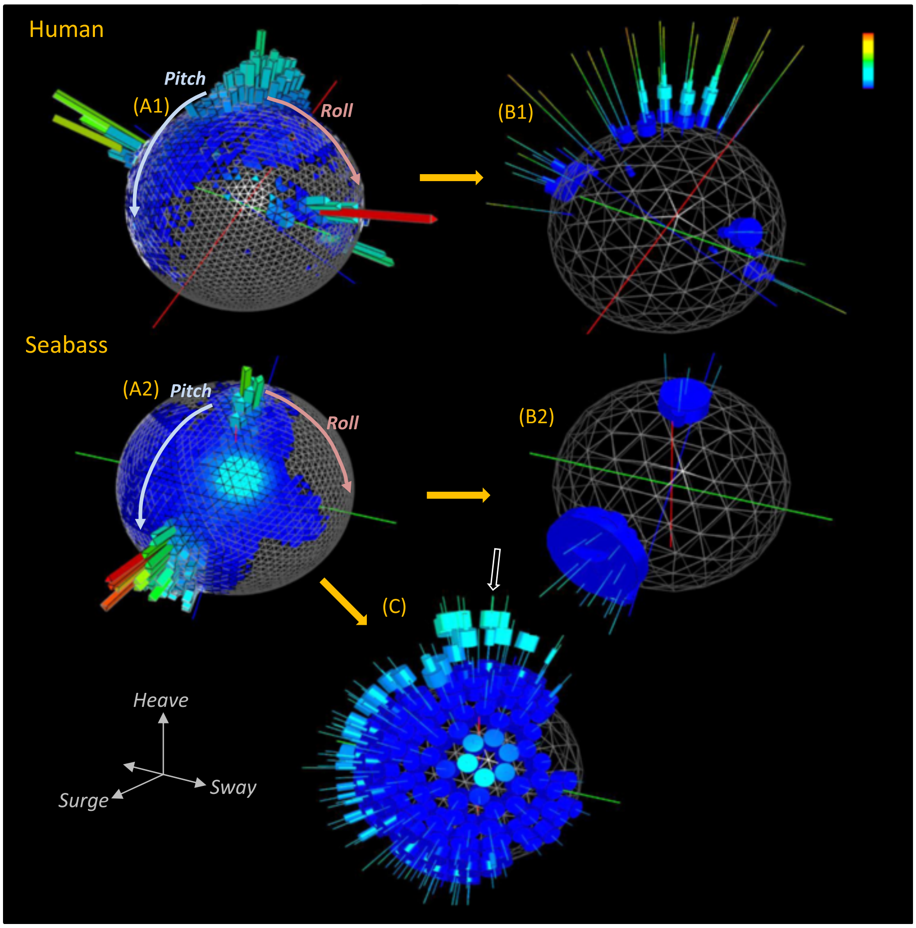

Fig. 2 Examples of posture and energy-linked posture visualised for two contrasting species (a human and a fish) over 24 h. The human data are taken from a person on a walking/camping tour while the fish data are from a hole-dwelling reef species that often rests by wedging itself at unusual angles. The left hand figures (**a**) show spherical histogram (Dubai) plots, indicating how time is allocated to different body postures [the 'North pole' position shows the species in the 'normal' upright position]. The first right-hand figure for each species (**b**) shows how each posture is linked to varying putative power levels. Note how the human has higher power-proxy levels associated with the vertical posture due to walking. Both the human and the fish have low power-proxy levels at low 'latitude' angles acquired during resting/sleep, exemplified by the large diameter blue discs. Data normalized to give a global percentage for all angles may hide infrequent, but higher-energy, activities. Normalising the data to 100 % per facet (**c**) highlights these though. In this case, the low-energy life style of the fish is still apparent (cf. B), with higher energies occurring fleetingly and only when the fish is vertical (*white arrow*). The colour coding has blue as low, and red as high, values

both the time and proxy for energy across the whole time period considered (Figs. 1c1 and 2b). Alternatively, data can be normalised within each facet to highlight the energetic proxies of particular postures irrespective of their time contribution (Figs. 1c2 and 2c). Urchin plots thus show differences between behaviours within species (Fig. 1c), differences in lifestyles between species (Fig. 2b, c), and differences in behaviour of any individual through time (Fig. 3).

Comparing behaviours and putative power uses - the differential g-urchin

The process of comparing individuals or the same individual over different times can be enhanced by subtracting one Dubai plot or one g-urchin from another. These differential plots can be colour-coded, for example, according to which DBA bin from which urchin has the higher value (Fig. 4). This highlights differences in assumed power use associated with posture and therefore behaviour, with notable changes even associated even with state [25] (Fig. 4a).

Simplifying outputs

G-sphere derivatives can be re-simplified to enhance e.g. inter- or intra- specific comparisons by plotting 2-d line graphs showing the time and/or the DBA allocated to percentage coverage of the g-sphere (Fig. 5). Such 'life-style' plots show consistent patterns within and between species (Fig. 5).

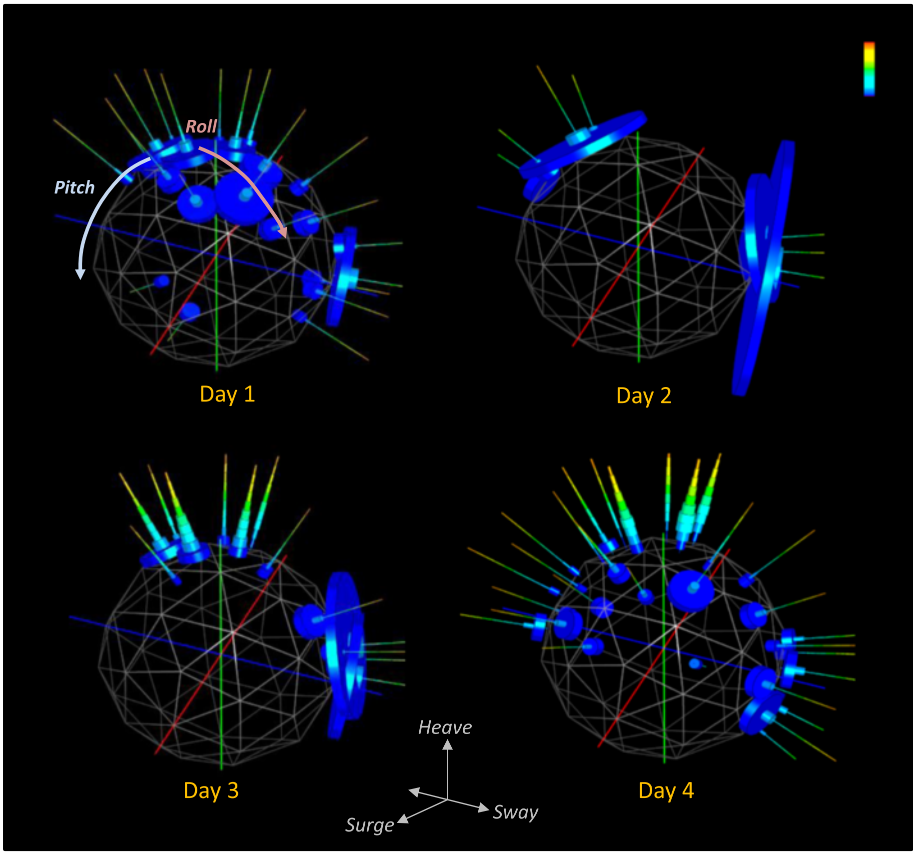

Fig. 3 Example urchin plots for four consecutive 24 h periods after the release of a European badger (wearing a collar-mounted accelerometer) following anaesthesia. The 'North pole' facets show when the animal was properly horizontal (ie in standing or walking posture). Note how the first two days show no high energy activity because the animal was either resting or asleep. The second day shows only four changes in position. By day three, higher energy, normal posture activities such as walking are apparent at the North pole. This process is further enhanced in day 4, with North pole spine DBA distributions having modes that have moved up the length of the spines to indicate higher power use. DBA values are colour-coded with maximum values (in *red*) of 1 *g*

Discussion

Application of g-spheres and their derivatives to raw tri-axial acceleration data adds another powerful tool to visualize and identify behaviour [19] that requires no knowledge of the animal in question for behaviour-specific patterns to emerge into groups. This approach concatenates 6 complex lines of acceleration data into one plot binding animal attitude and proxy for power use into one visualization that clearly shows modes of behaviour (Fig. 1). The immediate value lies in its potential for use as a template match approach for specific activity pattern identification across data [26]. Thus, behavioural description and identification (Figs. 1, 2 and 3) do not require matched observed behaviours with example data but stem from a visually apparent clustering within the plot. In particular, differences between various g-sphere derivatives, especially Dubai and urchin plots (Fig. 4), can be used to identify specific variation in posture and power-use proxies between behaviours. For example, the Dubai plots in Fig. 4a provide an example of how the posture of a subject changed according to whether they had watched a happy or sad film clip, with the allocation of time to facet position changing. Similarly, the posture and allocation of DBA to different body postures during walking changed after a fall (Fig. 4b). The g-spheres therefore employ fundamentally different principles to other methods in the manner of data visualization and interpretation.

In a first iteration, the most common behaviours are most easily identified because of the way they dominate the basic g-sphere visualization (Fig. 1), which could be argued is the most important feature of understanding time management in animals. However, even behaviour that is only a small fraction of the time budget, but is energetically distinct and therefore likely to be apparent in the DBA distributions on urchin spines, may be identified by moving from the globally normalized g-urchin to one that is normalized to facet (Fig. 2b, c).

Importantly, mono-, bi-, or even tri-modality in the frequency distributions of DBA allocated to particular

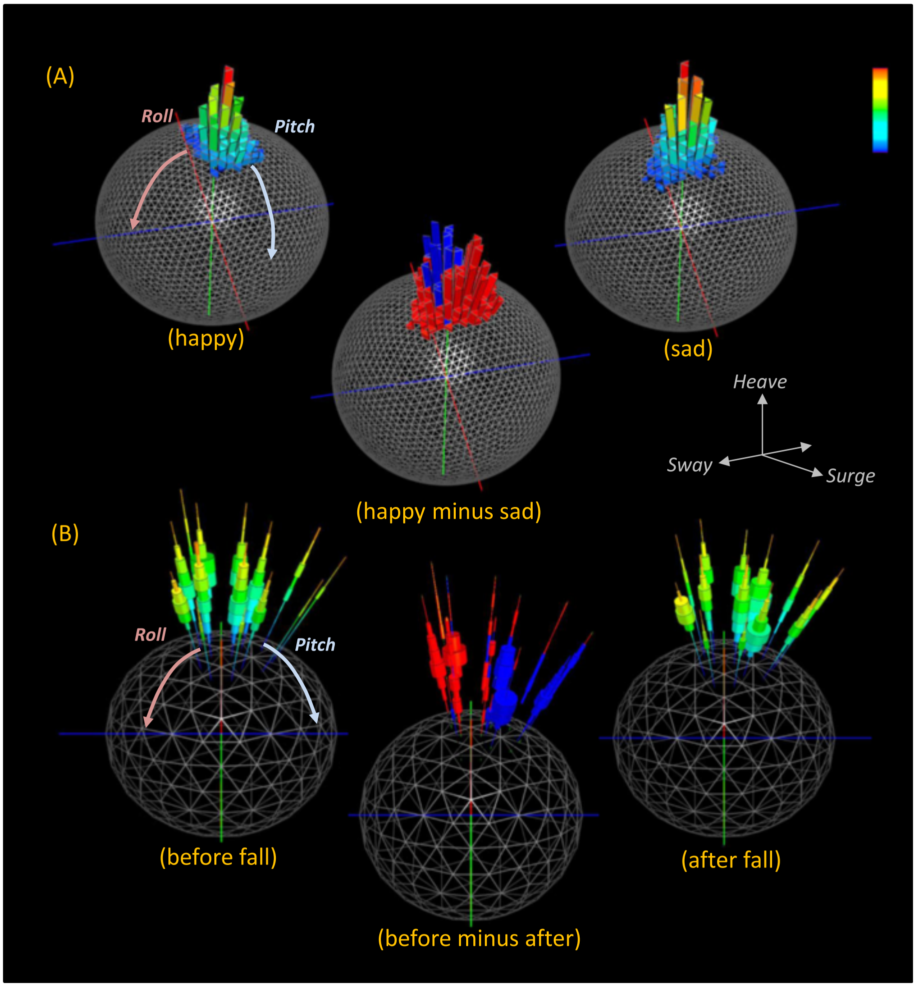

Fig. 4 Example posture and DBA values associated with 'state' in humans. **a** shows two Dubai plots for a person walking after seeing 'happy' and 'sad' film clips (higher frequencies are coded by warmer colours). A third differential Dubai plot highlights the difference between the two situations (*blue* = a higher relative frequency of 'happy' points per facet while red = a higher relative frequency of 'sad' points per facet). Note how the two conditions are reflected in the postural changes (**b**) shows urchin plots for someone trekking across snow pulling a sledge one minute before a fall and one minute after recovering from the fall. The differential urchin shows both differences in postures adopted between the two situations as well as the dynamism of the walking (red shows a higher relative DBA frequency 'before the fall' while blue shows the reverse)

facets or groups of adjacent facets, point to multiple behaviours occurring at similar animal postural attitudes. This is illustrated, for example, in the cormorant behaviour where the white arrow in Fig. 1c2 shows multimodality in DBA due to both dive ascent behaviour and flight behaviour being apparent in the same body attitude facet. It is also exemplified in the stationary and swimming behaviours in the seabass, shown in the bimodality of the DBA distributions along urchin spines at the North Pole (cf. Fig. 2c). The time-based adoption of behaviours can also be studied with this, for example, in the badger data presented (Fig. 3). Here, 'normal' walking behaviour is only manifest during day 4 post-sedation, when the urchin spines at the North Pole acquire a DBA mode that is greater than 1.0 g (Fig. 3). Such observations can then readily be incorporated into statistical classifiers and classification algorithms.

Generation of frequency distributions of DBA, as a proxy for power, thus enhances the process of separating behaviours. Importantly, it also helps visualize the overall allocation of power proxies, either to specific behaviours over short periods such as seconds or to collections of behaviour over longer periods (cf. Figs. 1, 2 and 3) extending to months or even years. Depending on the timescales, collections of particular behaviours should provide a representation of different lifestyles, as well as their considered associated energetic outlay, allowing powerful comparisons to be made between systems or scenarios. Examples include comparisons between species with contrasting lifestyles (Figs. 2 and 5) or within-

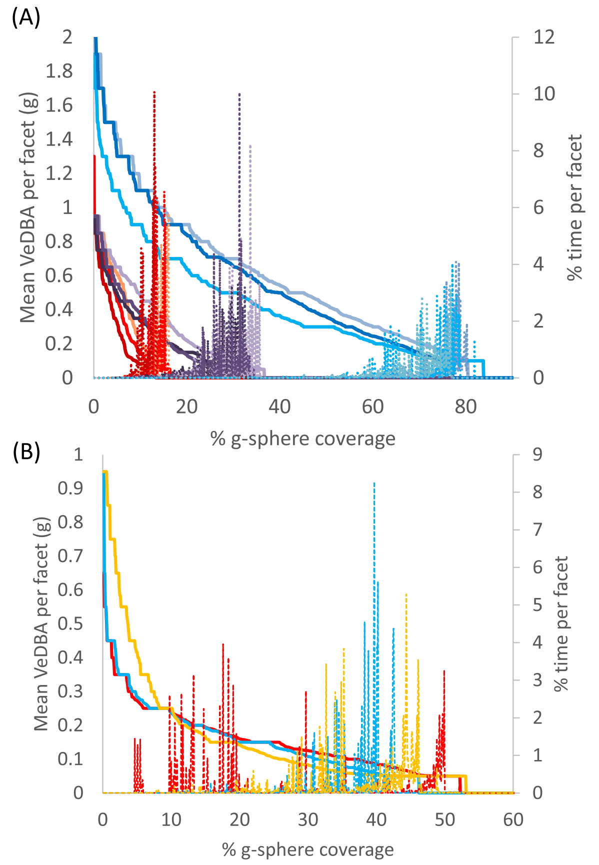

Fig. 5 Example 'lifestyle' plots for different species and situations. These show how DBA values are distributed across the surface of the g-sphere (*continuous lines*) and the time allocated to those values (*dashed lines of equivalent colour*) over 24 h for (**a**) 3 Magellanic penguins (*blue*), 3 Eurasian beavers (*purple*) and 3 domestic sheep (*red*) and (**b**) three people; a child (*yellow*) and 2 adults, one of whom hiked extensively during the period (*red*) while the other was essentially sedentary (*blue*). Note the species-specific similarities (species that employ most diverse body angles have the highest percentage of the sphere coverage) but that differences between individuals can be manifest in either the time or DBA allocations on the sphere

species lifestyle comparisons. Indeed, the precise form of 'lifestyle' plots (Fig. 5) may help in defining lifestyle taxa by defining animal capacities. The future may also benefit from the use of g-sphere approaches based on multiple accelerometers used on different parts of the body or even having accelerometers on hand-held objects. The expectation is that this will be particularly useful in sport applications (Additional file 1: Figure S7) where effective movement must be stylized for maximum performance because limb-, or sports equipment-mounted sensors will represent local forces and perhaps local power-usage proxies better than trunk-mounted systems which produce a body-integrated signal. Importantly, such power-proxy comparisons, from trunk-or limb-mounted sensors, can help identify efficient solutions to activities where performance, such as running speed over a given distance or animal breeding success over months, should be equatable with the putative energetic cost. This sort of consideration thus has advantages for elite athletes as well as for conservation bodies examining the costs of the lifestyle of their animals. Equally, changes in behaviour that occur with disease or illness, such as constrained activity stemming from rheumatoid arthritis [27], should be rapidly identifiable using this approach.

We expect g-spheres and their derivatives (e.g. Fig. 5) to form the basis for summary statistics which highlight particular aspects of performance, behaviour and lifestyle, which may function to be powerful descriptors of e.g. animal lifestyle, linked, among other things, to physical limitations based on taxonomic, allometric or environmental (e.g. water versus terrestrial) constraints [28]. In addition, such visualizations may help both children and adults to understand how the physical activity levels in their lifestyles compare to those recommended [29].

Conclusions

The treatment of tag-derived tri-axial acceleration data by creating a tri-axial plot of the gravity-based acceleration, leads to a spherical surface on which acceleration proxies for power use can be placed. This process has potential for highlighting behaviour-, and even state-, dependent clusters, irrespective of whether the user has a verified library or not and should illustrate how animals may allocate energy to the different behaviours. Subsequent simplification of the spherical plots into percentage of sphere occupied, mean dynamic body acceleration and time allocated per facet allows simple 2-d plots between these parameters to be created (Fig. 5). This approach should provide a powerful summary of putative energy allocation to behaviour and time, documenting intra-specific differences and showing how animals respond to their environment over time. Interspecific comparisons of these metrics show promise as a powerful behavioural tool with which to compare and quantify animal lifestyles.

Methods

The g-sphere visualization technique has been incorporated into publically available smart sensor analysis software, Framework4 [30, 31], available from http://www.framework4.co.uk. Walker et al. [32] give more details on this.

The basic g-sphere

In brief, the basic g-sphere is derived from tri-axial acceleration data, where the sensors have orthogonal placement, aligning with the major axes of the tagged animal's body.

Typically, the acceleration data will be recorded at infra-second rates (e.g. 40 Hz) on a deployment spanning anywhere from a few minutes up to a year. One day of data (24 h) recorded at these rates provides over 10 million measurements. For the g-sphere, we build on a method for visualising accelerometer data in Grundy et al. [23], using spherical coordinate plots to depict the distributions of data. To deal with large datasets, we utilise frequency-based approaches which show an overview of the data. Firstly, a spherical histogram shows the number of data items in each facet of the spherical coordinate system. Secondly, we build on the surface provided by the g-sphere using location-dependent frequency bins (the 'g-urchin' plot), for metrics such as DBA [17] as proxies for power usage. Multiple urchins can be compared difference operations to analyse across instances, behaviours groupings, or data sets.

Static and dynamic acceleration

Measured acceleration is the product of a static component due to gravity, manifest in accelerometers according to their orientation with respect to the Earth, and a dynamic component, due to the movement of the animal. Separating these components from the raw accelerometer measurements allows isolation of postural attitudes and movement.

The static component can be approximated by applying a low-pass filter over each the accelerometer axis components. Shepard et al. [21] suggest smoothing using a running mean over a period amounting to about twice the wavelength of any repetitive frequencies. The static component at data point i (SA_c,i) with a smoothing window of w is given by:

$$S_i = \frac{1}{w}\sum_{j=i-\frac{w}{2}}^{i+\frac{w}{2}} A_j$$

The corresponding dynamic components of acceleration (DA_c) per orthogonal axis are computed by subtracting the static components (SA_c) of acceleration from the raw acceleration values (A_c).

$$DA_c = A_c - SA_c$$

Power metrics

Dynamic acceleration-based metrics [17] have been argued as a predictor of power [18]. Two measures, Overall Dynamic Body Acceleration (ODBA) and Vectorial Dynamic Body Acceleration (VeDBA), have been used, and are essentially equivalent in terms of their power to predict VO_2 [33].

VeDBA (V) is calculated from the dynamic components of acceleration (DA_x, DA_y and DA_z) by taking the vectorial length of the dynamic acceleration vector using;

$$V = \sqrt{DA_x^2 + DA_y^2 + DA_z^2}$$

ODBA (O) is also calculated from the dynamic components of acceleration (DA_x, DA_y, and DA_z), instead taking the sum of the dynamic acceleration components using;

$$O = |DA_x| + |DA_y| + |DA_z|$$

Raw plot

The basic g-sphere plots the static accelerometer data in a three dimensional scatter plot with the animal's heave axis being allocated the y-axis, the surge the x-axis and the sway the z-axis (Fig. 1a). Each vector is considered as an offset from the origin, directly scatter-plotted in three-dimensional space with, for example, the colour of each data point being linked to any associated attribute in the data set (Fig. 1a). This representation shows short-lived behaviours well, providing a compelling visualization of when forces exceed that exerted by gravity (Additional file 1: Figure S1).

Spherical plot

Normalising the static acceleration vector, encodes posture information. Given the x, y, and z channels of the vector, the length of the vector L can be computed and the components normalised to x', y' and z' via:

$$L = \sqrt{SAX^2 + SAY^2 + SAZ^2}$$

$$X' = \frac{SAX}{L}\ Y' = \frac{SAY}{L}\ Z' = \frac{SAZ}{L}$$

This, projects the normalised vector onto the surface of a sphere in 3-d scatter plots which gives an implicit conversion to spherical coordinates (r, θ, ϕ) [34], where θ corresponds to the angle of inclination, ϕ is the angle of rotation on a two-dimensional plane, and the radius is constant ($r = 1$) throughout. Each vector is plotted as a point in the display and the size and radius of each point can be adjusted by a fixed amount, to link it to an attribute in the data set. Each point can be joined together in chronological order to show the temporal ordering of the vectors as a path in the three-dimensional space (Additional file 1: Figure S2) so that the spherical scatter plot shows an intuitive summary of the geometric distribution of posture and direction. Linking the radius, r of each coordinate to another attribute allows additional dimensions, such as depth, to be encoded which, in this case, provides a compelling illustration of diving patterns along with the associated state (Additional file 1: Figure S2).

Binning in three-dimensions

Large data set plots incur problems with occlusion and overplotting where data values in a point cloud obscure other values. For this, an overview and focus approach [35] can be employed which gives a contextual overview of the data while leaving potential to interact with further details in the data. Thus, we divide the surface of the sphere into facets (*sphere tessellation*) and treat the data within each facet to derive summary statistics (*binning*).

Sphere tessellation

To represent the underlying data on which the chart is based accurately [36], we employ a frequency-based approach using regular bin sizes to summarise the data although construction a sphere from a series of uniform geometric primitives is a problem from the cartography domain [37]. The traditional method of constructing a sphere via lines of latitude and longitude results in variable sized facets misrepresenting the underlying data [38]. We thus utilise a geodesic sphere, providing a close to uniform and regular sphere tessellation, using subdivision surfaces and spherical projection of an icosahedron platonic solid. The geodesic sphere starts with an icosahedron. Each facet is then repeatedly subdivided a predefined number of times with each of the acquired points projected onto a sphere. This results triangular facets, each of which is of a close to regular shape and area. Despite a slight variation in size and shape of each facet, this has a negligible effect in reconstructing the underlying data [38].

Binning data

Binning identifies the facet with which a data item intersects on the geodesic sphere. Teanby [38] propose a winding method which operates by linearly searching for an intersecting facet on the sphere which has a sum of angles with the test vector equating to 2π. Walker et al. [30] propose a more efficient method using the hierarchical structure of the geodesic sphere which operates in a similar manner to that of a search tree, dividing and dealing with the otherwise logarithmic complexity. The angle (θ) between the direction of the centre of each facet from the origin, (w) and the current vector (v) is computed using the dot product (below). The point is determined to be associated with the sphere facet with the smallest angle between them. This is recursively computed on the hierarchical structure until the lowest-level is reached.

$$\theta = \frac{v \cdot w}{|v|\ |w|}$$

For each facet, the following statistics are computed; (i) the number of data items intersecting each facet, (ii) the mean value of each data channel for the items in each facet and (iii) a frequency distribution of a user-defined data attribute consisting of a user-defined number of bins. The data for attributes (i) and (ii) are normalised so that the whole sphere adds up to 100 %. The distributions for (iii) are normalised locally which allows the creation of a histogram of each facet of the power usage occurring for a particular movement and postural state independent of the frequency of the underlying data in the facet (since the frequency equates to a percentage).

Dubai plot

The binned data for each facet can be displayed as a single histogram projecting perpendicularly from its respective facet (Figs. 1b, 2a and 4a; Additional file 1: Figure S3). Each histogram length and colour is nominally proportional to the normalised sample size for the sphere facet (Additional file 1: Figure S4). This gives an overview of the data distribution over the sphere, illustrating the frequency of postures or movements in the data set. The colour may be encoded as any other data attribute, in addition to the normalised frequency, along with the length.

G-urchin

In a final step of this method, the smoothed, tri-axial acceleration axes can be encoded in addition to the frequency of items in each facet. A histogram for each facet of the sphere is computed for the items residing in the facet, which can be combined in a manner that represents the power usage for each state. This 'g-urchin' has spines projecting from the sphere with each spine placed at a user-defined distance away from the sphere to avoid occlusion with any of the other layers of the visualization (although a line is drawn to the centre of the facet it represents). The length and width of each spine can be ascribed to any data attribute. It is most effective when the spine characteristics are linked to histogram frequency or the number of items residing in the facet (Figs. 1c, 2b,c and 3). Each spine consists of a number of stacks, the width of which corresponds to the histogram bin width (Additional file 1: Figure S4 overview):

Differential g-sphere

The binning procedure standardizes the data for time to allow a sphere from one situation (species, individual, time period) to be applied with another, providing the g-spheres are of the same sphere tessellation and bin size. We use two operations for this; firstly subtraction, which is used for highlighting differences, and summation, which combines g-spheres together. This gives the notion of two sphere types; a data g-sphere generated from raw data, and an operation g-sphere, generated by applying an operation. The standardization process means that operations can be applied to any combination of the two g-sphere representations.

(a) Difference is used to subtract two g-spheres (GA, GB) from each other. The absolute difference between the two spheres, for each facet in the sphere (f), and each corresponding bin (b) in the frequency distribution is computed. The result is a new operation g-sphere which highlights the difference between GA and GB (Fig. 4b).

$$G' = \sum_{i=0}^{f}\sum_{j=0}^{b} Abs\left(GA_{ij} - GB_{ij}\right)$$

(b) Summation is used to combine two g-spheres together. The items in each bin are added together. The result is a new operation g-sphere which combines the spheres GA and GB together.

$$G' = \sum_{i=0}^{f}\sum_{j=0}^{b} Abs\left(GA_{ij} + GB_{ij}\right)$$

Each frequency distribution is normalised to eradicate any bias towards data sets containing different number of data points. The effect in the frequency distribution is a percentage where each bin contributes towards a subset of the distribution. As such, the entire frequency distribution totals 100 %. When combining the distributions together by addition or subtraction, the result is the difference in percentage between the two histograms. Percentages of distributions are used to protect against bias resulting from the size of the underlying data.

Additional file

Additional file 1: Methods. Changing shapes for frequency distributions. **Figure S1.** A 3-d scatter plot (g-sphere) of static (orthogonal) tri-axial acceleration data. **Figure S2.** A spherical coordinate's visualization of (a) postural state plotted onto the surface of a sphere in three-dimensional space, (b) points joined together in chronological order, (c) projecting the data outwards from the sphere according to other parameters. **Figure S3.** A spherical histogram (Dubai plot) visualization to depict frequent postural states. **Figure S4.** Histogram, Frequency shape (stacked), fixed shape (skittle) from urchin plots. **Figure S5.** G-urchin of skittle shape and stacked frequency urchins emitted from the centre of each facet of the sphere. **Figure S6.** Overview of user interface for a program in which spherical plots can be created. **Figure S7.** G-spheres and comparable g-urchins derived from a rod-mounted tri-axial accelerometer showing fly-fishing visualisations. (DOCX 5289 kb)

Abbreviations

DBA: Dynamic body acceleration; VeDBA: Vectorial dynamic body acceleration

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Availability of data and materials

All data generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Authors' contributions

RPW provided the initial concept after discussion with MDH, JSW, MWJ and ELCS. MDH and JSW developed the software. VLW, GIW, MAM, KAM and BT provided human-based data including analysis and interpretation, FQ, AG-L, J-ES, DMS, JC, LQ, FR, and PMG gathered animal data and provided analyses and interpretation. MG contributed to general analyses and all authors contributed to the manuscript and to the ideas contained therein. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

See above. No named person within this study.

Ethics approval and consent to participate

The fish work was performed under permits from the "Secretaría de Pesca del Chubut" while the bird manipulations were carried out in accordance with the legal standards of the Argentine government and fieldwork approved by The Organismo Provincial de Turismo and Dirección de Fauna y Flora Silvestre of Chubut Province, Argentina. Permission was granted from UK Home Office and protocols approved by the Department of Agriculture, Environment & Rural Affairs, Northern Ireland for all mammal work except for beavers, for which the work was approved by the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management. The study procedures for humans were approved by the Swansea University ethics committee and complied with the Declaration of Helsinki. All the participants and their parents/guardians were informed in writing about the demands of the study, and subsequently gave their written informed assent and consent, respectively, for participation prior to commencing the study.

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Supplementary Information

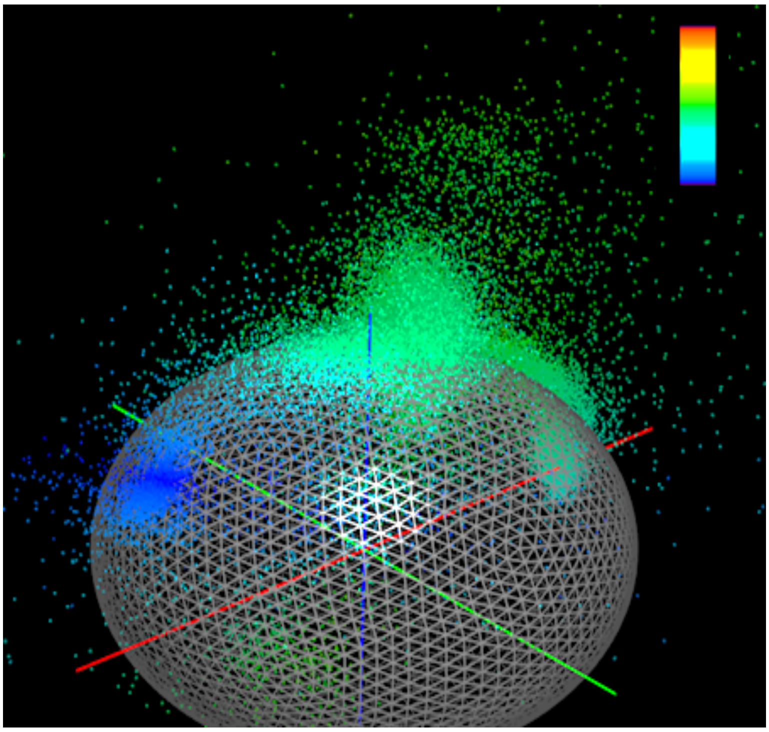


Fig. S1 *– A 3-d scatter plot (g-sphere) of static (orthogonal) tri-axial acceleration data recorded from an Imperial Cormorant; diving, sitting on the water surface and flying.*

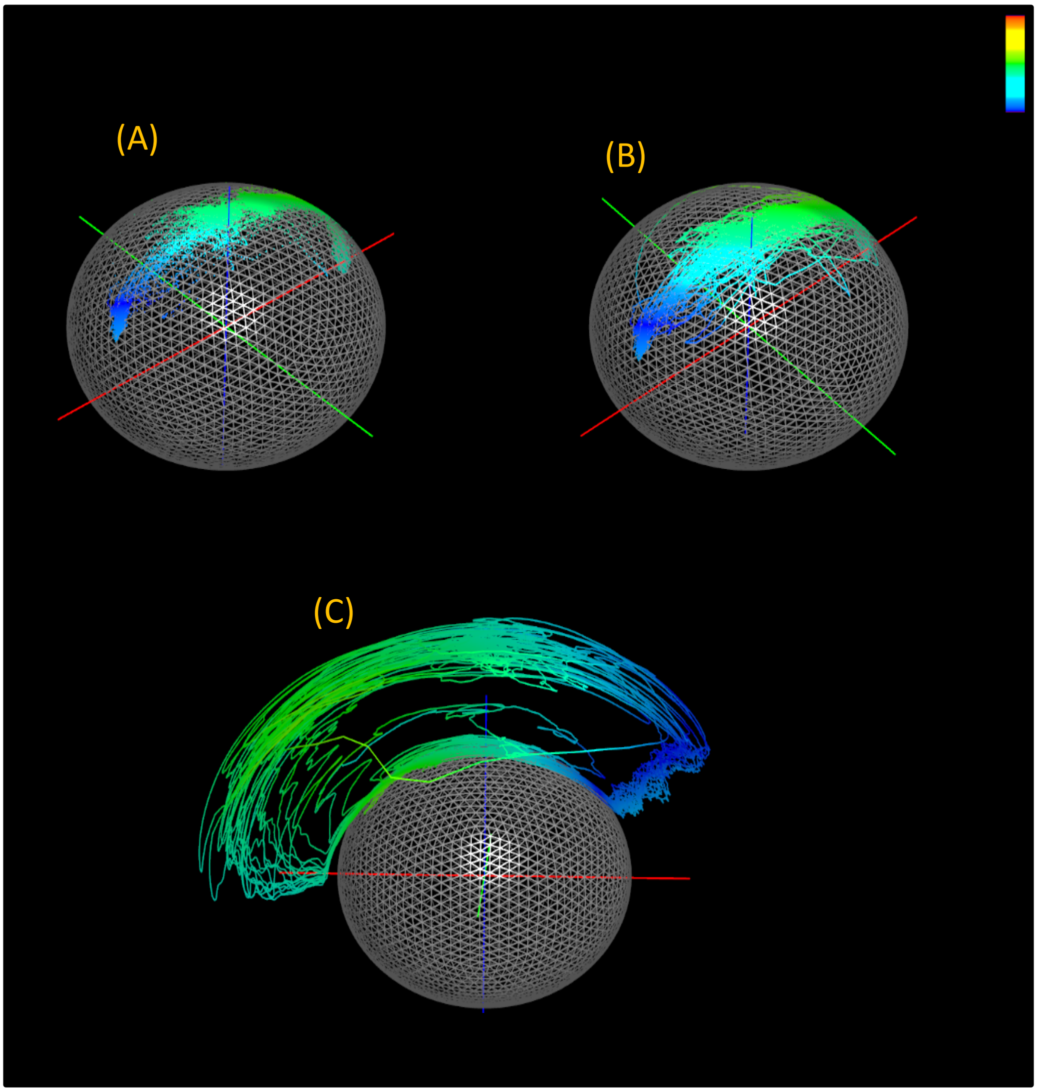


Fig. S2 *– A spherical coordinate's visualisation of* ***(A)*** *postural state plotted onto the surface of a sphere in three-dimensional space.* ***(B)*** *Each point is joined together in chronological order to show the temporal structure of the data.* ***(C)*** *The data are further projected outwards from the sphere according to depth. This shows a compelling visualisation of orientation combined with depth to aid in behaviour analysis.*

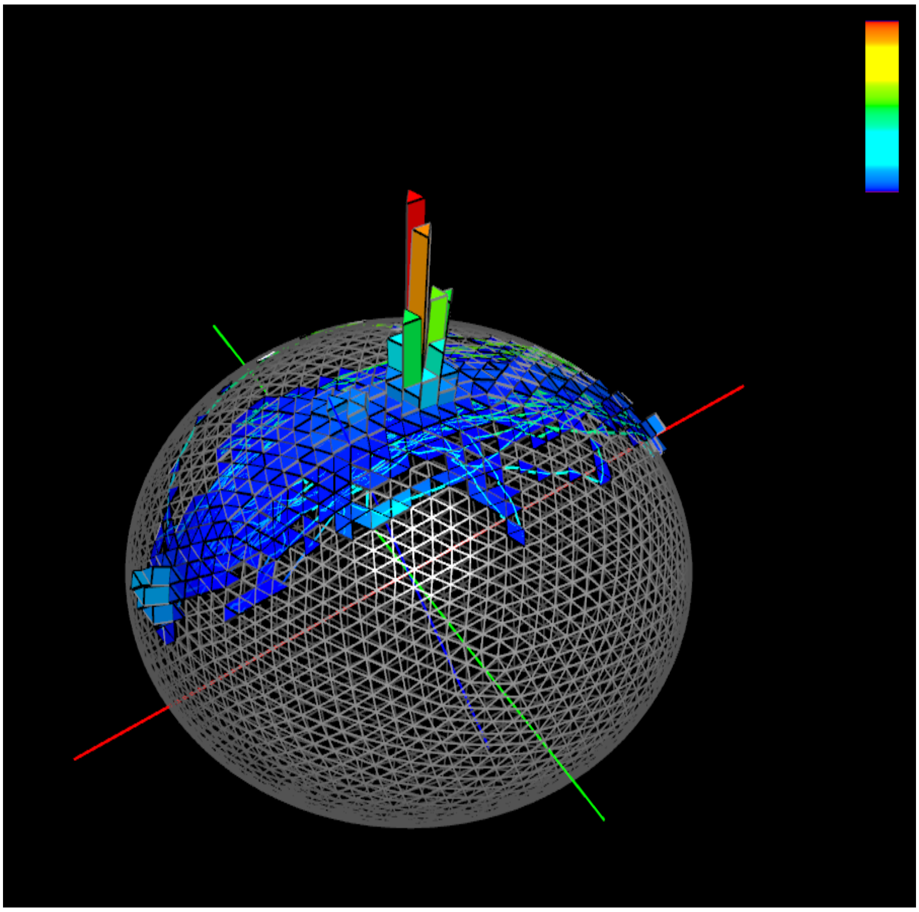


Fig. S3 *– A spherical histogram (Dubai plot) visualisation to depict frequent postural states. The cormorant spends most time horizontally; on the surface of the water, swimming along the seabed and flying. Variations of the orientation depict less frequent diving and flying patterns.*

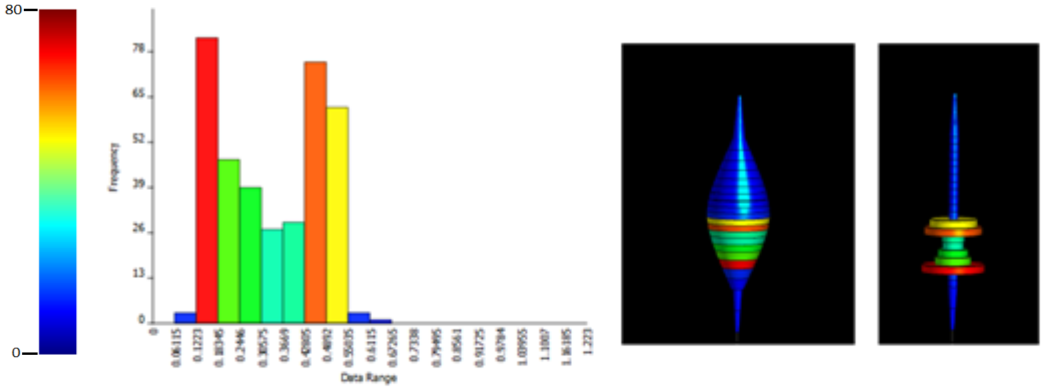


Fig. S4 *– Left to right: Histogram, Frequency shape (stacked), fixed shape (skittle). Note the bimodality apparent in the frequency distributions (second left and far right images), which may correspond to different behaviours.*

Changing shapes for frequency distributions

(a) Fixed shape (Skittle)
Firstly, a fixed shape spine derived from spinning tops using a Hermite spline[9] creates a smooth curve. The start and end points of the spline are fixed at the respective top and bottom centre of the spine, with control points leading orthogonally outwards at a radius defined by the facet frequency. The resulting spline is revolved through 360 degrees around the spine axis to create a skittle like object. The skittle is split into segments defined by the number of bins, with each segment colour coded accordingly to the histogram size as per the corresponding bin (Fig. 5 (top)).

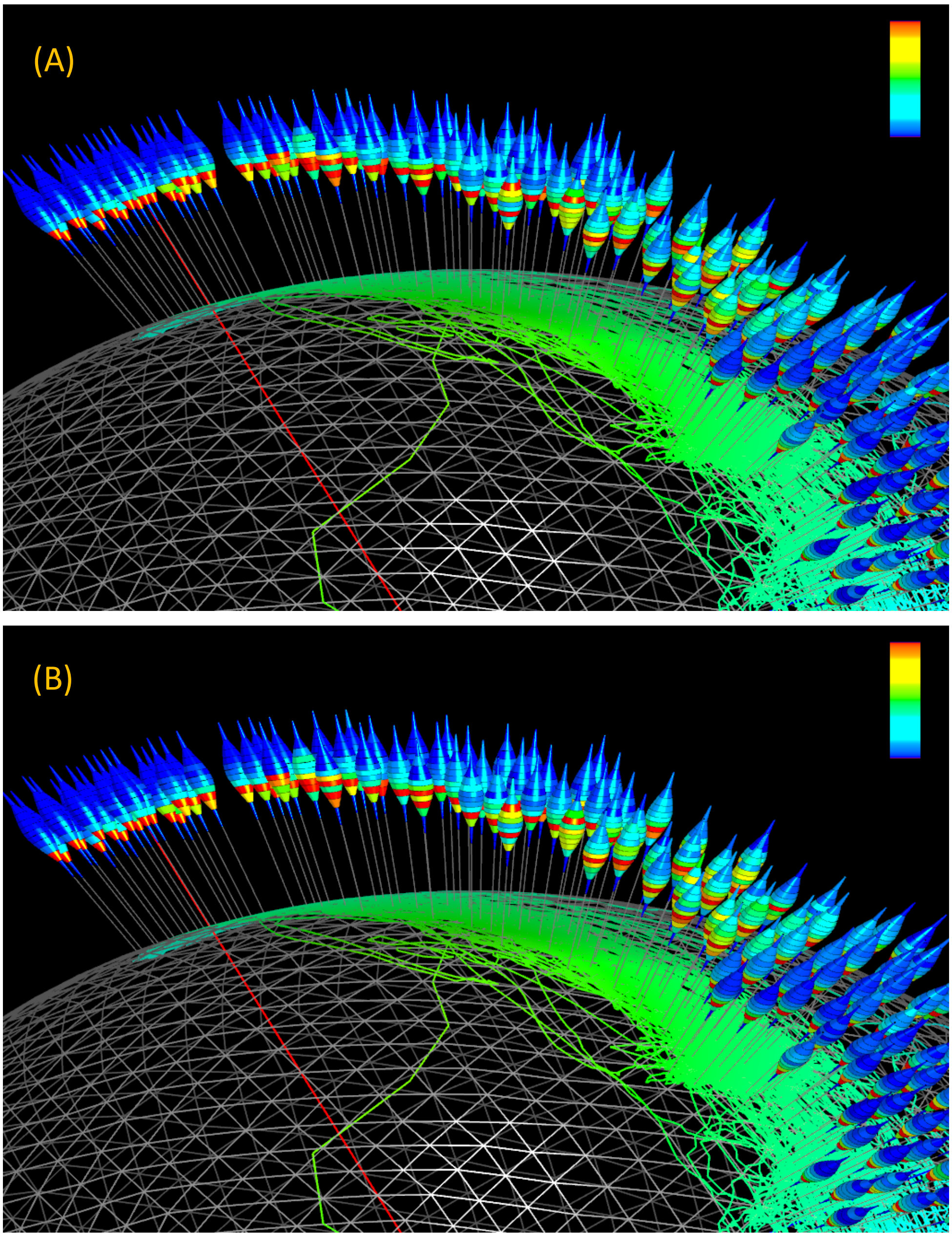


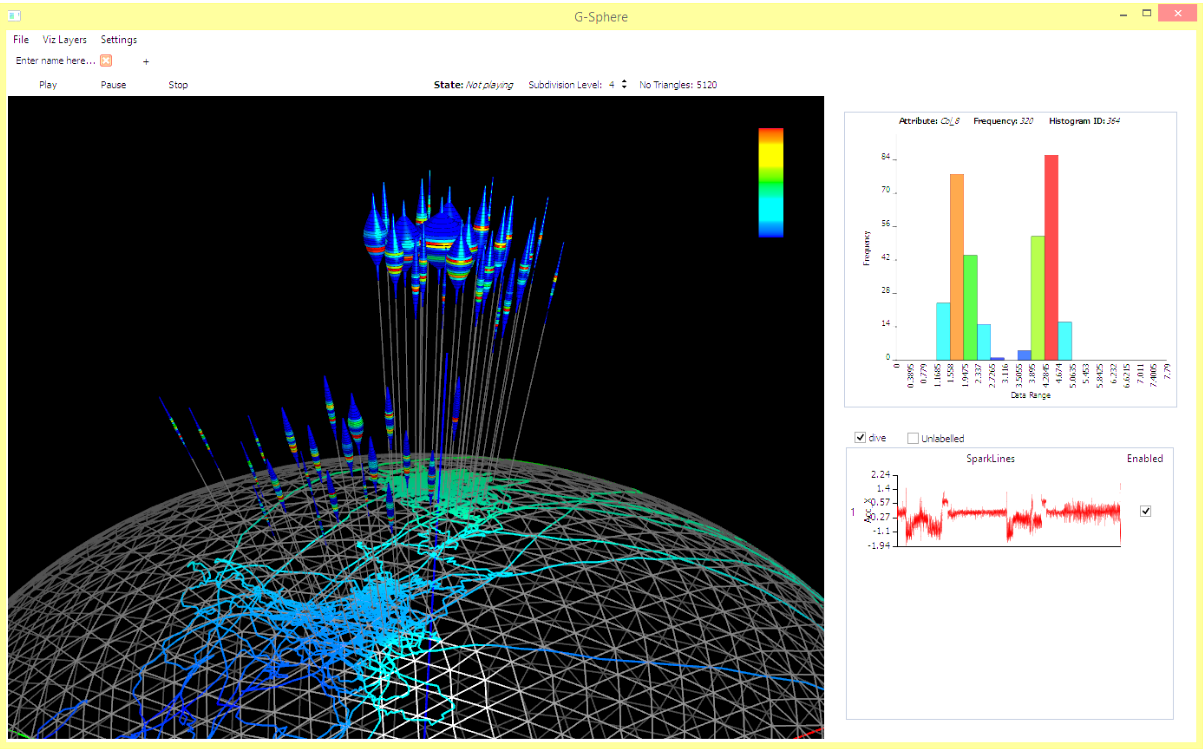
Fig. S5 *– G-Urchin of skittle shape* ***(A)****, and stacked frequency* ***(B)*** *urchins emitted from the centre of each facet of the sphere. Each urchin represents the underlying data within the corresponding facet. The size of each histogram bin is colour-coded accordingly.*

(b) Frequency shape (Stacked)

Another option is to treat each bin in the histogram as a cylinder, with a fixed height corresponding to bin width, but for which the diameter corresponds to the number, or percentage, of elements inside the corresponding bin. Each cylinder is stacked and the resulting height and width scaled by item frequency which is then colour-coded appropriately. The resulting visualisation allows the incorporation of power usage and behavioural state together in one visualisation. For example, a highly energetic state will be presented as a large cylinder or red highlight near the top of the urchin (Fig. S5 (bottom)).

User interface

The g-sphere user interface is built into Framework4 and made accessible via the tools menu. Framework4 uses a multi-tab interface to allow multiple data sets to be loaded and labelled in the software. The g-sphere operates on the data sets and associated classified behaviours. The g-sphere also uses a multi-tab interface for the same purpose and creates multiple g-spheres from different data, attributes, and operations. Upon creation of a g-sphere, a new tab is created which is named by the user for later reference throughout the software. Each tab represents a separate interface specific for interacting with the corresponding g-sphere. The interface (Fig. S6) is split into three components. At the centre is the g-sphere visualisation panel, with which the user can interact by rotating, moving, and scaling to zoom in and out. In the top right, the histogram panel shows an individual instance of a histogram in two-dimensions when a histogram or urchin is double clicked. In the bottom right of the display, the details of the g-sphere are shown. For a data g-sphere, the behaviour classification grouping for the data are shown. Here, the user can select which behaviours to visualise in the g-sphere, which updates the visualisation instantly.



State: *Not playing* Subdivision Level: 4 No Triangles: 5120

Attribute: *Col_8* Frequency: *320* Histogram ID: *364*

☑ dive ☐ Unlabelled

Fig. S6 *– Overview of the user interface. Top – Toolbar for constructing a new G-Sphere. Left – Visualisation panel of the G-Sphere. Top Right – Histogram view of a selected g-*

urchin in the visualisation panel. Bottom Right – Interface to select specific behaviours and data subsets to utilise in the visualisation.

Menu options allow the user to enable and disable each visualisation technique, along with a settings panel to interact with the visualisations, change bin size and attributes throughout as specified previously. A playback function allows the user to playback the visualisation over time to see how the visualisation evolves. Finally, the user can save the g-sphere workspace and load it back in the work panel at any later date.

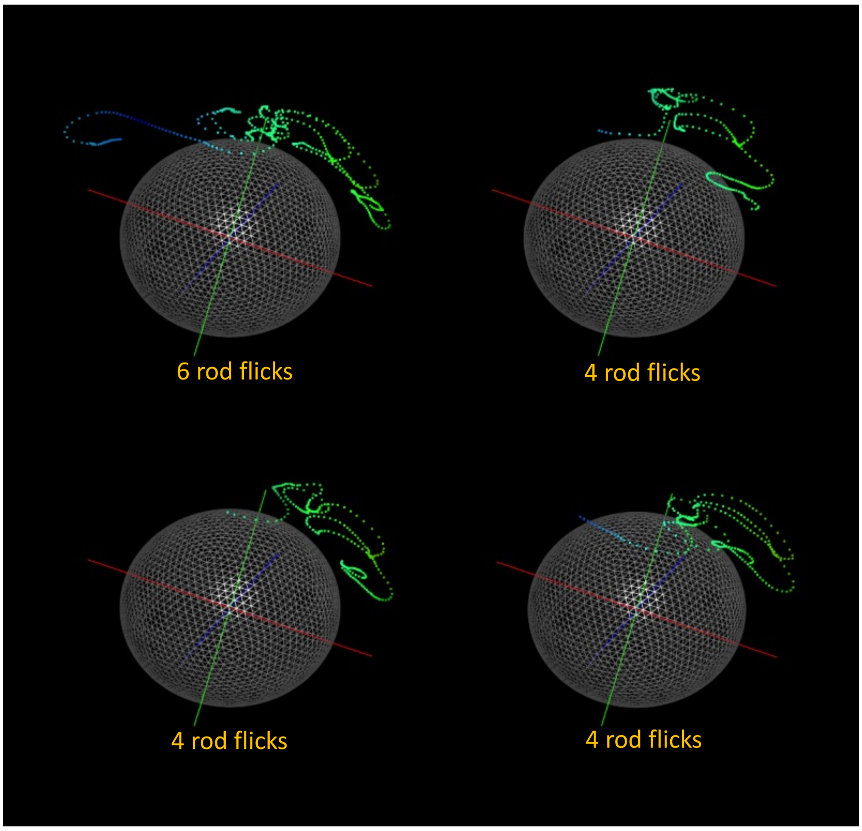


Fig. S7 *– G-spheres showing periods when an angler was flicking a rod back and forth in preparation for the final cast during fly-fishing with a tri-axial accelerometer attached to the base of the rod. In this case, the radial distance of the points from the sphere was set to be manifest by the vectorial sum of the smoothed acceleration values. During a full casting sequence, the rod is typically flicked backwards and forwards a number of times before the final cast. The cases above show one session consisting of 6 flicks before the final cast and three different sessions, each of 4 flicks before the final cast. Note the differences between sequences, both in the number of flicks and in the variation around the 4-flick casts. Points are separated by 0.025 s.*

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