Animal lifestyle affects acceptable mass limits for attached tags

Rory P. Wilson1, Kayleigh A. Rose1, Richard Gunner1, Mark D. Holton2, Nikki J. Marks3, Nigel C. Bennett1, Stephen H. Bell3, Joshua P. Twining2, Jamie Hesketh1, Carlos M. Duarte5, Neil Bezdice6, Milos Jezek7, Michael Painter7, Vaclav Silovský7, Margaret C. Crofoot8, Roi Harel8,9, John P. Y. Arnould10, Blake M. Allan10, Desley A. Whisson10, Abdulaziz Alagaili11 and D. Michael Scantlebury3

1Max Planck Institute of Animal Behavior, D-78315 Radolfzell, Germany
2College of Science, Swansea University, Fabian Way, Swansea SA1 8EN, UK
3School of Biological Sciences, Queen’s University Belfast, Belfast BT9 5DL, UK
4Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa
5Red Sea Research Centre, King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia
6Applied Sports, Technology, Exercise and Medicine (A-STEM) Research Centre, College of Engineering, Swansea University, Bay Campus, Swansea SA1 8EN, UK
7Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague 165 00, Czech Republic
8Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Bücklestraße 5, Konstanz D-78467, Germany
9Germany and Department of Biology, University of Konstanz, Konstanz 78457, Germany
10School of Life and Environmental Sciences, Deakin University, Melbourne Burwood Campus, 221 Burwood Highway, Burwood, VC 3125, Victoria, Australia
11KSU Mammals Research Chair, Zoology Department, King Saud University, Riyadh, Saudi Arabia

RPW, 0000-0003-3177-0107; KAR, 0000-0001-7023-2809; RG, 0000-0002-2054-9944; NCB, 0000-0001-9748-2947; JPT, 0000-0002-0881-9665; JPYA, 0000-0003-1124-9330; DMS, 0000-0001-8327-0556

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5672341.

1. Introduction

The use of animal-attached devices is transforming our understanding of wild animal ecology and behaviour [1,2]. Indeed, tags containing multiple sensors...
and position-determining systems have been used across scales of time and space to measure everything from the extraordinary details of high performance hunts in cheetahs [3], to vast cross-taxon comparisons of animal behaviour and space-use over whole oceans (e.g. [1,4]). A critical proviso is, however, that such devices do affect survival or change the behaviour of their carriers, for both animal welfare issues as well as for scientific rigor [5]. Defining acceptable device loads for animals is critical because even diminishingly small tags can cause detriment. For example, Saraut et al. [6] showed that the addition of flipper rings to penguins can affect their populations, with adults having a survival rate 16% lower than untagged conspecifics and producing 39% fewer chicks, presumed to be because of the tags increasing the drag force in these fast-swimming birds. Performance is relevant in this case because drag-dependent energy expenditure to swim increases with the cube of the speed [7].

Although consideration of the physics of drag has been shown to be a powerful framework with which to understand tag detriment in aquatic animals (e.g. [8,9]), drag is negligible in terrestrial (though not aerial) systems even though tag detriment in terrestrial animals has been widely reported and is multi-faceted [10]. Reported issues range from minor behavioural changes [11] through skin-, subcutaneous- and muscle damage with ulceration [12,13] to reduced movement speed [14] and dramatically increased mortality [15]. As with drag, we advocate that a force-based framework is necessary to help understand such detriment. Indeed, force is implicit in ethics-based recommendations for acceptable tag loads because, for example, a central tenet is that animal tag mass should never exceed 3% or 5% of the animal-carrier body mass [16], this being based on early observations that tags weighing less than 5% of animal body masses apparently caused no change in behaviour [17]. Importantly though, there are now numerous studies that have reported highly variable impacts of animals carrying tags of masses less than the 3–5% limit [18–21] for reasons that are not always clear [20–22]. Implicit in this limit is that consequences, most particularly the physical forces experienced by animals owing to tags, are similarly limited. This cannot be true because Newton showed that mass, force and acceleration are linked via \( F = ma \), so animal performance, specifically their acceleration, will affect the tag forces applied to the carriers. Tag forces on the animal carrier can therefore be assessed by measuring acceleration experienced by the tag as the animal moves. Specifically, reference to Newton’s force/mass acceleration formulation shows that any time the tag acceleration exceeds \( 1 \, g \) (corresponding to Earth’s gravity), the carrier animal will be subject to correspondingly higher tag-derived forces. We note here though, that this necessitates gathering on-animal data because simple consideration of acceleration from rigid-non-living bodies is inappropriate for living systems composed of multiple interacting segments [23].

Here, we examine the forces exerted by collar-mounted tags on moving animals. We investigate four species within the order Carnivora in detail; lions *Panthera leo*), European badgers *Meles meles*, pine martens *Martes martes* and a cheetah *Acinonyx jubatus* (with body masses roughly spanning 2–200 kg) equipped with accelerometers undertaking their normal activities in the wild for 1–21 days. In particular, because gait is known to affect acceleration in body-mounted tags [24] we examined how walking, trotting and bounding affected the forces imposed on the animals by the tags. We also equipped six other species of mammal from diverse animal families (a cercopithecid, a phascolarctid, a phalangerid, a bovid, a cervid and a suid) with different lifestyles with accelerometers *in situ* for periods between 7 and 168 days to examine the general patterns of forces they exhibited and compared them to the carnivores.

Because the act of travelling is known to produce particularly high forces [25], we also carried out controlled trials with 12 domestic dogs *Canis familiaris* (2–45 kg) equipped with the same tags moving at defined speeds to investigate how movement speed, body mass and tag mass interact to affect tag forces.

We document how the forces imposed by the collars changed with activity across all these species and conditions. Based on this, we propose a method based on acceleration data that allows researchers to define the breadth of forces exerted by tags on animals and their relative frequency of occurrence. We show how this information can then be used to derive appropriately force-based acceptable limits for tag masses, recognizing the effect of animal lifestyle and athleticism.

## 2. Material and methods

### (a) Tag deployments on free-ranging species

We selected four species of free-living carnivores for detailed analysis, exemplifying about two orders of magnitude of mass; 10 lions *Panthera leo* (mean mass ca 152 kg), one cheetah *Acinonyx jubatus* (mass ca 41 kg), 10 badgers *Meles meles* (mean mass ca 9.1 kg) and five pine martens *Martes martes* (mean mass 1.9 kg), and fitted them with collar-mounted tri-axial accelerometers (*Daily Diaries—Wildbyte Technologies* [http://www.wildbyte-technologies.com/]; measurement range 0–16 g (resolution 0.49 mg), recording frequency 40 Hz), all of which constituted less than 3% of the mass of the animal carriers (electronic supplementary material, table S1). Owing to the weighting of the loggers, and more particularly their associated batteries, the units and sensors were positioned on the underside of the collar although during movement the collars could rotate, which could occasionally, temporarily bring the measuring system off the ventral position. After being equipped, the animals roamed freely, behaving normally, for periods ranging between 3 and 21 days before the devices were recovered.

In addition to these, we also deployed collar-mounted accelerometers constituting less than 3% of the carrier mass (electronic supplementary material, table S1) on six select free-ranging animal species. We chose these species by capitalizing on available data from animals equipped with high temporal resolution acceleration tags on collars from different mammal families with varying lifestyles for comparison with the carnivores. The species and lifestyles were: a savannah-dwelling monkey—the olive baboon *Papio anubis* (mean mass 15 kg, \( n = 5 \)); an arboreal herbivorous marsupial—the koala *Phascolarctos cinereus* (mean mass 10.3 kg, \( n = 5 \)); a nocturnal, semi-arboreal, herbivorous marsupial—the mountain brushtail possum *Trichosurus cunninghami* (mean mass 3.2 kg, \( n = 5 \)); a grass-eating, desert-dwelling bovid—the Arabian oryx *Oryx leucoryx* (mean mass 74 kg, \( n = 5 \)); a grass-eating, wood- and moor-dwelling cervid—the red deer *Cervus elaphus* (mean mass 135 kg, \( n = 5 \)); and a forest-dwelling, omnivorous pig—the wild boar *Sus scrofa* (mean mass 67 kg, \( n = 5 \)). Extensive details on species-specific tagging procedures are included in the electronic supplementary material.

### (b) Trials with domestic dogs

Twelve domestic dogs (*Canis lupus domesticus*) of seven different breed combinations and three main body types (small, racers and northern breeds), ranging 2–45 kg in body mass (electronic
supplementary material, table S2), were volunteered by their owners and the Royal Society for the Prevention of Cruelty to Animals (RSPCA) Llys Nini Wildlife Centre (Penllergaer, Wales) to take part in this study. Dog body masses were obtained from the most recent measurements taken by a veterinarian, or the RSPCA, and we measured body length, forelimb length and hindlimb length to the nearest cm. Two leather dog collars (short and long) of the same width were used to cover the range in dog neck size. Combinations of pre-prepared lead plates (up to 10 cm in length) and varying in mass (25, 35, 45, 50, 100, 150 and 175 g) were fashioned into collar loads equivalent to 1, 2 and 3% of each carrier dog’s body mass. The lead plates were stacked, the longest of them (for the greatest masses) being bent to replicate a 10 cm section of the collar circumference and attached securely to the ventral collar along their full-length using Tesa® tape. A tri-axial accelerometer and its supporting battery (3.2 V lithium ion) were taped securely to the load. The tag and battery combined weighed 11.9 g and, in the absence of any additional load, were considered negligible in mass and used as a control (0% carrier body mass). All trials were approved by the Swansea University Animal Welfare Ethical Review Body (ethical approval number IP-1617-21D).

Each dog was encouraged to traverse along a 25 m stretch of level, short-cut grass at slow (walk/amble), moderate (pace/trot) and fast (canter/gallop) speeds (because gait affects acceleration signatures substantially [24]) wearing collar-tags equivalent to 0, 1, 2 and 3% of their body mass (12 gait and tag mass combinations) and trial order was randomized. Posts were spaced every 5 m along the track. A stopwatch was used to record the time taken (to the nearest s) for a dog to travel 20 m in order to calculate an average speed of travel (m s$^{-1}$).

(c) Data processing
In all cases of animals equipped with accelerometers, the three channels of raw acceleration data were converted to a single metric by calculating the vectorial sum of the acceleration following $\text{Vect sum} = \sqrt{a_x^2 + a_y^2 + a_z^2}$, where $a_i$ is the instantaneous acceleration and the subscripts denote the different (orthogonally placed) acceleration axes. We chose to use the Vect sum rather than dynamic body acceleration (DBA) metrics [26] because DBA values do not represent peak accelerations owing to the gravity-based component being removed [27]. The specifics of the surge, heave and sway accelerations were not considered separately owing to some collar roll. In the case of the free-living carnivores, we examined how travel gait affected the Vect sum by plotting the cumulative frequency distribution from each species during periods of walking, trotting and bounding.

For the domestic dogs, we selected the maximum four peak accelerations in the Vect sum from the gait waveforms using the peak analysis tool in OriginLab (2020) to examine them as a function of average speed, gait, body mass and tag mass as a percentage of carrier body mass. We standardized the use of four peaks because at the highest speeds some dogs only had four full waveforms during the test stretch. The relative forces (% body mass) exerted by the tags on their animal carriers were calculated using $F = ma$, where $m$ is the mass of the tag plus collar as a percentage of carrier mass and $a$ is the acceleration (g).

(d) Tag-based acceleration method
Finally, in a full cross-species comparison of the free-living animals, we plotted the cumulative frequency distribution of the Vect sum from each species during periods when they were active (by excluding periods where the acceleration signals were constant) to define the vector sum of the acceleration at species-specific 95% and 99% limits.

3. Results
(a) Changing acceleration according to activity in carnivores
Accelerometer data for periods when our carnivores travelled, displayed clear peaks in the waveforms with measurable frequency and, summarized as a frequency distribution of the vectorial sum of the three orthogonal axes, showed tri-modal distributions except for the pine martens which were mono-modal. Following [29] and examination of videos of the study animals engaged in travelling using different gaits with measurable step frequency, we could ascertain that these corresponded to walking, trotting and bounding (e.g. figure 1, which also tallied with our direct and filmed observations of the domestic dogs below); these were further exemplified by variation in the amplitude in this acceleration metric (figure 2). Cumulative frequencies of all acceleration values showed increasing acceleration from walking through trotting to bounding and typically had a roughly logarithmic-type curve for all gaits and animals (figure 1). The percentage time during which the tags carried by the carnivores had acceleration exceeding 1g during specified activity, varied between a mean minimum of 31% for walking badgers to 88% for bounding cheetahs (electronic supplementary material, table S3). Furthermore, while differences in species acceleration distributions were not readily apparent for their walking gaits, the percentage time during which acceleration was in excess of 1 g was greatest during bounding, with cheetahs showing the highest values in this category (green line with circles in figure 1). Mean peak accelerations per stride across species varied between 1.37 g (s.d. 0.05) and 6.25 g (s.d. 0.79) for walking and bounding cheetahs, respectively (electronic supplementary material, table S4). The maximum recorded value was 18.1 g in a cheetah assumed to be chasing prey.

Across the four species, gait was the main factor dictating peak acceleration (figure 2) and there were no significant effects of body mass, nor period between peaks (linear mixed-effects model: log period: $F_{1,210} = 0.01$, $p = 0.908$; gait:

(e) Statistical analyses
Linear mixed-effects models were conducted in R (v. 4.0.3, [28]) within the ‘lme4’ package (v. 1.1-26) in order to investigate how the period between peak accelerations, gait and body mass influenced peak accelerations across four species of wild carnivores, and separately in domestic dogs. Additionally, we investigated how travel speed (covariate), body mass (covariate), collar mass as a percentage of carrier body mass (fixed factor with four levels) and gait (fixed factor with three levels for slow, moderate and fast gaits) influenced peak accelerations and consequent forces exerted by the tags. Dog identity was included as a random factor in all models to account for repeated measures. All potential interaction effects were first investigated and a step-wise back-deletion of non-significant interaction terms was conducted. Standard model diagnostics were conducted in order to ensure that model assumptions were met (examining quantile-quantile plots and plotting the residuals against fitted values) and data transformations were conducted in order to meet assumptions where appropriate. The F statistic and marginal and conditional $R^2$ were determined using the ‘car (3.0-5)’ and ‘MuMIn (1.46.6)’ packages, respectively. Coefficients for best-fit lines in the figures were extracted from the final outputs of the models.
In dogs, stride peak accelerations increased linearly with travel speed (electronic supplementary material, figure S2), but at greater rates with increasing relative tag mass (there was a significant interaction effect between travel speed and tag per cent body mass: $F_{3,500.77} = 4.34$, $p = 0.004$; electronic supplementary material, table S6). There was also a significant interaction effect between gait and tag per cent body mass on stride peak accelerations ($F_{6,498.57} = 4.34$, $p = 0.0002$; electronic supplementary material, table S6). Peak tag accelerations ranged from 4 to 18 $g$ during fast category (canter/gallop) trials in dogs wearing collar tags equivalent to 3% of their body mass (electronic supplementary material, figure S3). In this scenario, movement of the tag relative to the body (flapping/swinging) was exacerbated and, as a consequence, the force exerted by the tags ranged from 20–50% of the gravitational force exerted on the carrier animal’s body mass (electronic supplementary material, figure S4).

Stride peak accelerations were largely invariant with body mass ($F_{1,10.12} = 3.51$, $p = 0.090$; electronic supplementary material, table S6) across dog breeds for any given gait (electronic supplementary material, figure S3). Consequently, the peak forces exerted by the tags were directly proportional to tag mass and body mass. Accordingly, relative tag forces (percentage of the gravitational force exerted on the carrier animal’s body mass) were independent of carrier body
mass (electronic supplementary material, table S6 and figure S4).

(b) Using accelerometry to derive an over-arching tag-force rule

Although travelling is a major component across species, animal activity across all behaviours contributes to the acceleration, and therefore the tag force profiles, that animals experience. We produced cumulative frequency curves of the vectorial sum of the acceleration (cf. figure 1) for all 10 study species for periods when animals were considered active and these all showed a characteristic sigmoid pattern (figure 4a). These relationships were displaced further to the right as higher acceleration activities accounted for an increasing proportion of any animal’s time (figure 4a). In order to have a scientifically robust acceptable threshold to limit the forces produced by a tag on an animal carrier, we suggest a tag-based acceleration method; that researchers limit the forces produced by a tag on an animal carrier, we suggest a tag-based acceleration method; that researchers should derive a similar cumulative acceleration profile for their study species and use a minimum of the 95% limits on the plot (although higher limits may be more appropriate). Assuming, in the case of our study animals, that these limits were intended to cater for a tag that should exert forces that are less than 3% of the gravitational force exerted on the animal’s body, this limit would lead to corrected tag masses constituting between 1.6% and 2.98% of our study animals’ masses (figure 4b). We note, however, that even these corrected tag masses would effectively exceed the 3% rule conditions for one-twentieth of the animals’ active periods: the difference between the 95% and 99% thresholds for our study species indicates the extent of the force development for this period with some, such as the koalas, showing virtually no difference, whereas badgers, baboons and martens exhibited substantial differences (figure 4b). Importantly though, this method would allow researchers to define any tag force thresholds, not just 3%, and the times these were exceeded by the animal, not just 95%.

Figure 2. Body mass and stride period do not dictate peak tag acceleration. Distributions of peak amplitudes of (the vectorial sum of) accelerations and stride periods for four free-living carnivores (see symbols, with mean masses of ca. 2 kg, 9 kg, 41 kg and 152 kg for the pine martens, badgers, cheetah and lions, respectively) travelling using different assumed gaits (colours). Each individual point shows a mean from a duration of activity greater than 5 s from a single individual. See also the electronic supplementary material, figure S1 for similar data from domestic dogs. (Online version in colour.)

4. Discussion

The subject of detriment caused by tags on animals is complex because the general term ‘detriment’ has many facets [20], not least because the tag itself may cause the animal to move in an atypical manner, which may change how a device would affect an animal that did not respond to the device. One direct aspect that exemplifies this is, for example, measurable physical harm to the animal, such as pressure sores [12], the severity of which might be expected to depend on movement patterns. However, physical harm can also effectively occur if tagged animals or their offspring cannot balance energy budgets owing to compromised foraging stemming from tag interference [6,30,31]. Often, this is simply a result of higher movement costs or reduced performance in tagged animals as they travel [18]. This also means though, that precise limb kinematics may be different in travelling tagged animals, and this will affect acceleration signals recorded by animal-attached tags, which is relevant to a study such as ours. So, measurement affects performance [32] and we must bear this caveat in mind when we advocate that our tag data represent the norm of untagged animals. Against this, however, we can and should use proper physical frameworks to assess tag detriment because this is precisely what our tagged animals experience, whether their movement is ‘normal’ or not, because we have specifically equipped them with the source of detriment. Indeed, this is the fundamental premise behind our work although the issue of what untagged animals may experience remains problematic [5].

A rigid vehicle accelerating in a straight-line only experiences acceleration in the longitudinal axis. By contrast, the multiple limb-propelled motion of an animal with a flexible body produces complex three-dimensional trunk accelerations owing to the changing limb accelerations [23] caused by multiple muscle groups that ultimately transfer mechanical energy and affect shock absorption [33], and the mechanical work conducted within each stride [34]. Ultimately, the magnitude of trunk accelerations depends on the combined acceleration of the limbs, and the masses of those limbs (cf. [23]). Thus, animals engaging in high performance activities are expected to produce high body accelerations, and have physiological and anatomical adaptations to enhance performance, such as fast twitch muscles [35], and tendons designed for greater storage and release [36], which will increase this. Through all these complexities, tags mounted on the trunk of an animal result in greater forces being imposed that scale linearly with the acceleration of the tag and its mass. Consideration of animal lifestyle then, can already inform prospective tag users of the likely scale-up of the tag forces beyond the 1 g normally considered for tag detriment because force = mass × acceleration, the repercussions of which are discussed below in terms of potential detriment. Consequently, the 3–5% mass limits for slow-moving animals, such as sloths (Bradypodidae) or koalas (Phascolarctidae) (figure 4), seem most appropriate, though this does not mean that tags will not affect the animals. Against this, the 3–5% mass limits may be less appropriate for pursuit predators, such as wild dogs (Lycaon pictus), regularly jumping animals like kangaroos (Macropodidae) or martens (Mustelidae) (figure 4) and rutting ungulates (Ungulata). Beyond that, in our small sample of carnivores at least, which nonetheless covers about two orders of magnitude in
mass, it seems that peak acceleration associated with gait varies little with mass, although larger animals have longer stride periods (figure 2, cf. [37]). If these animals were to carry tags constituting 3% of their normal body mass, mean peak forces imposed by the tags would constitute ca 4.5%, 6% and 12% of the gravitational forces exerted on the animals’ bodies for walking, trotting and bounding gaits at frequencies of between 1.6 and 4 times per second (for walking lions and trotting badgers, respectively; figure 2; electronic supplementary material, table S4). We also note how minor differences in sex-dependent tag masses coupled with differences in performance affect the forces imposed by the tags, as exemplified by the lions (figure 3) and how, were the tags in this study to constitute 3% of the animals’ masses, the tag-based forces would scale up accordingly.

Against all this, we recognize two important trends: (i) that as animals get larger, deployed tags on them are likely to be a smaller fraction of their mass anyway; but that (ii) despite miniaturization advances in tag technology, researchers continue to deploy systems that are around the 3–5% mass limit on smaller animals [21].

Importantly, tag attachment is relevant in translating the acceleration experienced by the animal’s trunk into tag-dependent forces acting on the animal, with collars predicted to be particularly problematic. A tag that couples tightly with its carrier’s trunk, such as one attached with tape to a bird [38] or glue to a marine mammal [39], experiences acceleration that closely matches that of its substrate, so it exerts forces at a site where most of the animal’s mass lies. By contrast, a device on a looser-fitting collar of a moving tetrapod not only exerts forces on the (less massive) head and neck areas, rather than the animal’s trunk, but the tag also oscillates between essentially two states: one is analogous to ‘freefall’, which occurs between pulses of animal trunk acceleration in the stride cycle which project the collar in a particular direction owing to its inertia and lack of a tight couple with the neck. The collar is therefore subject to peaks in acceleration when it interacts with the animal’s neck, causing greater collar acceleration than would be the case if it were tightly attached to the animal’s body (cf. peaks in figure 1). This explains why Dickinson et al. [40] reported that acceleration signatures from collar-mounted tags deployed on (speed-controlled) goats Capra aegagrus became increasingly variable with increasing collar looseness, and is analogous to the concerns related to injuries sustained by people in vehicles depending on seatbelt tightness [41].

Partial answers to minimizing such problems may involve having padded collars that should reduce acceleration peaks, making sure that the tags themselves project minimally beyond the outer surface of the collar and having wider collars to reduce the pressure.

Having identified how animal movement changes the 3% tag rule, it is more problematic to understand how the identified forces translate into detriment. Within a general tag detriment framework, heavier tags require that animals perform more work (J) during movement because work done = force × distance, which helps clarify why the additional forces from a tag, on top of the animal weight, should relate to energy expenditure (cf. [42]). However, with respect to load carrying, how various tri-axial acceleration metrics such as DBA [26] relate to force and energy needs further research [43]. A prime effect of vectorially summed acceleration is that higher associated forces (because mass is constant) and smaller contact areas will lead to higher pressure at the tag-animal interface because pressure = force/area. This can affect anything from fur/feather wear [44] to changing the underlying tissue [45] and, as would be predicted, is notably prominent in species wearing thin collars.
<a><figure><table></table></figure></a>Figure 4. Defining tag mass limits based on cumulative time spent experiencing tag forces. Panel (a) shows the mean cumulative frequency (bars = s.d.) of the vectorial sum of the acceleration for two arboreal animals with very different athleticisms: five koalas (black line concentrated around 1 g) and five pine martens (blue line with much greater spread around 1 g). The 95% limit is shown by the dashed (green) line. Panel (b) shows these two species points (and the 99% limits in red triangles) adjacent to a broader species list highlighting variation in lifestyles. Assuming that a tag should only exert a force amounting to 3% of the gravitational force exerted on the carrier animal’s body, the translation of these species-specific acceleration limits can be used to correct tag masses to be an appropriate percentage of the carrier animal mass (blue axis on the right). (Online version in colour.)

(e.g. howler monkeys Alouatta palliatai, where 31% of animals wearing ball-chain radio-collars constituting just 1.2% of their mass sustained severe damage extending into the subcutaneous neck tissue and muscle [12]). However, pressure-dependent detriment will also depend on the proportion and length of time to which an animal is exposed to excessive forces, with animals that spend large proportions of their time travelling, such as wild dogs, being particularly susceptible [46].

Perhaps more esoteric, is the extent to which the inertia of a variable force-exerting tag ‘distracts’ its wearer, aside from the physical issues of load-bearing by animals, and in this context, peak forces per stride are liable to be critical. The tag mass as a percentage of carrier mass did not affect the gait-specific speeds selected by the domestic dogs in this study. However, it remains to be seen the extent to which a typical 30 kg cheetah wearing a collar that is 3% of its body mass, and therefore experiencing an additional force equivalent to up to 16 kg during every bound of a prey pursuit, might have its hunting capacity compromised. We note that the survival of such animals is believed to be especially sensitive to the proportion of successful hunts (cf. [47]), which calls for critical evaluation of performance between tag-sensitive to the proportion of successful hunts (cf. [47]), which might have its hunting capacity compromised. We note that seasonal variation in animal behaviours, such as occurs in rutting ungulates, have potential to affect the distribution substantially, emphasizing the importance of considering the context under which the data were gathered.

Importantly, we do not advocate the 3% rule as such, but recognize that it has been widely adopted and could serve as a useful starting point with which to consider tag detriment if calculated as we have suggested here. In this, cognizance should also be given to the extent of tag forces for periods above the 95% threshold because, where these are excessive, it may be appropriate to use a 99% threshold or higher to derive appropriate tag masses. Notably though, even 99% limits do not highlight the high tag forces developed during prey pursuits exhibited by the cheetah. We suggest that the solution to this lies in more detailed consideration of the animal’s lifestyle; in particular, identifying survival-critical behaviours with exceptionally high accelerations. Such periods may persuade ethics bodies to raise their thresholds still further. Underpinning this will be ongoing miniaturization, where tags benefit from the sensor revolution in human wearables, which will undoubtedly percolate through to animal applications: advanced smart phones have greater than 10 sensors, along with significant memory and data transmission capabilities, and typically weigh 150–200 g or about 0.2% of average human body mass, although human wearables benefit from regular contact with charging systems while many wildlife tag applications are projected for long-term deployments (e.g. [48]) that either necessitate correspondingly large batteries or autonomous charging systems, both of which increase the mass of tags [49].
Finally, consideration of the acceleration-based forces generated by animal-attached tags does not cover all forms of detriment because other forces are at play, such as greater drag in swimming- and flying species (cf. [6]), and more esoteric elements, such as device colour, that affect animal behaviour [50]. However, our framework should take the current ‘one-size-fits-all’ basic 3% rule into an arena where quantitative assessment of acceleration can be compared to the myriad of tag-influenced behaviours recognised by the community to link animal lifestyle to putative detriment. Most importantly, these considerations should give ethics bodies a more useful rule of thumb than is currently the case and enable us to develop systems that minimize force-based tag effects, to the benefit of both animals and the science that their studies underpin.

**Ethics.** All trials with domestic dogs were approved by the Swansea University Animal Welfare Ethical Review Body (ethical approval number IP-1617-21D). Live trapping and collar deployment with badgers and pine martens was conducted at two sites under UK Home Office License and Northern Ireland Environment Agency, License 2228 between August and November 2019. For work with lions, all procedures followed recommendations of SANPark’s Standard Operating Procedures for the Capture, Transportation and Maintenance in Holding Facilities of Wildlife. Conditions, permits and approvals for fieldwork on lions were granted from South African National Parks (permit number SCAM 1550), from Swansea University College of Science Ethics Committee (SU (SU-Ethics-Student-260919/1229)), the Animal Welfare Ethical Review Committee at Queens University Belfast (QU-B-BS-AREC-18-006) and the University of Pretoria (NAS061-19). For work with olive baboons, research activities described in this paper were approved by the Republic of Kenya’s National Council for Science and Technology (permit no. NCF-2011, B33-2012) and conducted under permit by the Victoria Department of Sustainability and Environment. For mountain brushtail possum work, methods were approved by the Deakin University Animal Ethics Committee (A312010) and conducted under permit (10005379) by the Victorian Department of Sustainability and Environment. For data accessibility. Data pertaining to this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sdjf2xbm [51].

**Authors’ contributions.** R.P.W.: conceptualization, formal analysis, funding acquisition, investigation, writing—review and editing; N.C.B.: investigation, writing—review and editing; S.H.B.: investigation, writing—review and editing; J.H.: data curation, investigation, writing—review and editing; C.M.D.: investigation, writing—review and editing; N.B.: investigation, writing—review and editing; M.J.: investigation, writing—review and editing; M.P.: investigation, writing—review and editing; V.S.: investigation, writing—review and editing; R.H.: investigation, writing—review and editing; M.C.C.: investigation, writing—review and editing; J.P.Y.A.: investigation, writing—review and editing; B.M.A.: investigation, writing—review and editing; D.A.W.: investigation, writing—review and editing; A.A.: investigation, writing—review and editing; D.M.S.: investigation, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

**Funding.** This work benefited by funding from the CAASE project (King Abdullah University of Science and Technology (KAUST)) under the KAUST Sensor Initiative (R.P.W., R.G., M.H., C.M.D.); the Royal Society/Wolfson Laboratory refurbishment scheme (R.P.W.); the Department of Learning and the Challenge Funding, and access provided by the National Trust and Forest Service NI (D.M.S., J.P.T.); the Vice Deanship of Research Chairs at the King Saud University, Saudi Arabia (A.A., D.M.S., N.C.B.); The Royal Society 2009/R3 JP009604 (D.M.S.); Natural Environment Research Council NE/1002030/1 (D.M.S.); The Department for Economy Global Challenges Research Fund (D.M.S.); the Department of Agriculture and Rural Development (DARD) Northern Ireland (currently the Department of Agriculture, Environment and Rural Affairs) through various studentships (D.M.S., N.J.M.); the Department for the Economy studentship to J.P.T. (D.M.S., N.J.M.); the National Science Foundation IIS-1514174, I05-1250895 (M.C.C.); the Packard Foundation Fellowship 2016-65130 (M.C.C.); the Alexander von Humboldt Foundation in the framework of the Alexander von Humboldt Professorship endowed by the Federal Ministry of Education and Research (M.C.C.), Deakin University, the advanced research supporting the forestry and wood-processing sector’s adaptation to global change and EVA4.0, no. CZ.02.1.01/0.0/0.0/16_019/ 000803 financed by OP RDE and supported by grant KQ1910462.

**Acknowledgements.** We gratefully acknowledge the access provided by the National Trust and Forest Service NI. We are also grateful to the RSPCA’s Llys Nini Wildlife Centre in Penllergaer, Wales, and to Judy Corbett and Peter Welford at Gwydir Castle in Llanrwst, Wales, for allowing us to work on their property with their lurchers. We thank Derek van Heerden and the staff at Harnas Wildlife Foundation in Namibia for their kindness and supporting our work. We thank SANParks and the Department of Wildlife and National Parks, Botswana for allowing our research in the Kgalagadi Transfrontier Park (permit number SCAM 1550). We are grateful to Angela Bruns, Sam Ferreira and Danny Govender and Paul Viljoen for facilitating the research and to the many field staff and volunteers that conducted the fieldwork including Wayne Oppel, Corera Links, Martin van Rooyen and Mads Frost Bertelsen. We are grateful to Fraser Meszies and all the field staff at the Department of Agriculture, Environment and Rural Affairs, DAFF. We are also grateful to the Vincent Wildlife Trust for supporting this research. A.A., D.M.S and N.C.B. are particularly grateful to Prince Bander bin Saud Al-Saud, past President of the Saudi Wildlife Authority (SWA), for his unlimited and enthusiastic support to undertake these studies on the Arabian oryx, managed by the SWA.

**References**

1. Brown DD, Kays R, Wikelski M, Wilson R, Klimley AP. 2013 Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry* 1, 1–20.
2. Cates R, Crofoot MC, Jetz W, Wikelski M. 2015 Terrestrial animal tracking as an eye on life and planet. *Science* 348, aaa2478. (doi:10.1126/science.aaa2478)
3. Wilson AM, Lowe JC, Roskilly K, Hudson PE, Golabek KA, McNutt JW. 2013 Locomotion dynamics of hunting in wild cheetahs. *Nature* 498, 185–189. (doi:10.1038/nature12295)
4. Block BA et al. 2011 Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86–90. (doi:10.1038/nature10082)
5. Wilson RF, McMahon CR. 2006 Measuring devices on wild animals: what constitutes acceptable practice? *Front. Ecol. Environ.* 4, 147–154. (doi:10.1890/1540-9295(2006)004[0147:MDOWAW]2.0.CO;2)
6. Sarda C et al. 2011 Reliability of flipper-banded penguins as indicators of climate change. *Nature* 469, 203–206. (doi:10.1038/nature09630)
