

Research article

## Multi-sensor biologgers and innovative training allow data collection with high conservation and welfare value in zoos

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**Abstract**

Zoos are valuable resources for research, allowing scientists to observe rare and elusive species. Animal-attached loggers (biologgers) offer profound insight into animal behaviour. Their use in zoos has great yet largely untapped potential to collect data relevant for wild animal research and conservation, and zoo animal welfare and enrichment monitoring. However, affixing biologgers to study animals can be problematic in captive settings, limiting their use for species such as large carnivores which ordinarily must be sedated for device fitting. Two yearling female Endangered African wild dogs *Lycaon pictus* were fitted with tri-axial accelerometer and magnetometer loggers while sedated in preparation for translocation from London to Whipsnade Zoo, with data collected for 10–26 hours until collar detachment. Two adult males at London Zoo were trained to accept collars in a modified crate in exchange for food—which removed the need for sedation—with data collected for 28 days. Biologger data detected fine-scale individual differences in recovery from sedation as well as within- and between-individual variation in activity patterns in relation to feeding regimes. The vectorial dynamic body acceleration metric, a proxy for movement-related energy expenditure, shows that daily energy expenditure was higher on days with partial pony carcass feeds compared to rabbit feeds but varied considerably between days where flesh pieces were fed with tongs. The dead-reckoning method allowed visualisation and quantification of fine-scale (1 Hz locations) movement paths within indoor and outdoor enclosures, and space use differences between individuals and over time. Combining multi-sensor biologgers with training captive animals to accept collars without the use of anaesthetic can enable flexible, experimental approaches to data collection with minimal impact on study animals, providing novel understanding of relevance for both zoo and wild animals.

**Introduction**

Biologgging, i.e. data collection of multiple variables using animal-attached tags, has seen considerable technological advancement in recent years (Ropert-Coudert and Wilson 2005; Williams et al. 2020; Wilmers et al. 2015). Modern biologgers such as Daily Diaries (DDs; Wildbytes Ltd., Swansea University, UK) can collect fine-scale data at sub-second intervals, recording acceleration and compass data as well as ambient temperature, pressure and light levels (Williams et al. 2020; Wilson et al. 2008). This level of detail allows insight into

animal activity and behaviour patterns, movements and space use, and individual state from the logger outputs (Wilson et al. 2018). Loggers such as DDs are typically used to investigate the behaviour of wild animals that cannot easily be observed (Brown et al. 2013) but also hold considerable potential in improving livestock management practices (Barker et al. 2018; Vázquez Diosdado et al. 2018) and optimising animal welfare in captive environments (Shorter et al. 2017). Understanding the behaviour of animals in human care can ensure effective welfare measures are in place under the reduction, refinement and replacement framework (3Rs; Flecknell 2002; Russell and

Burch 1959), particularly regarding refinement. Note that while the 3Rs framework was initially developed for laboratory animal experiments, the framework is increasingly being applied to other contexts. There are mounting calls to consider this framework for wildlife, particularly in studies which manipulate animals such as those involving trapping and tagging (Caravaggi et al. 2021; Field et al. 2019). Logging data from captive animals can also aid behavioural interpretation of data from wild animals (English 2018; Ladds et al. 2018; Rast et al. 2020; Studd et al. 2019; Williams et al. 2014), allowing refinements to data collection and analysis before logger deployment on wild animals.

Zoos can benefit from logged data collected on their animals to examine behaviour and improve enclosure design, enrichment activities and feeding schedules to create more stimulating environments for zoo animals (Bassett and Buchanan-Smith 2007; Mason et al. 2007). In particular, space use by captive animals is a potential indicator of enclosure appropriateness with implications for welfare (Hunter et al. 2014). Providing sufficient space for captive animals has knock-on effects for social interactions and stress experienced in shared enclosures (Greggor et al. 2018), as enclosures with more usable space facilitate exploratory movement and social companion choice (Browning and Maple 2019). This also affects reproductive success, which is particularly important in the captive management of endangered species (Carlstead and Shepherdson 1994; Morgan and Tromborg 2007). Stereotypic behaviours and high infant mortality rates in captive carnivores are often more prevalent in wide-ranging species (Clubb and Mason 2007). As accelerometers and magnetometers record the necessary information to derive estimates for both heading (Han and Wang 2011) and speed (Bidder et al. 2012), the movement path of an animal fitted with these sensors can be reconstructed at a very fine scale, both indoors and outdoors, in a process known as dead-reckoning (Bidder et al. 2015; Gunner et al. 2021; Wilson and Wilson 1988; Wilson et al. 1991). This could provide specific, useful data with which to evaluate enclosure use and housing conditions of zoo animals, for example by detecting pacing, a common food anticipatory activity in captive carnivores (Bassett and Buchanan-Smith 2007).

Although behavioural information can be collected unobtrusively in zoos with relative ease by simple observation, this approach is generally limited to zoo opening hours. This largely precludes the collection of nocturnal behaviour, as well as failing to collect data without the presence of a human observer. Closed-circuit television (CCTV) recordings can be used to fill in some of these knowledge gaps (Ferguson and Turner 2013; Walsh 2017), but these also have limitations, including missing data when the study animals are out of sight of the cameras and the extent to which environmental factors (such as snow and rain) may affect film quality (Hall and Roshier 2016).

Some of the advantages of biologgers in a zoo environment are, however, seemingly negated by problems—both ethical and technical (Hawkins 2004; Minter and Collins 2013)—of the animal capture and sedation process. Against this, biologging data, e.g. from accelerometers and magnetometers, has the potential to reveal and quantify even fine-scale individual differences in recovery from sedation. Capture and sedation is not always necessary because crate-training allows zoo-keepers to interact safely with zoo-housed animals without the use of sedation (AZA Canid TAG 2012; Phillips et al. 1998). Crate-training has successfully been used to collect blood samples from nyala *Tragelaphus angasii* (Grandin et al. 1995), treat wounds and collect milk from bongo *Tragelaphus eurycerus* (Phillips et al. 1998) and transport marabou storks *Leptoptilos crumeniferus* (Miller and King 2013). It is standard practice for large canids to be familiarised with crates prior to translocation (Rodden et al. 2012) and crate-training has been used to detect pregnancy in

maned wolves *Chrysocyon brachyurus* (Aitken-Palmer et al. 2017). As well as being key to captive animal transportation (Linhart et al. 2008) and veterinary interventions (Phillips et al. 1998), training exercises can provide additional opportunities for behavioural stimulation and enrichment (Savastano et al. 2003; Szokalski et al. 2012; Westlund 2014). Crate-training may therefore provide a safe method for deploying collars with loggers on carnivores while ensuring zoo-keeper safety, avoiding unnecessary sedation of animals and providing a source of enrichment.

Here, a methodological case study is provided to showcase the opportunities and potential for zoos from combining innovative training and the use of multi-sensor biologgers for data collection with high conservation as well as animal welfare value. Data are reported from fitting DD-equipped collars (Wilson et al. 2008) to four captive African wild dogs *Lycaon pictus* in London and Whipsnade zoos. African wild dogs are the second most endangered canid species in Africa, with an estimated wild population of 6,600 individuals (Woodroffe and Sillero-Zubiri 2012). Having experienced a range contraction of 93% (Wolf and Ripple 2017), captive studies have a potentially significant role to play in the conservation of this species. Furthermore, African wild dogs have an average pack territory size of ~500 km<sup>2</sup> (Gorman et al. 1998), potentially leaving them at higher risk of developing stereotypic behaviours in captivity (Hunter et al. 2014). Previous attempts to assess the efficacy of wild dog enrichments have focused on zoo-keeper surveys rather than quantitatively assessing variation in activity between days with and without enrichment, and on days with different enrichment types (Cloutier and Packard 2014). DDs can effectively quantify changes in activity levels and prevalence of stereotypic behaviours (such as pacing) resulting from enrichment and allow assessment of enclosure use. Fitting captive members of a species with loggers also facilitates the construction of preliminary logger-based ethograms (Rast et al. 2020; Williams et al. 2014). This can inform studies deploying this technology in the wild, allowing more accurate behavioural interpretation even when in-person observations are not possible, thus benefiting conservation research.

This paper outlines how captive African wild dogs were successfully trained for collar deployment and retrieval, while providing example applications of biologging collars in zoos. Using wild dog data from these two zoos, this study: (i) compares procedures for collar fitting with and without sedation, outlining for the latter a process for collaring captive African wild dogs through crate-training, (ii) assesses post-sedation recovery, and enclosure use and activity patterns in relation to feeding regimes and (iii) determines fine-scale movements and space use within enclosures through dead-reckoning. These analyses were chosen due to zoo staff interest in sedation recovery and activity in response to feeding and the value of the zoo context for refining dead-reckoning analysis in known, enclosed areas. A descriptive overview of sedation recovery in two individuals is provided for adaptation in other contexts with larger datasets. Activity level changes due to prolonged interaction with food items on days with pony or rabbit carcass feeds are assessed and use of dead-reckoning to generate highly resolved movement paths is demonstrated.

## Materials and methods

### Ethics statement

Ethical approval was obtained for this study from Swansea University under the approval codes STU\_BIOL\_29066\_280817112012\_2 and SU-Ethics-Student-180917/2, and the AWERB approval code IP-1617-8. The Zoological Society of London approved the work under the reference code ZDZ78.

### Collar fitting strategies: Sedation and crate-training

Captive African wild dog collar deployments began following a series of initial trials on domestic dogs *Canis lupus familiaris*, conducted to test and improve collar design and formulate biologging data analysis procedures. On 27 March 2017, two collars equipped with a DD multi-sensor biologging tag (details below) and an automated drop-off mechanism, designed and constructed in Swansea University, were deployed on two female African wild dogs being moved from London to Whipsnade Zoo. These individuals weighed 29 and 30 kg respectively and were part of a pack of five female litter-mate yearlings. The collars were attached to the wild dogs whilst sedated by London Zoo veterinarians. These individuals were sedated so they could be placed in crates for transport via truck from London to Whipsnade Zoo and were not sedated explicitly to fit the collars.

Next, two adult males in London Zoo were trained to accept collars without being sedated over a period of 12 weeks from April to July 2017. These individuals were the oldest from a pack of eight, and responded better to training than the other pack members who were litter-mate yearlings. Both males weighed >30 kg. All pack members were born in captivity. Collars were designed in conjunction with ongoing behavioural training performed by London Zoo staff, and the final design was approved by zoo-keepers, a veterinarian and an animal behaviour expert in London Zoo before deployment. A modified crate was made in London Zoo, featuring a weighing platform as its base and an end slat with a hole where the head could fit through to rest on a wooden platform, surrounded by a wire mesh (Figure 1). First, the chosen individuals were familiarised with the crate, located in the indoor section of the enclosure. It was left in this position to allow free entry for wild dogs at any time they had indoor access. A food reward (i.e. meat pieces, typically horse meat) was given when a wild dog touched a metal rod used in contact training (Figure 1). This reward was dispensed via metal tongs to ensure the zoo-keeper was not at risk of being bitten. A leather strap of the same material used to make the collars was hooked over the top of the hole and screwed into the sides of the platform. This allowed each wild dog space to fit their head through, while familiarising them with the feeling of the leather strap. Further training took place to familiarise the wild dogs with neck contact, using rope as this was a familiar and durable material. This was swapped for a noose when the wild dogs repeatedly took the rope into the enclosure. The noose facilitated approximate measurements of neck circumference per individual with a tape measure and collar deployment.

The London Zoo enclosure consisted of two paddocks, affording a combined space of 1,852.76 m<sup>2</sup>. The larger paddock was 98.75 m × 14.5 m while the smaller paddock was 28.5 m × 14.5 m. These paddocks could be separated when necessary (e.g. males and females were separated prior to translocation of the female wild dogs to Whipsnade), but remained connected for the duration of London Zoo collar data collection. The indoor section of the enclosure featured three dens, measuring 4.6 × 3.3 m each. All individuals in the pack had access to the full enclosure throughout the study period, including at night. CCTV cameras were set up in the London Zoo enclosure for the duration of collar deployment (Figure 2). A HandyKam© system with seven cameras was used. While efforts were made to include as much of the enclosure in camera range as possible, camera positions were chosen based on zoo-keeper knowledge of wild dog space use. Due to the wild dogs' unique coat patterns, it was possible to distinguish individuals consistently from the video footage. Times were recorded to the second by the CCTV system and noted during behavioural observations. All times for cameras, behavioural observations and collar calibrations were standardised using the website time.is. This allowed matching of behavioural observations to

collar outputs using the visualisation and analysis software Daily Diary Multiple Trace (DDMT; Wildbyte Technologies <http://www.wildbytetechnologies.com/>).

Throughout the study period, the wild dogs were fed according to their normal feeding schedule, with daily feeds consisting of either a partial pony carcass (twice a week), whole rabbit carcasses (once a week) or 1 kg of meat pieces administered by tongs (four times a week). The study period for the two London Zoo wild dogs consisted of 14 days during which wild dogs received meat pieces via tongs (typically horse, 1 kg per individual), 8 days where a partial pony carcass was shared amongst the pack and 4 days where each wild dog received a rabbit carcass. Crate training continued during the period in which collars were worn. Collars were removed through use of the collar's quick-release buckle while the wild dogs were in the crate receiving their food reward.

### Collar design

For the Whipsnade Zoo deployment, standard leather dog collars were cut and sewn back together with nylon string. They featured a DD, with tri-axial accelerometers and magnetometers and environmental sensors (Wilson et al. 2008), and a drop-off mechanism governed by the DD turning on a separate battery connected to a burn resistor and double nylon line (60 kg resistance), and a battery for each component. The DD was powered by two 2/3 A Lithium batteries and the burn resistor was powered by a 100 mAh 3.7 V Lipo rechargeable battery. The DD was programmed to trigger the drop-off at a set time by passing high current through the resistor, which then became hot, causing the nylon line used to sew the collar to melt and sever, allowing the collar to drop. All components were contained in a robust 3D-printed nylon housing attached to a leather strap. This was adjusted to a suitable circumference, as determined by zoo veterinary staff, closed with a standard clasp and excess material was cut.

The London Zoo collars were made using leather belt blanks with a thickness of 4 mm and width of 28 mm (Figure 1). A quick release clasp with a breaking load of 200 kg (Pets Bits Online, UK) was chosen so that collars could be snapped on, and later released, in one swift motion. The collars were not adjustable, due to concerns that a pack mate might manipulate a looped collar, making it too tight on the neck. Conversely, if a collar was pulled loose, there was potential risk of a forelimb getting caught. The collars were initially riveted on one side only, so that adjustments could be made to get the best fit for both individuals. After zoo-keepers had adjusted the other side appropriately to fit the neck of the animals, collars were sent back to Swansea University to complete riveting and attach the logger housing. The housing was attached to sit at the ventral side of the neck so that the collar was bottom-weighted to reduce the incidence of collar roll, which affects accelerometer and magnetometer data. A supplementary training collar was provided while final adjustments were made. This allowed zoo-keepers to maintain regular training as collar manufacture was completed. Training took place four days a week, from Tuesday to Friday inclusive, over a four-month training period. The training collar had a housing attached, containing two batteries and a DD, so that the weight would match that of the collars for deployment. The final weight of the collars, including all parts, was 258 g, approximately 0.86% of the wild dogs' body mass and thus well below the 3% rule in accordance with standard welfare guidelines (Kenward 2000) and with collar size and weight conforming with recommendations for high quality biologging data (Dickinson et al. 2020).

Housing units were designed in Swansea University, with space for two A batteries and a DD. Data were stored on 2 GB micro SD cards within the DDs. Two SAFT (Levallois-Perret, France) 2/3 A Lithium batteries connected by diodes were used to power

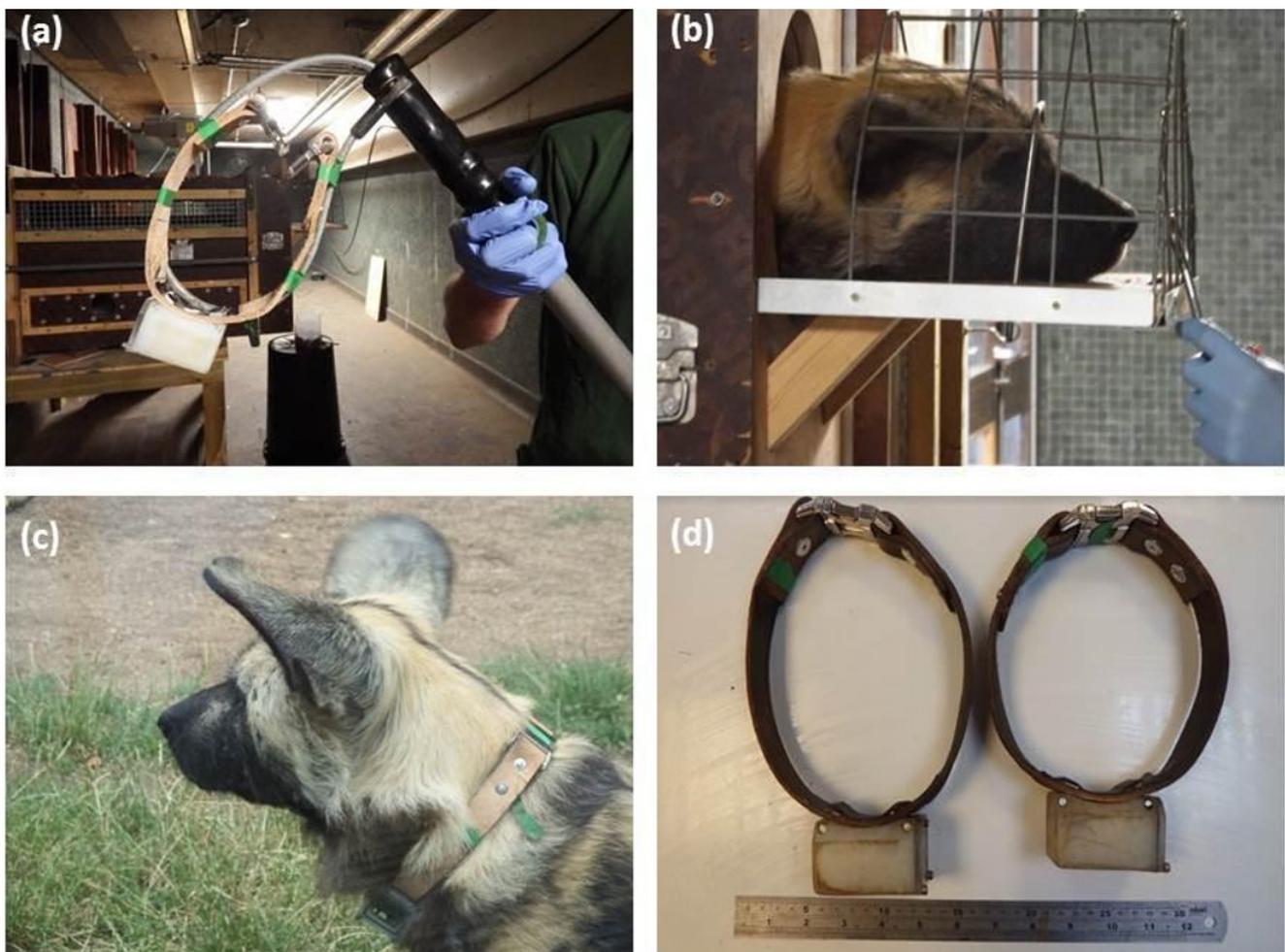
the DD. These housings and loggers were used for both the Whipsnade and London deployments. However, as the drop-off mechanism was not robust enough to withstand wear by wild dogs (see Results), the collars for use in London Zoo did not feature a drop-off mechanism. The protective nylon housing for the DD and batteries was attached with countersunk screws and taped over with Tesa® tape to ensure no irritation to the neck. The DD was set to record acceleration at 40 Hz, magnetometry at 16 Hz and environmental data at 4 Hz for one individual in London Zoo; data from the other three wild dogs were recorded at 20 Hz, 8 Hz and 2 Hz by the respective sensors. This decision was taken following consideration of the advantages and disadvantages of sampling rate on data value and information content, in relation to power requirements and battery size (English 2018). DD start time was noted to the second using the website [time.is](https://www.time.is/) to later define a start time in the logged data. Upon collar switch on, collars were immediately calibrated using a series of distinct motions. These set motions were easily distinguishable in the logged data and the start and end points of each motion were noted to the second, confirming that timing was accurate. Behavioural observations and video footage were also timed using [time.is](https://www.time.is/) for consistency.

#### Data interpretation

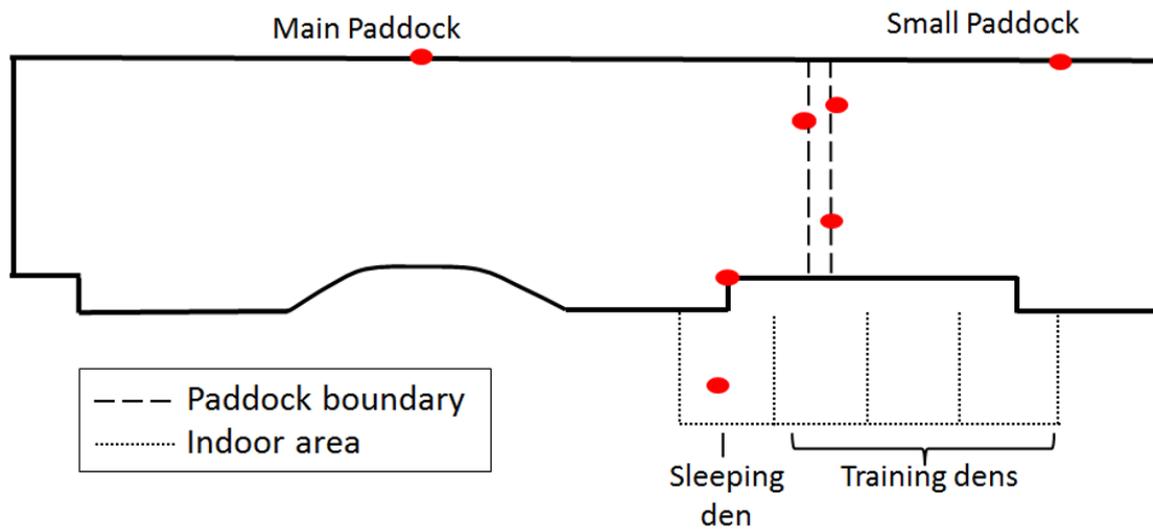
Upon collar retrieval, DD data were inspected using the complementary data visualisation software DDMT (Wildbyte Technologies Ltd., UK; available from <https://github.com/DDMT->

Software/DDMT). The data were calibrated to perform soft and hard iron corrections to the magnetometry channels (Bidder et al. 2015; Gunner et al. 2021), accounting for any interference in magnetic data caused by metal on the collars themselves. Three-dimensional m-sphere visualisations (Williams et al. 2017) were used to inspect the data before and after corrections to confirm that magnetometry data had been corrected adequately to account for potential interference from metal enclosure fences.

Data were time-matched to concurrent behavioural observations for interpretation. Traces from the sedation recovery period for the two wild dogs moved to Whipsnade Zoo were visually inspected in DDMT. The time period from wild dogs being placed in their transport crates (i.e. the time point at which all manipulation including placement in crates had finished) until they were fully alert was considered. Longer consideration of micro-movements once alert was not possible due to subsequent transport to Whipsnade Zoo. As well as graphing raw sensor data, DDMT computes a range of metrics calculated from acceleration and magnetometry data, including vectorial dynamic body acceleration (VeDBA; Wilson et al. 2008, 2020). VeDBA is a reliable proxy for movement-related energy expenditure (Wilson et al. 2020) and speed (Bidder et al. 2012). It was used to examine activity patterns and space use via dead-reckoning (see below) over 12-hour active periods, from approximately 0600–1800, for the London Zoo data. This period was chosen to correspond with the daily active period of the wild dogs, as determined from



**Figure 1.** (a) The collar was attached to a nose with weak tape prior to deployment. (b) African wild dog in an early training session. (c) An African wild dog wearing the deployed collar. (d) Collars after retrieval.



**Figure 2.** A schematic of the London Zoo African wild dog enclosure indicating the position of CCTV cameras in red. These cameras were used to extract longitude and latitude coordinates to correct the dead-reckoned tracks.

visual inspection of biologging traces in DDMT and CCTV footage. For the Whipsnade Zoo data, tracks were reconstructed over approximately two-hour periods for both wild dogs upon arrival in a small outdoor enclosure and indoor house, and for the initial exploration of the main outdoor enclosure for one individual the following day.

#### Statistical analyses

The R Environment for Statistical Computing was used for statistical analyses (version 4.0.0; R Core Team 2020). Logger data were first visualised and the relevant sections extracted using DDMT. All figures were plotted using ggplot2 (Wickham 2016) and dead-reckoned tracks were mapped using ggmap (Kahle and Wickham 2013). Segmented regression was used to determine the start and end points of rapid awakening from sedation using the segmented R package. Total daily activity levels in response to food received were tested for significance through non-parametric permutation testing for linear models with the lmPerm package (Wheeler and Torchiano 2016). Permutation testing with lmPerm package ran for 5,000 iterations. Significance asterisks were plotted with the R package ggsignif (Ahlmann-Eltze and Patil 2021).

VeDBA derived from the acceleration data and heading values derived from the acceleration and magnetometry data were used to reconstruct fine-scale animal movement paths, in a process termed dead-reckoning (Bidder et al. 2015; Wilson and Wilson 1988). Accumulation of errors along successive dead-reckoned location estimates can cause dead-reckoned paths to drift from true positions unless corrected using ground-truthed location data collected at a coarser temporal scale (Bidder et al. 2015). To correct for this, location data were obtained by searching through CCTV footage and finding the longitude and latitude coordinates of known enclosure landmarks with Google Earth. These verified locations were used to correct the dead-reckoned tracks (Gunner et al. 2021). As dead-reckoning allows path reconstruction with location data supplied at flexible, irregular time intervals, the time periods between coordinates were not equal. VeDBA and heading data were smoothed to 1 Hz to minimise accumulated error in dead-reckoned tracks and reduce computational power requirements, then exported from DDMT to compute dead-reckoned tracks in

R, including location-based error correction, following methods outlined in Gunner et al. (2021). Briefly, location-based error correction involves providing time-stamped verified locations for the dead-reckoned path to pass through, to prevent the path drifting as errors are accumulated over time (typically verified locations may come from additional sensors such as GPS units, but here the camera-extracted locations performed the same role). Walking, trotting and running behaviours were identified in DDMT using a Boolean time series approach (English 2018; Wilson et al. 2018). Data from a two-hour observation session at Whipsnade Zoo were used to match behavioural observations to DD outputs. Separate CSV files were created whereby each file represented repeated bouts of a single gait. These files were used in classification tree analyses in R using the packages rpart (Therneau et al. 2022) and tree (Ripley 2005) to determine which sensor outputs were most appropriate for classifying movement gaits. Approximate value ranges for these metrics were identified, corresponding to discrete behaviours. These value ranges were used as initial guidelines to assist manual development of rules for the DDMT Behaviour Builder, aided by further visual inspection in DDMT so that all occurrences of individual behaviours could be classified within a given range or dataset. Following this procedure, only data associated with walking, trotting and running bouts were exported for the calculation of dead-reckoned tracks. This avoided the path being affected by non-movement behaviours, as initial inspection indicated that frequent lifting and lowering of the head while resting could affect the path if not excluded. Instances of collar roll were rare but easily detected through visual inspection in DDMT due to changes in axes positions. These were removed from the subset of data exported to create dead-reckoned tracks. For Whipsnade Zoo, dead-reckoned tracks were reconstructed following arrival of the wild dogs in their new enclosure to capture initial exploratory behaviour. For the London Zoo wild dogs dead-reckoned tracks were created over 12-hour time periods, from approximately 0600–1800, corresponding with days where different food types were provided. As with VeDBA data extraction, these times were chosen to correspond with the activity patterns of the wild dogs. The sleeping den was the start and end location for all tracks (Figure 2).

## Results

### Collar deployment via sedation versus crate-training

The resistor-powered drop-off mechanism was not robust enough to withstand the high activity levels and social manipulation of collars exhibited by African wild dogs. The first collar dropped off after 10 hours (1,749,880 acceleration events collected at 20 Hz) and the second after 26 hours (2,307,400 events at 20 Hz)—significantly shorter than the planned three weeks of data collection. The non-drop-off collars with a quick-release clasp deployed in London Zoo collected data for the full planned four-week collar deployment period and were both deployed and retrieved without complications. These collars were deployed on 13 July 2017 and recorded until 9 August 2017, providing approximately 1,344 hours of data, 672 hr per individual (93,246,120 acceleration events at 40 Hz and 46,908,828 at 20 Hz respectively). Collared wild dogs were monitored to ensure the collars did not attract negative attention from conspecifics. Particular care was taken to observe and film the wild dogs following initial collar fitting, but no collar-directed aggression was observed, apart from initial inspections by pack members upon arrival in Whipsnade Zoo.

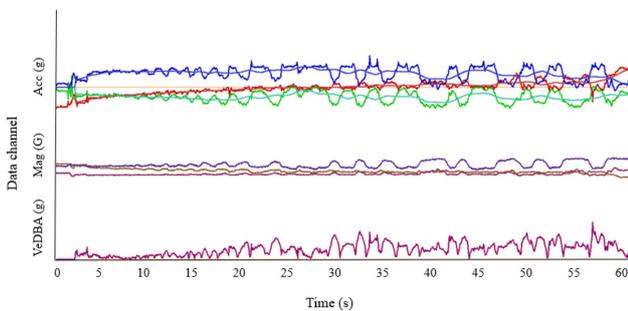
Awakening after sedation showed similar VeDBA traces for both sedated wild dogs. The acceleration and VeDBA traces for the first minute after waking up for each individual show distinctive shallow and repetitive waveforms, suggesting that both individuals were raising and lowering their heads repeatedly

upon awakening, though without otherwise changing posture. The magnetometer traces highlight individual differences in the recovery between the two individuals, with one showing non-overlapping traces (Figure 3a) while the second shows a periodic, repeated crossing of magnetometer channels (Figure 3b), with the latter indicating changes in head orientation. Plots of VeDBA over a ten-minute interval from the moment each sedated individual had been placed in the transport crate and left to recover (Figure 4) show that both individuals ‘woke’ from sedation approximately five minutes after being placed in their crates. The rapid wake-up phase lasted 28.8 seconds for one individual and 50.5 seconds for the other. VeDBA traces stabilised 3 and 3.4 minutes after wake-up respectively for the two wild dogs (Figure 4).

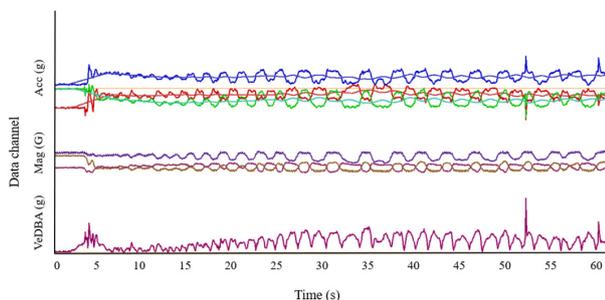
### Activity patterns in relation to feeding regimes

Adjusted P-values were computed with post-hoc pairwise comparisons of food types, which found significant differences between pony carcass and rabbit feeds ( $P=0.039$ ), but not tong and pony carcass feeds ( $P=0.07$ ) or tong and rabbit feeds ( $P=0.666$ ). There were significant differences in daily activity levels, measured by total daily VeDBA, both between individuals ( $P=0.006$ ) and between days where different foods were provided ( $P=0.036$ ). Tong feeds of meat pieces showed the most variation in total daily VeDBA values, with both the lowest and highest activity days corresponding with tong feeding for both individuals (Figure 5). Carcass feeds were associated with higher daily total VeDBA values than rabbit feeds (Figure 5).

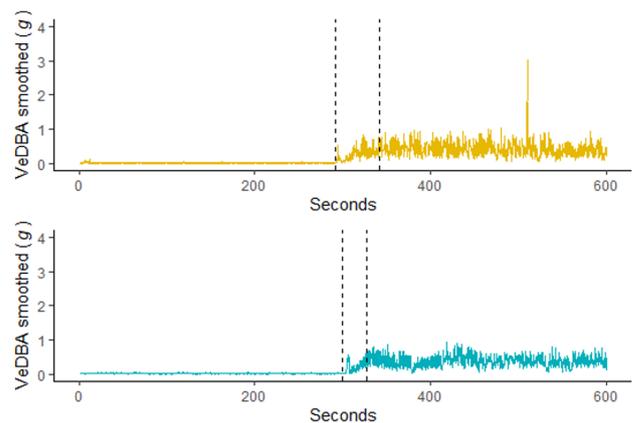
(a)



(b)



**Figure 3.** Acceleration, magnetometry and VeDBA traces from the first minute after waking up from sedation for the two wild dogs moved to Whipsnade Zoo (a) Brandy, (b) BeeBee, respectively. Tri-axial acceleration data were recorded at 20Hz (blue = heave, red = surge, green = sway). Raw acceleration depicts movement, while the smoothed line running through each acceleration axis indicates a lack of postural change. Acceleration data were smoothed at the default rate of 80 events in DDMT.



**Figure 4.** VeDBA over time for 600 s following two African wild dogs, (a) Brandy and (b) BeeBee, being placed into the transport crate following a veterinary check and collar fitting. Both individuals became fully alert after approximately 300 seconds. The dashed lines identify the breakpoints identified by segmented regression analysis, representing the start and end points of the rapid wake-up phase for each individual.

**Enclosure use via dead-reckoning**

Paths were successfully reconstructed encompassing both indoor and outdoor areas of the enclosures and showed no indication of pacing behaviour in any of the study individuals (Figure 6). A dead-reckoned track representing the first exploration of the main outdoor enclosure area in Whipsnade the morning following translocation shows wide coverage of the new enclosure, traveling a cumulative distance of 1,238 m (Figure 7). The dead-reckoning procedure was considered highly accurate as paths approach, but stay within, the confines of the enclosure boundaries.

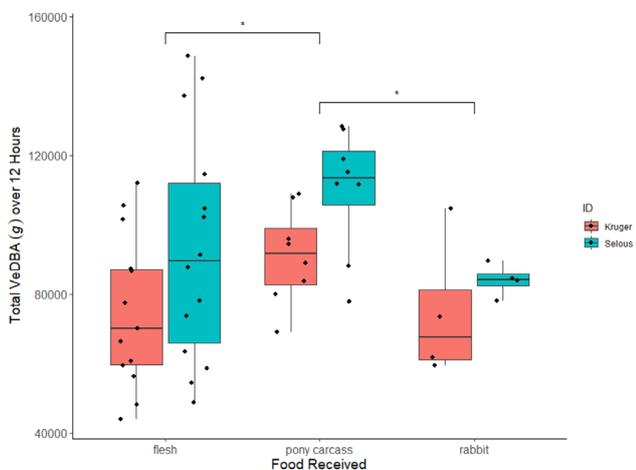
The dead-reckoned tracks shown in Figure 8 were created using 24 longitude and latitude coordinates for location correction which had been extracted from CCTV camera footage. While the overall shape of these paths can be generated with fewer correction locations, this affects the cumulative distance estimates (Figure 9). Visual inspections of carcass feeds showed clustering at the carcass position, but rabbit and meat pieces did not have discernible effects on daily enclosure use (Figure 8). The cumulative distance moved by both individuals was highest for the rabbit feed days, at 466.1 m and 507.4 m respectively, compared to 332.3 m and

296.9 m for carcass feeds and 310.0 m and 249.7 m for tong feeds (Figure 9). The London Zoo dead-reckoned tracks show markedly more restricted movements than the initial enclosure exploration seen in Whipsnade Zoo, as not all areas of the enclosure were visited daily.

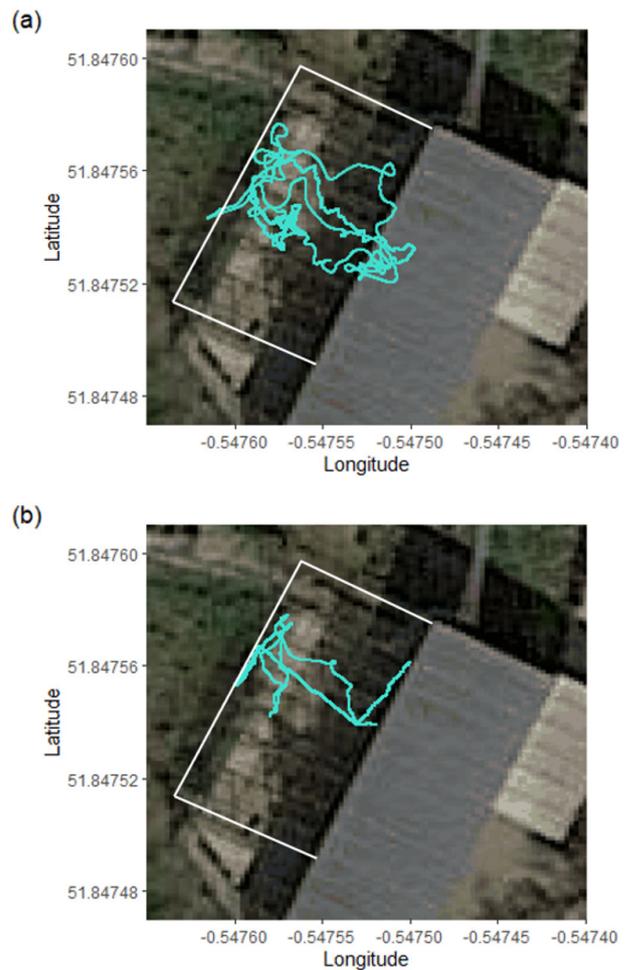
**Discussion**

The potential of biologging in zoo-based research with positive implications for animal welfare is demonstrated using biologging data collected from four wild dogs from two zoos. The resulting data can be used to quantify responses to sedation, activity levels and enclosure use, with potential benefits to captive welfare management decisions and trialling methods to inform studies on wild counterparts.

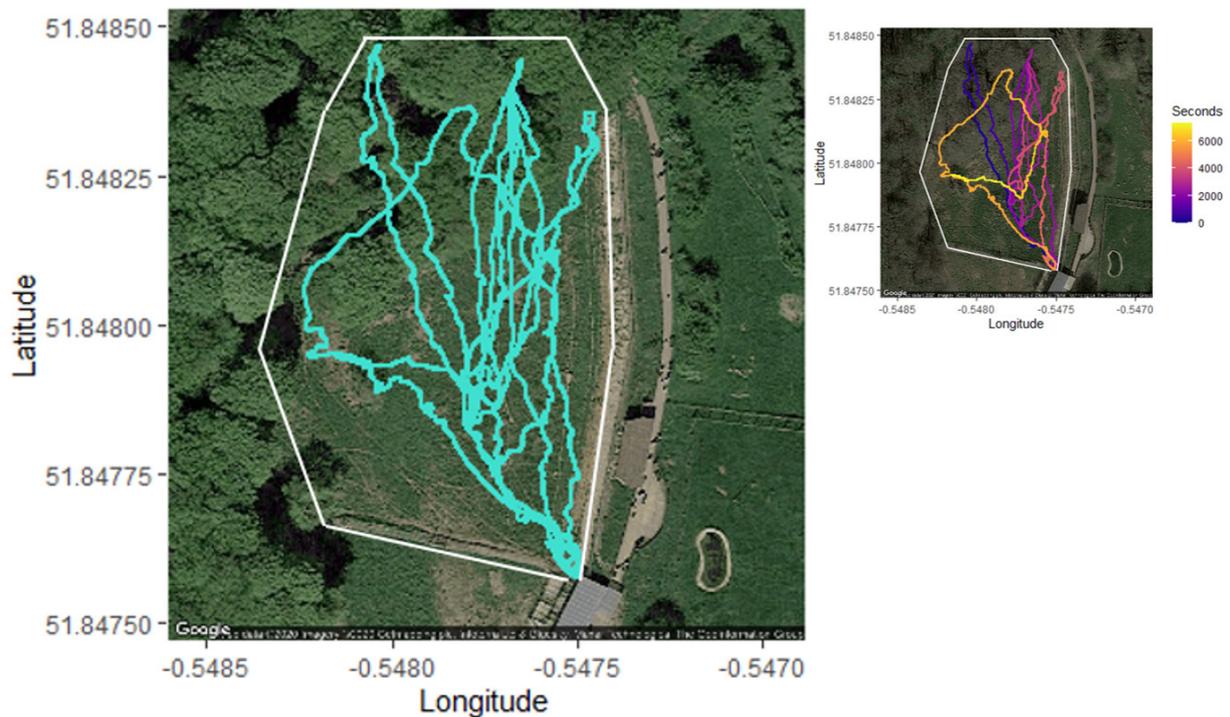
Though the available timeframe for sedation recovery analysis before translocation affected the logger data through crate lifting and transport via truck was short, the data presented here indicate quick recovery times. However, where longer term consideration is possible, VeDBA may be examined over several days post-sedation



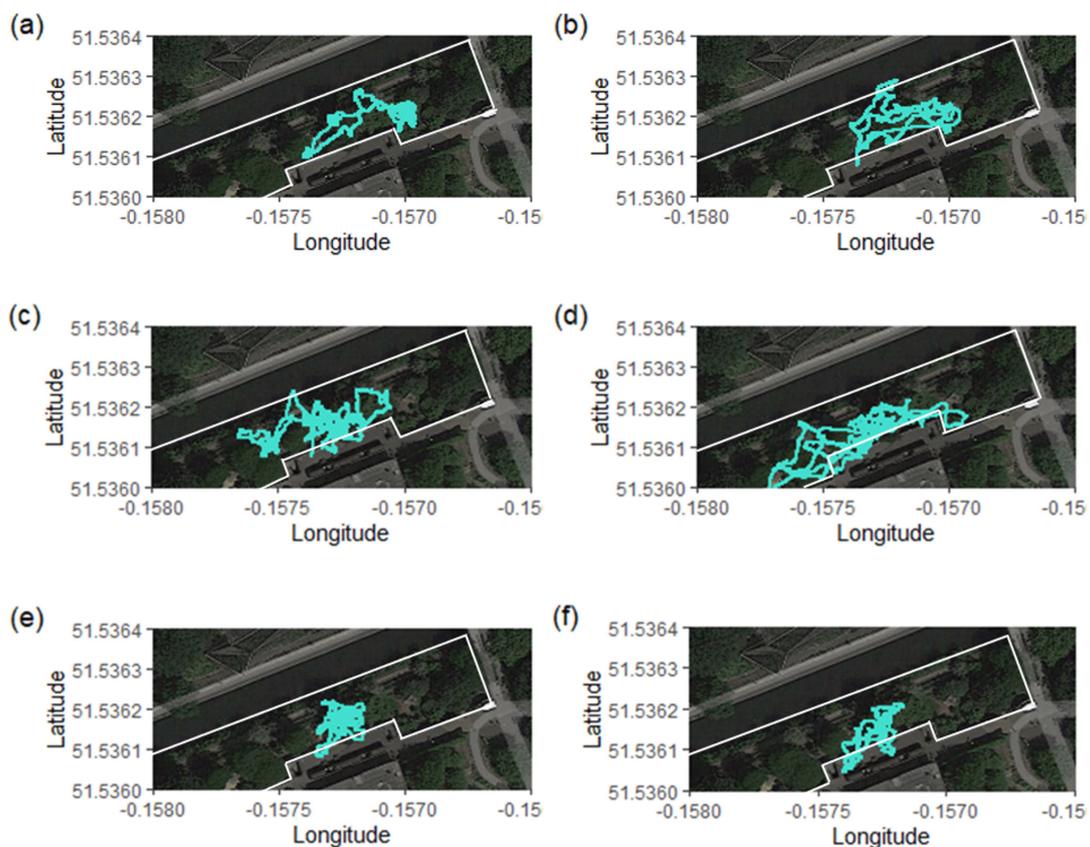
**Figure 5.** Total VeDBA values over a 12-hour period for two individuals in relation to food type received on a given day at 40Hz (Kruger, salmon shading) and 20Hz (Selous, blue shading).



**Figure 6.** Moving in and out of the house to the small outdoor area on the night the wild dogs arrived in Whipsnade (a) Brandy, (b) BeeBee. The tracks relate to the same two-hour period with 6 and 14 longitude and latitude coordinates for correction respectively, taken opportunistically based on confirmed individual presence at a landmark location.



**Figure 7.** A 1 Hz dead-reckoned track obtained from 20Hz Daily Diary data representing the first exploration of a new outdoor enclosure at Whipsnade Zoo by a female African wild dog yearling. 27 longitude and latitude coordinates were used in path correction over the two-hour period. The inset represents the same track coloured by time, moving from darker (blue) to lighter (yellow) colours. The boundaries of the outdoor paddock are marked in white.



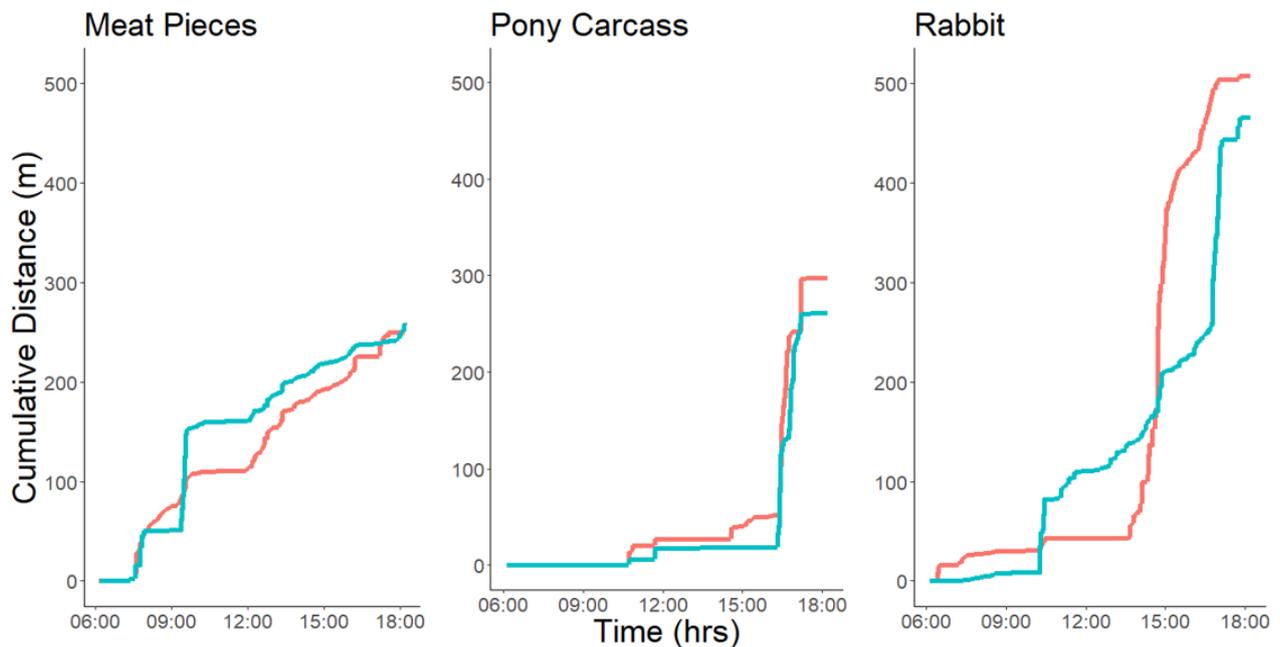
**Figure 8.** Three 12-hour dead-reckoned tracks for each of the two male African wild dogs which were collared in London Zoo, corresponding with different food days. The left column shows data from Selous (20Hz) and the right column shows data from Kruger (40Hz). The upper row shows tracks from a day where a partial pony carcass was fed (15 July 2017), the middle row shows tracks when rabbits were fed (16 July 2017) and the lower row shows tracks from a day where meat pieces were fed via tongs (19 July). Carcass feeds appeared to bias wild dog space-use to where the carcass was deposited in the outdoor enclosure, whereas when meat pieces were tong fed, space-use was biased towards the middle of enclosure, close to the indoor access point, where these feeds took place. All dead-reckoned tracks were produced at 1 Hz. The white lines indicate outdoor enclosure boundaries, though access to underground indoor housing was available to the south as shown in Figure 2.

to assess impacts on activity (Wilson et al. 2019). Nonetheless, here, despite the short timeframe available, VeDBA was useful in examining immediate responses and activity following sedation recovery. The success of the crate-training and the second collar design that followed suggest that future translocations may implement similar training procedures and thus negate the need for sedation prior to transport. Conversely, future cases where sedation is still required for veterinary procedures without translocations would allow individual differences in sedation recovery to be examined over longer time frames. Sedating animals comes with many risks, such as hypothermia, respiratory depression and even mortality in rare cases (Muir and Hubbell 2014; Stegmann 2000). Avoiding anaesthetic in the second deployment allowed collection of valuable data without these risks with the added advantage that training exercises in captive animals provide a source of enrichment (Melfi 2013).

Increased activity levels are often associated with improved captive welfare, but not if the activity stems from stereotypic behaviours (Andrews and Ha 2014; Bashaw et al. 2003): using dead-reckoned tracks allowed this to be investigated in unprecedented detail (see below). Both individuals collared in London Zoo showed higher daily VeDBA values when a partial pony carcass had been fed compared to rabbits but days where meat pieces had been fed showed greatest variability in VeDBA. This could be an artefact of sample size, as meat piece feed days were the most prevalent, occurring four times a week compared to twice a week (partial

pony carcass) and once a week (rabbits). Variety in feeding times and spatial distribution of food items are widely reported to be effective enrichment techniques for captive carnivores (Cummings et al. 2007; Kistler et al. 2009; Shepherdson et al. 1993; Wagman et al. 2018). Feeding in London Zoo occurred at approximately the same time each day during the study period, but the different foods provided were given from different enclosure locations and required different handling behaviours from the wild dogs. Hence, food type variation may play a role in the absence of stereotypies detected from the logger data or CCTV footage. Food items which stimulate natural foraging and food handling behaviours, such as the partial pony carcasses and whole rabbits provided here, can positively stimulate captive carnivore behaviour for several days after being given and may account for the high variability in activity levels on days when meat pieces were fed (Shepherdson et al. 1993; Wagman et al. 2018).

In Whipsnade Zoo, the exploratory behaviour of African wild dogs released into a new enclosure for the first time was quantified. Translocating animals between zoos is crucial for maintaining genetic integrity of species in captive breeding programmes (Lacy 2013). Despite the importance and prevalence of this activity, there is relatively little consideration of the effects of between-zoo translocation in the literature. The preliminary data here depicting space use immediately following a translocation event highlight the use of logging devices as a promising method for understanding post-translocation behaviour of endangered



**Figure 9.** Cumulative distance moved per individual derived from the dead-reckoned data for three days with three different feeding schedules. The meat pieces and pony carcass feed days (which occurred on 19 and 15 July 2017 respectively) shown depict similar distances moved, while the rabbit feed day (16 July 2017) shows larger distance covered. (Kruger data shown in salmon, Selous data shown in blue).

captive species. Future work should consider prolonged logger deployment, with data also collected in the zoo occupied before translocation for comparative purposes where feasible.

'Pacing' is a locomotory stereotypy which typically involves pacing over and back along a fixed route, typically a straight line but sometimes in circles or figures of eight (Clubb and Vickery 2006). This distinctive movement behaviour should form clear patterns in dead-reckoned tracks where it occurs, but no evidence of stereotypic pacing was detected in the African wild dogs in this study. Stereotypies are thought to arise when captive animals cannot conduct their natural behaviours, especially those related to ranging and foraging (Clubb and Mason 2003). While conditions in captivity can never match the large territory sizes of free-roaming African wild dogs, feeding enrichment is feasible and widely implemented (Cloutier and Packard 2014; Packard et al. 2010; Price 2010). Food-related enrichment is thought to be the most effective in reducing or eliminating African wild dog stereotypies (Cloutier and Packard 2014) but positive benefits have been found from adding even short training periods to the care schedules of pacing captive wild dogs (Shyne and Block 2010). The rotation of food type given and incorporation of whole rabbits and partial pony carcass feeds may contribute to the absence of stereotypic pacing. The regular training exercises for collar fitting may also be considered as enrichment (Fernandez et al. 2019; Westlund 2014).

The lower cumulative distance estimates for the London Zoo dead-reckoned tracks are in accordance with the advanced age of both adult males and, though cumulative distance estimates vary with the frequency of location corrections, this study highlights the value of this metric as a relative measure to compare between days. This has wider implications for other studies implementing dead-reckoning methods and may provide guidance for selecting sampling frequency in wild deployments where loggers are being used in conjunction with units collecting location data such as through GPS or Argos satellite telemetry. Performing behaviour classification to isolate movement from non-movement behaviours prior to reconstructing dead-reckoned paths was an important methodological step to ensure tracks stayed within enclosure boundaries. This too has wider implications, suggesting that at least preliminary behaviour classification is an important and under-utilised step of the dead-reckoning procedure. This study provides important evidence in response to pertinent questions regarding sampling frequencies and behaviour classification in track reconstruction procedures and warrants further study, particularly involving animals in enclosures.

Developing new training regimes such as that outlined here facilitates the collection of useful activity data which can inform animal welfare in captive settings, which is broadly applicable to a range of species living in zoos. These training activities also have positive consequences for captive animal health. Continued training with the modified crate has facilitated regular collection of individual body mass data. A number of veterinary interventions have also been streamlined by continued crate training while avoiding anaesthesia, including administering eye drops to an individual that developed an ulcer and taking samples of facial lesions which broke out in multiple pack members with unknown cause (L. Harvey personal observation). Where sedation is still required, crate training has also been used in London Zoo to calmly separate two wild dogs for procedures requiring general anaesthesia. Crate training is felt by staff to have increased the general training standard by increasing the trust between keeper and animal, with one individual having successfully undergone venepuncture without sedatives in another training area. As such, of the two different collaring approaches used, the quick-release collars and associated training procedures were more

advantageous for the zoo environment than the drop-off collars.

There is a lack of consensus regarding whether tags on collars, or even collars themselves, have negative impacts on animal behavioural patterns and a resultant need for species-specific, and perhaps even individual-specific, assessments (Horback et al. 2012). Wide-ranging carnivores are particularly vulnerable to stereotypic behaviours (Clubb and Mason 2003), and so training captive carnivores to accept collars for the collection of logging data could be beneficial to their welfare by offering detailed insight into behavioural patterns. However, social carnivores should be monitored to assess reactions from conspecifics to collars. Another important consideration for tagging animals in zoos is the reactions of visitors, as entrance fees are often an important source of funding for zoos. Here, both London and Whipsnade zoos used this study as an opportunity to educate the public about the research that these zoos support, with relevant signage added to wild dog enclosures.

## Conclusion

Biologging studies conducted in captivity provide information on the space use and activity patterns of captive animals. As well as the implications for captive carnivore welfare, this study highlights the enormous research potential of zoos to contribute to biologging studies by providing opportunities to develop new collar designs and trial data interpretation methods in a setting where non-domesticated animals can be observed with ease. The training exercise outlined here showcases a creative mechanism for fitting collars on a captive carnivore, with benefits for captive animal welfare and veterinary care.

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## References

- Ahlmann-Eltze C., Patil I. (2021) ggsignif: R package for displaying significance brackets for 'ggplot2'. *PsyArXiv*. doi:10.31234/osf.io/7awm6
- Aitken-Palmer C., Ware L.H., Braun L., Lang K., Joyner P.H. (2017) Novel radiographic technique for pregnancy detection in the maned wolf (*Chrysocyon brachyurus*) without anesthesia. *Journal of Zoo and Wildlife Medicine* 48(1): 204–207. doi:10.1638/2015-0041.1
- Andrews N.L.P., Ha J.C. (2014) The effects of automated scatter feeders on captive grizzly bear activity budgets. *Journal of Applied Animal Welfare Science* 17(2): 148–156. doi:10.1080/10888705.2013.856767
- AZA Canid TAG (2012) *Large Canid (Canidae) Care Manual*. Silver Spring, Maryland: Association of Zoos and Aquariums.
- Barker Z.E., Vázquez Diosdado J.A., Codling E.A., Bell N.J., Hodges H.R., Croft D.P., Amory J.R. (2018) Use of novel sensors combining local positioning and acceleration to measure feeding behavior differences associated with lameness in dairy cattle. *Journal of Dairy Science* 101(7): 6310–6321. doi:10.3168/jds.2016-12172
- Bashaw M.J., Bloomsmith M.A., Marr M.J., Maple T.L. (2003) To hunt or not to hunt? A feeding enrichment experiment with captive large felids. *Zoo Biology* 22(2): 189–198. doi:10.1002/zoo.10065
- Bassett L., Buchanan-Smith H.M. (2007) Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science* 102(3–4): 223–245. doi:10.1016/j.applanim.2006.05.029
- Bidder O.R., Soresina M., Shepard E.L.C., Halsey L.G., Quintana F., Gómez-Laich A., Wilson R.P. (2012) The need for speed: Testing acceleration for estimating animal travel rates in terrestrial dead-reckoning systems. *Zoology* 115(1): 58–64. doi:10.1016/j.zool.2011.09.003

- Bidder O.R., Walker J.S., Jones M.W., Holton M.D., Urge P., Scantlebury D.M., Marks N.J., Magowan E.A., Maguire I.E., Wilson R.P. (2015) Step by step: Reconstruction of terrestrial animal movement paths by dead-reckoning. *Movement Ecology* 3: 23. doi:10.1186/s40462-015-0055-4
- Brown D.D., Kays R., Wikelski M., Wilson R., Klimley A.P. (2013) Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry* 1: 20. doi:10.1186/2050-3385-1-20
- Browning H., Maple T.L. (2019) Developing a metric of usable space for zoo exhibits. *Frontiers in Psychology* 10: 791. doi:10.3389/fpsyg.2019.00791
- Caravaggi A., Amado T.F., Brook R.K., Ciuti S., Darimont C.T., Drouilly M., English H.M., Field K.A., Iossa G., Martin J.E., McElligott A.G., Mohammadi A., Nayeri D., O'Neill H.M.K., Paquet P.C., Périquet S., Proulx G., Rabaiotti D., Recio M.R., Soulsbury C.D., Tadich T., Wynn-Grant R. (2021) On the need for rigorous welfare and methodological reporting for the live capture of large carnivores: A response to de Araujo et al. (2021). *Methods in Ecology and Evolution* 12(10): 1793–1799. doi:10.1111/2041-210X.13664
- Carlstead K., Shepherdson D. (1994) Effects of environmental enrichment on reproduction. *Zoo Biology* 13(5): 447–458. doi:10.1002/zoo.1430130507
- Cloutier T.L., Packard J.M. (2014) Enrichment options for African painted dogs (*Lycaon pictus*). *Zoo Biology* 33(5): 475–480. doi:10.1002/zoo.21155
- Clubb R., Mason G. (2003) Captivity effects on wide-ranging carnivores. *Nature* 425: 473–474. doi:10.1038/425473a
- Clubb R., Mason G.J. (2007) Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. *Applied Animal Behaviour Science* 102(3–4): 303–328. doi:10.1016/j.applanim.2006.05.033
- Clubb R., Vickery S. (2006) Locomotory stereotypes in carnivores: Does pacing stem from hunting, ranging or frustrated escape? In: Mason G., Rushen J. (eds.). *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*. Trowbridge, UK: Cromwell Press, 58–85.
- Cummings D., Brown J.L., Rodden M.D., Songsasen N. (2007) Behavioral and physiologic responses to environmental enrichment in the maned wolf (*Chrysocyon brachyurus*). *Zoo Biology* 26(5): 331–343. doi:10.1002/zoo.20138
- Dickinson E.R., Stephens P.A., Marks N.J., Wilson R.P., Scantlebury D.M. (2020) Best practice for collar deployment of tri-axial accelerometers on a terrestrial quadruped to provide accurate measurement of body acceleration. *Animal Biotelemetry* 8: 9. doi:10.1186/s40317-020-00198-9
- English H.M. (2018) *Behaviour, Energetics and Movement through Biologging in the Canidae*. MRes thesis, Swansea University.
- Ferguson A., Turner B. (2013) Reproductive parameters and behaviour of captive short-beaked echidna (*Tachyglossus aculeatus acanthion*) at Perth Zoo. *Australian Mammalogy* 35(1): 84–92.
- Fernandez E.J., Kinley R.C., Timberlake W. (2019) Training penguins to interact with enrichment devices for lasting effects. *Zoo Biology* 38(6): 481–489. doi:10.1002/zoo.21510
- Field K.A., Paquet P.C., Artelle K., Proulx G., Brook R.K., Darimont C.T. (2019) Publication reform to safeguard wildlife from researcher harm. *PLoS Biology* 17(4): e3000193. doi:10.1371/journal.pbio.3000193
- Flecknell P. (2002) Replacement, reduction, refinement. *Altex* 19(2): 73–78.
- Gorman M.L., Mills M.G., Raath J.P., Speakman J.R. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* 391: 479–481. doi:10.1038/35131
- Grandin T., Rooney M.B., Phillips M., Cambre R.C., Irlbeck N.A., Graffam W. (1995) Conditioning of nyala (*Tragelaphus angasi*) to blood sampling in a crate with positive reinforcement. *Zoo Biology* 14(3): 261–273.
- Greggor A.L., Vicino G.A., Swaisgood R.R., Fidgett A., Brenner D., Kinney M.E., Farabaugh S., Masuda B., Lamberski N. (2018) Animal welfare in conservation breeding: Applications and challenges. *Frontiers in Veterinary Science* 5: 323. doi:10.3389/fvets.2018.00323
- Gunner R.M., Holton M.D., Scantlebury M.D., van Schalkwyk O.L., English H.M., Williams H.J., Hopkins P., Quintana F., Gómez-Laich A., Börger L., Redcliffe J., Yoda K., Yamamoto T., Ferreira S., Govender D., Viljoen P., Bruns A., Bell S.H., Marks N.J., Bennett N.C., Tonini M.H., Duarte C.M., van Rooyen M.C., Bertelsen M.F., Tambling C.J., Wilson R.P. (2021) Dead-reckoning animal movements in R: A reappraisal using Gundog. Tracks. *Animal Biotelemetry* 9: 23. doi:10.1186/s40317-021-00245-z
- Hall C., Roshier A. (2016) Getting the measure of behavior... is seeing believing? *Interactions* 23(4): 42–46. doi:10.1145/2944164
- Han S., Wang J. (2011) A novel method to integrate IMU and magnetometers in attitude and heading reference systems. *Journal of Navigation* 64(4): 727–738. doi:10.1017/S0373463311000233
- Hawkins P. (2004) Bio-logging and animal welfare: Practical refinements. *Memoirs of the National Institute of Polar Research* 58: 58–68.
- Horback K.M., Miller L.J., Andrews J., Kuczaj II S.A., Anderson M. (2012) The effects of GPS collars on African elephant (*Loxodonta africana*) behavior at the San Diego Zoo Safari Park. *Applied Animal Behaviour Science* 142(1–2): 76–81. doi:10.1016/j.applanim.2012.09.010
- Hunter S.C., Gusset M., Miller L.J., Somers M.J. (2014) Space use as an indicator of enclosure appropriateness in African wild dogs (*Lycaon pictus*). *Journal of Applied Animal Welfare Science* 17(2): 98–110. doi:10.1080/10888705.2014.884401
- Kahle D., Wickham H. (2013) ggmap: Spatial visualization with ggplot2. *The R Journal* 5(1): 144–161. doi:10.32614/RJ-2013-014
- Kenward R.E. (2000) *A Manual for Wildlife Radio Tagging*. London, UK: Academic Press.
- Kistler C., Hegglin D., Würbel H., König B. (2009) Feeding enrichment in an opportunistic carnivore: The red fox. *Applied Animal Behaviour Science* 116(2–4): 260–265. doi:10.1016/j.applanim.2008.09.004
- Lacy R.C. (2013) Achieving true sustainability of zoo populations. *Zoo Biology* 32(1): 19–26. doi:10.1002/zoo.21029
- Ladds M.A., Salton M., Hocking D.P., McIntosh R.R., Thompson A.P., Slip D.J., Harcourt R.G. (2018) Using accelerometers to develop time-energy budgets of wild fur seals from captive surrogates. *PeerJ* 6: e5814. doi:10.7717/peerj.5814
- Linhart P., Adams D.B., Voracek T. (2008) The international transportation of zoo animals: Conserving biological diversity and protecting animal welfare. *Veterinaria Italiana* 44(1): 49–57.
- Mason G., Clubb R., Latham N., Vickery S. (2007) Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science* 102(3–4): 163–188. doi:10.1016/j.applanim.2006.05.041
- Melfi V. (2013) Is training zoo animals enriching? *Applied Animal Behaviour Science* 147(3–4): 299–305. doi:10.1016/j.applanim.2013.04.011
- Miller R., King C.E. (2013) Husbandry training, using positive reinforcement techniques, for marabou stork *Leptoptilos crumeniferus* at Edinburgh Zoo. *International Zoo Yearbook* 47(1): 171–180. doi:10.1111/izy.12001
- Minteer B.A., Collins J.P. (2013) Ecological ethics in captivity: Balancing values and responsibilities in zoo and aquarium research under rapid global change. *ILAR Journal* 54(1): 41–51. doi:10.1093/ilar/ilt009
- Morgan K.N., Tromborg C.T. (2007) Sources of stress in captivity. *Applied Animal Behaviour Science* 102(3–4): 262–302. doi:10.1016/j.applanim.2006.05.032
- Muir W.W., Hubbell J.A.E. (2014) *Handbook of Veterinary Anesthesia-E-Book*. Elsevier Health Sciences.
- Packard J.M., Turner S.J., Shepard S. (2010) Behavioral enrichment for African wild dogs (*Lycaon pictus*): Response to stimuli used in an ongoing program at the Houston Zoo. Biodiversity Stewardship Report No. BS10-2. College Station, Texas: Biodiversity Stewardship Lab, TAMUS.
- Phillips M., Grandin T., Graffam W., Irlbeck N.A., Cambre R.C. (1998) Crate conditioning of bongo (*Tragelaphus eurycerus*) for veterinary and husbandry procedures at the Denver Zoological Gardens. *Zoo Biology* 17(1): 25–32.
- Price L.J. (2010) A preliminary study of the effects of environmental enrichment on the behaviour of captive African wild dogs (*Lycaon pictus*). *Bioscience Horizons: The International Journal of Student Research* 3(2): 132–140. doi:10.1093/biohorizons/hzq017
- Rast W., Kimmig S.E., Giese L., Berger A. (2020) Machine learning goes wild: Using data from captive individuals to infer wildlife behaviours. *PLoS ONE* 15(5): e0227317. doi:10.1371/journal.pone.0227317
- Ripley B. (2005) *tree: Classification and Regression Trees*. R package version 1.0-19.
- Ropert-Coudert Y., Wilson R.P. (2005) Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* 3(8): 437–444. doi:10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2
- R Core Team (2020) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Russell W.M.S., Burch R.L. (1959) *The Principles of Humane Experimental Technique*. London, UK: Methuen and Co Ltd.
- Savastano G., Hanson A., McCann C. (2003) The development of an operant conditioning training program for New World primates at the Bronx Zoo. *Journal of Applied Animal Welfare Science* 6(3): 247–261.
- Shepherdson D.J., Carlstead K., Mellen J.D., Seidensticker J. (1993) The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology* 12(2): 203–216.

- Shorter K.A., Shao Y., Ojeda L., Barton K., Rocho-Levine J., van der Hoop J., Moore M. (2017) A day in the life of a dolphin: Using bio-logging tags for improved animal health and well-being. *Marine Mammal Science* 33(3): 785–802. doi:10.1111/mms.12408
- Shyne A., Block M. (2010) The effects of husbandry training on stereotypic pacing in captive African wild dogs (*Lycaon pictus*). *Journal of Applied Animal Welfare Science* 13(1): 56–65. doi:10.1080/10888700903372069
- Stegmann G.F. (2000) Isoflurane anaesthesia in an African wild dog, *Lycaon pictus*. *Journal of the South African Veterinary Association* 71(4): 246.
- Studd E.K., Boudreau M.R., Majchrzak Y.N., Menzies A.K., Peers M.J.L., Seguin J.L., Lavergne S.G., Boonstra R., Murray D.L., Boutin S., Humphries M.M. (2019) Use of acceleration and acoustics to classify behavior, generate time budgets, and evaluate responses to moonlight in free-ranging snowshoe hares. *Frontiers in Ecology and Evolution* 7: 154. doi:10.3389/fevo.2019.00154
- Szokalski M.S., Litchfield C.A., Foster W.K. (2012) Enrichment for captive tigers (*Panthera tigris*): Current knowledge and future directions. *Applied Animal Behaviour Science* 139(1–2): 1–9. doi:10.1016/j.applanim.2012.02.021
- Therneau T., Atkinson B., Ripley B. (2022) *Package 'rpart'*. <https://cran.pau.edu.tr/web/packages/rpart/rpart.pdf> (Accessed 9 November 2022).
- Vázquez Diosdado J.A., Barker Z.E., Hodges H.R., Amory J.R., Croft D.P., Bell N.J., Codling E.A. (2018) Space-use patterns highlight behavioural differences linked to lameness, parity, and days in milk in barn-housed dairy cows. *PLoS ONE* 13(12): e0208424. doi:10.1371/journal.pone.0208424
- Wagman J.D., Lukas K.E., Dennis P.M., Willis M.A., Carroscia J., Gindlesperger C., Schook M.W. (2018) A work-for-food enrichment program increases exploration and decreases stereotypies in four species of bears. *Zoo Biology* 37(1): 3–15. doi:10.1002/zoo.21391
- Walsh B. (2017) Asian elephant (*Elephas maximus*) sleep study – Long-term quantitative research at Dublin Zoo. *Journal of Zoo and Aquarium Research* 5(2): 82–85. doi:10.19227/jzar.v5i2.174
- Westlund K. (2014) Training is enrichment—and beyond. *Applied Animal Behaviour Science* 152: 1–6. doi:10.1016/j.applanim.2013.12.009
- Wheeler B., Torchiano M. (2016) *Package 'lmpPerm': Permutation Tests for Linear Models*.
- Wickham H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. New York, New York: Springer.
- Williams T.M., Wolfe L., Davis T., Kendall T., Richter B., Wang Y., Bryce C., Elkaim G.H., Wilmers C.C. (2014) Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* 346(6205): 81–85. doi:10.1126/science.1254885
- Williams H.J., Holton M.D., Shepard E.L.C., Largey N., Norman B., Ryan P.G., Duriez O., Scantlebury M., Quintana F., Magowan E.A., Marks N.J., Alagaili A.N., Bennett N.C., Wilson R.P. (2017) Identification of animal movement patterns using tri-axial magnetometry. *Movement Ecology* 5: 6. doi:10.1186/s40462-017-0097-x
- Williams H.J., Taylor L.A., Benhamou S., Bijleveld A.I., Clay T.A., de Grissac S., Demšar U., English H.M., Franconi N., Gómez-Laich A., Griffiths R.C., Kay W.P., Morales J.M., Potts J.R., Rogerson K.F., Rutz C., Spelt A., Trevail A.M., Wilson R.P., Börger L. (2020) Optimising the use of biologists for movement ecology research. *Journal of Animal Ecology* 89(1): 186–206. doi:10.1111/1365-2656.13094
- Wilmers C.C., Nickel B., Bryce C.M., Smith J.A., Wheat R.E., Yovovich V. (2015) The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology* 96(7): 1741–1753. doi:10.1890/14-1401.1
- Wilson R.P., Wilson M.P. (1988) Dead reckoning: A new technique for determining penguin movements at sea. *Meeresforschung* 32(2): 155–158.
- Wilson R.P., Wilson M.P.T., Link R., Mempel H., Adams N.J. (1991) Determination of movements of African penguins *Spheniscus demersus* using a compass system: Dead reckoning may be an alternative to telemetry. *Journal of Experimental Biology* 157: 557–564.
- Wilson R.P., Shepard E.L.C., Liebsch N. (2008) Prying into the intimate details of animal lives: Use of a daily diary on animals. *Endangered Species Research* 4(1–2): 123–137. doi:10.3354/esr00064
- Wilson R.P., Holton M.D., di Virgilio A., Williams H., Shepard E.L.C., Lambertucci S., Quintana F., Sala J.E., Balaji B., Lee E.S., Srivastava M., Scantlebury D.M., Duarte C.M. (2018) Give the machine a hand: A Boolean time-based decision-tree template for rapidly finding animal behaviours in multisensor data. *Methods in Ecology and Evolution* 9(11): 2206–2215. doi:10.1111/2041-210X.13069
- Wilson R.P., Holton M., Wilson V.L., Gunner R., Tysse B., Wilson G.I., Quintana F., Duarte C., Scantlebury D.M. (2019) Towards informed metrics for examining the role of human-induced animal responses in tag studies on wild animals. *Integrative Zoology* 14(1): 17–29. doi:10.1111/1749-4877.12328
- Wilson R.P., Börger L., Holton M.D., Scantlebury D.M., Gómez-Laich A., Quintana F., Rosell F., Graf P.M., Williams H., Gunner R., Hopkins L., Marks N., Geraldi N.R., Duarte C.M., Scott R., Strano M.S., Robotka H., Eizaguirre C., Fahlman A., Shepard E.L.C. (2020) Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology* 89(1): 161–172. doi:10.1111/1365-2656.13040
- Wolf C., Ripple W.J. (2017) Range contractions of the world's large carnivores. *Royal Society Open Science* 4(7): 170052. doi:10.1098/rsos.170052
- Woodroffe R., Sillero-Zubiri C. (2020) *Lycaon pictus* (amended version of 2012 assessment). The IUCN Red List of Threatened Species 2020: e.T12436A166502262.