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## Animal lifestyle affects acceptable mass limits for attached tags

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**Running headline:** A method to clarify acceptable tag mass limits

**Media summary**

Electronic tags attached to wild animals can provide unprecedented information about species habits. To minimize potential tag detriment to the animals, it has long been suggested that tags should be less than 3% of the carrier's weight. We note though, that this does not take into account species athleticism (rucksacks on sprinters are more injurious than on walkers). We measured acceleration in animal-attached tags in 10 species ranging in mass from 2 to 200 kg (pine martens to lions) to derive the tag forces and suggest how to correct for animal lifestyle by changing tag weights accordingly.

**Abstract**

Animal-attached devices have transformed our understanding of vertebrate ecology. To minimize any associated harm, researchers have long advocated that tag masses should not exceed 3% of carrier body mass. However, this ignores tag forces resulting from animal movement. Using data from collar-attached accelerometers on 10 diverse free-ranging terrestrial species from koalas to cheetahs, we detail a tag-based acceleration method to clarify acceptable tag mass limits. We quantify animal athleticism in terms of fractions of animal movement time devoted to different collar-recorded accelerations and convert those accelerations to forces (acceleration x tag mass) to allow derivation of any defined force limits for specified fractions of any animal's active time. Specifying that tags should exert forces that are less than 3% of the gravitational force exerted on the animal's body for 95% of the time led to corrected tag masses that should constitute between 1.6% and 2.98% of carrier mass, depending on athleticism. Strikingly, in four carnivore species encompassing two orders of magnitude in mass (*ca.* 2-200 kg), forces exerted by '3%' tags were equivalent to 4-19% of carrier body mass during moving,

with a maximum of 54% in a hunting cheetah. This fundamentally changes how acceptable tag

mass limits should be determined by ethics bodies, irrespective of the force and time limits

specified.

## 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, Saraux 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 due to 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

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90    (though not aerial) systems even though tag detriment in terrestrial animals has been widely

91    reported and is multi-facetted [10]. Reported issues range from minor behavioural changes [11]

92    through skin-, subcutaneous- and muscle damage with ulceration [12, 13] to reduced movement

93    speed [14] and dramatically increased mortality [15]. As with drag, we advocate that a force-

94    based framework is necessary to help understand such detriment. Indeed, force is implicit in

95    ethics-based recommendations for acceptable tag loads because, for example, a central tenet is

96    that animal tag mass should never exceed 3% or 5% of the animal-carrier body mass [16], this

97    being based on early observations that tags weighing less than 5% of animal body masses

98    apparently caused no change in behaviour [17]. Importantly though, there are now numerous

99    studies that have reported highly variable impacts of animals carrying tags of masses less than

100   the 3-5% limit [18-21] for reasons that are not always clear [20-22]. Implicit in this limit is that

101   consequences, most particularly the physical forces experienced by animals due to tags, are

102   similarly limited. This cannot be true because Newton showed that mass, force and acceleration

103   are linked *via* F = ma, so animal performance, specifically their acceleration, will affect the tag

104   forces applied to the carriers. Tag forces on the animal carrier can therefore be assessed by

105   measuring acceleration experienced by the tag as the animal moves. Specifically, reference to

106   Newton's force/mass acceleration formulation shows that any time the tag acceleration exceeds 1

107   *g* (corresponding to Earth's gravity), the carrier animal will be subject to correspondingly higher

108   tag-derived forces. We note here though, that this necessitates gathering on-animal data because

109   simple consideration of acceleration from rigid-non-living bodies is inappropriate for living

110   systems composed of multiple interacting segments [23].

111

Here, we examine the forces exerted by collar-mounted tags on moving animals. We investigate 4 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, since 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 6 other species of mammal from diverse animal families (a cercopithecid, a phascolarctid, a phalagerid, 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.

Since the act of travelling is known to produce particularly high forces [25], we also carried out controlled trials with twelve 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.

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## 2.  MATERIALS AND METHODS

### 2.1 Tag deployments on free-ranging species

We selected 4 species of free-living carnivores for detailed analysis, exemplifying about 2 orders of magnitude of mass; 10 lions *Panthera leo* (mean mass *ca.* 152 kg), 1 cheetah *Acinonyx jubatus* (mass *ca.* 41 kg), 10 badgers *Meles meles* (mean mass *ca.* 9.1 kg) and 5 pine martens *Martes martes* (mean mass 1.9 kg), and fitted them with collar-mounted tri-axial accelerometers ('Daily Diaries - Wildbyte Technologies [http://www.wildbytetechnologies.com/]; measurement range 0-16 *g* [resolution 0.49 m*g*], recording frequency 40 Hz), all of which constituted less than 3% of the mass of the animal carriers (Table S1). Due 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 <3% of the carrier mass (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

Supplementary Materials.


**2.2 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 (Table S2),

were volunteered by their owners and the RSPCA's 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 %

181     carrier body mass). All trials were approved by the Swansea University Animal Welfare Ethical

182     Review Body (ethical approval number IP-1617-21D).

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184     Each dog was encouraged to traverse along a 25 m stretch of level, short-cut grass at slow

185     (walk/amble), moderate (pace/trot) and fast (canter/gallop) speeds (because gait affects

186     acceleration signatures substantially [24]) wearing collar-tags equivalent to 0, 1, 2 and 3% of

187     their body mass (twelve gait and tag mass combinations) and trial order was randomized. Posts

188     were spaced every 5 m along the track. A stopwatch was used to record the time taken (to the

189     nearest s) for a dog to travel 20 m in order to calculate an average speed of travel (m s$^{-1}$).

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191     **2.3 Data processing**

192

193     In all cases of animals equipped with accelerometers, the 3 channels of raw acceleration data

194     were converted to a single metric by calculating the vectorial sum of the acceleration following

195     Vect sum = $\sqrt{(a_x^2+a_y^2+a_z^2)}$, where a is the instantaneous acceleration and the subscripts denote

196     the different (orthogonally placed) acceleration axes. We chose to use the Vect sum rather than

197     dynamic body acceleration metrics [26] because DBA values do not represent peak accelerations

198     due to the gravity-based component being removed [27]. The specifics of the surge, heave and

199     sway accelerations were not considered separately due to some collar roll. In the case of the free-

200     living carnivores, we examined how travel gait affected the Vect sum by plotting the cumulative

201     frequency distribution from each species during periods of walking, trotting and bounding.

202

For the domestic dogs, we selected the maximum 4 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 in the dogs.

We standardized the use of four peaks because at the highest speeds some dogs only had four full

waveforms during the test stretch. Gait was assessed visually in the dogs as a walk, trot or bound.

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*).


**2.4 Tag-based acceleration method (TbAM)**


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.


**2.5 Statistical analyses**


Linear mixed-effects models were conducted in R (version 4.0.3, [28]) within the 'Lme4'

package (version 1.1-26) in order to investigate how the period between acceleration peaks, 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 (covariate) and gait (fixed

factor) influenced peak accelerations and consequent forces exerted by the tags. Dog ID 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 q-q 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.

3. **RESULTS**

**3.1 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. Fig 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 (Fig. 2). Cumulative frequencies of all acceleration values showed increasing acceleration from walking through

249    trotting to bounding and typically had a roughly logarithmic-type curve for all gaits and animals

250    (Fig. 1). The percentage time during which the tags carried by the carnivores had acceleration

251    exceeding 1 $g$ during specified activity, varied between a mean minimum of 31% for walking

252    badgers to 88% for bounding cheetahs (Table S3). Furthermore, while differences in species

253    acceleration distributions were not readily apparent for their walking gaits, the percentage time

254    during which acceleration was in excess of 1 $g$ was greatest during bounding, with cheetahs

255    showing the highest values in this category (green line with circles in Fig. 1). Mean peak

256    accelerations per stride across species varied between 1.37 $g$ (SD 0.05) and 6.25 $g$ (SD 0.79) for

257    walking and bounding cheetahs, respectively (Table S4). The maximum recorded value was 18.1

258    $g$ in a cheetah assumed to be chasing prey.

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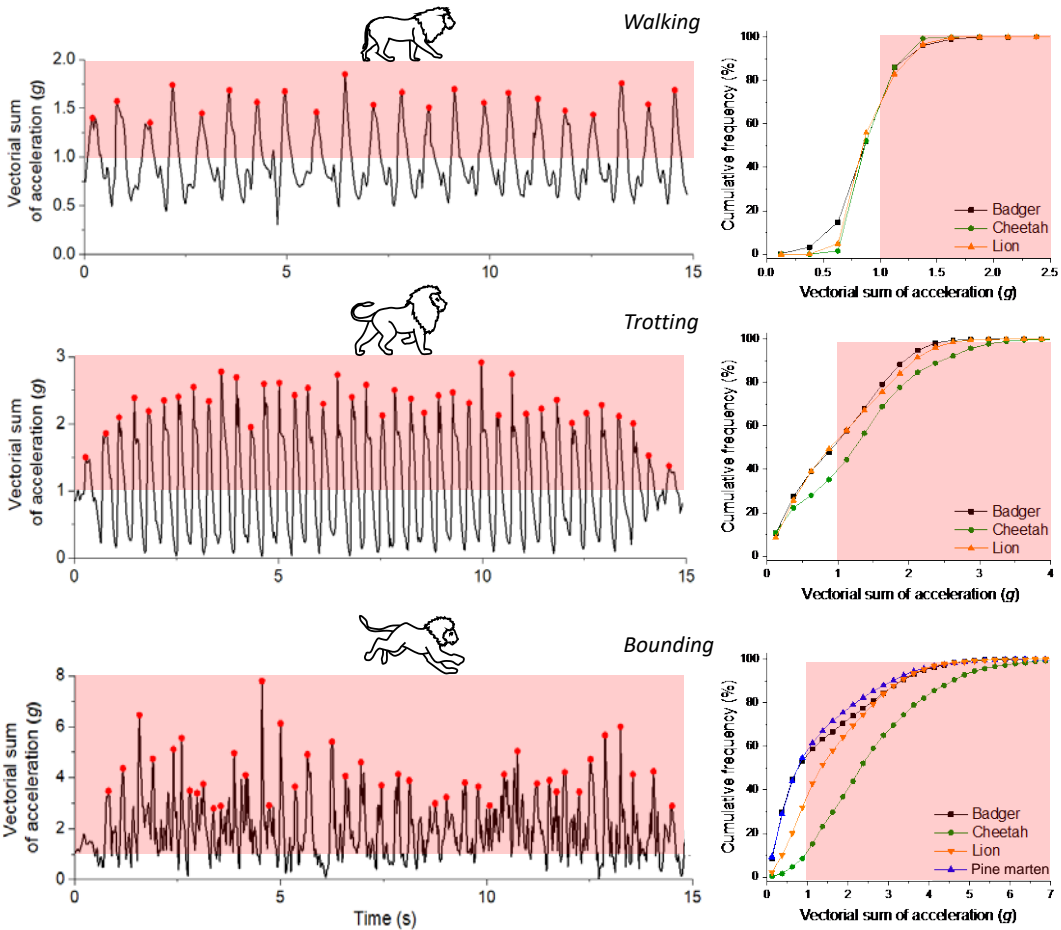
**FIGURE 1 Acceleration signatures vary according to gait and lifestyle**. Left-hand panels;

Acceleration signatures recorded by collar-mounted tags on a lion according to activity. The red

areas show when the acceleration exceeded that of gravity (note the changing scales with gait).

Right-hand panels; Cumulative frequency of all acceleration values for four free-living

carnivores according to gait. Note that the pine martens never walked or trotted.

Across the four species, gait was the main factor dictating peak acceleration (Fig. 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: $F_{2,\,208}$=1083.07, $P$<0.0001; body mass: $F_{1,\,19}$= 3.00;

$P$=0.100, Table S5). The period between acceleration peaks was greater for larger species during

271  slower gaits, but not for bounding (a linear mixed-effects model demonstrated a significant

272  interaction effect between body mass and gait: $F_{2, 209}= 3.00$, $P<0.0001$, Table S5).
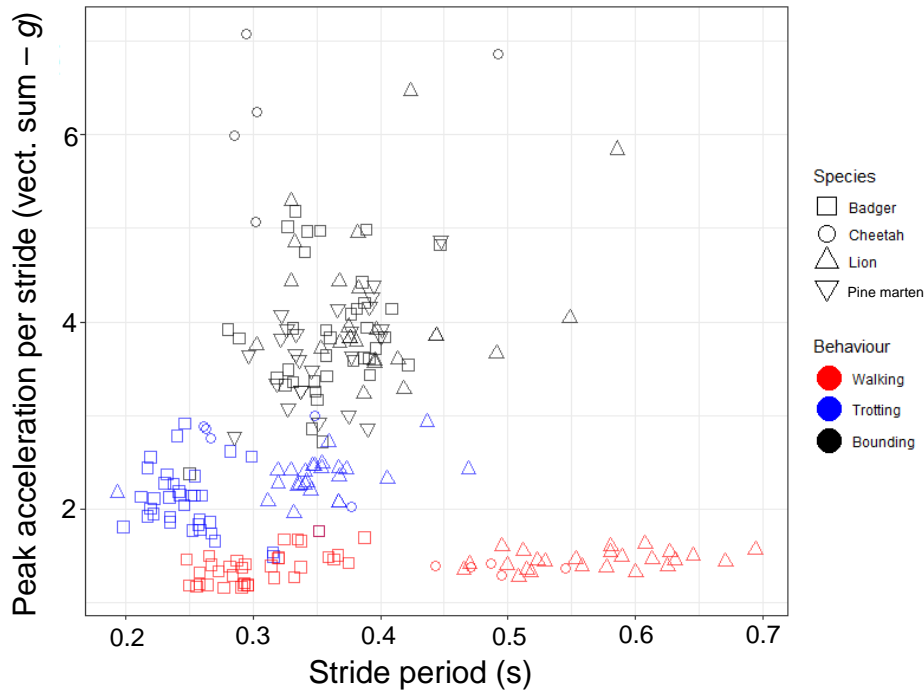


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274  **FIGURE 2 Body mass and stride period do not dictate peak tag acceleration.** Distributions

275  of peak amplitudes of (the vectorial sum of) accelerations and stride periods for four free-living

276  carnivores (see symbols, with mean masses of *ca.* 2 kg, 9 kg, 41 kg and 152 kg for the pine

277  martens, badgers, cheetah and lions, respectively) travelling using different assumed gaits

278  (colors). Each individual point shows a mean from a duration of activity >5 s from a single

279  individual. See also Fig. S1 for similar data from domestic dogs.

280

281  There was also appreciable variation in the vectorial sum of the acceleration within gaits and

282  between sexes, as exemplified by prey chases by lions. Here, mean peak acceleration per stride

283  across females and males increased from about 3 *g* at the outset to a maximum of about 3.8 *g*

284  before decreasing again (Fig. 3). However, female peak acceleration was approximately 1 *g*

higher than males for the duration of the chase (Fig. 3). Given that females and males were

wearing tags that amounted to 0.72% and 1.02% of their mean body masses, respectively (Table

S1), this translates to tag-dependent forces corresponding >2% and >4% of the gravitational

force exerted on the animal's body masses, respectively (Fig. 3). In the case of the cheetah, which

showed the highest peak vectorial acceleration sum of our study animals, a 3% tag would impose

forces equivalent to 54% of the gravitational force exerted on the animal's body at this time.
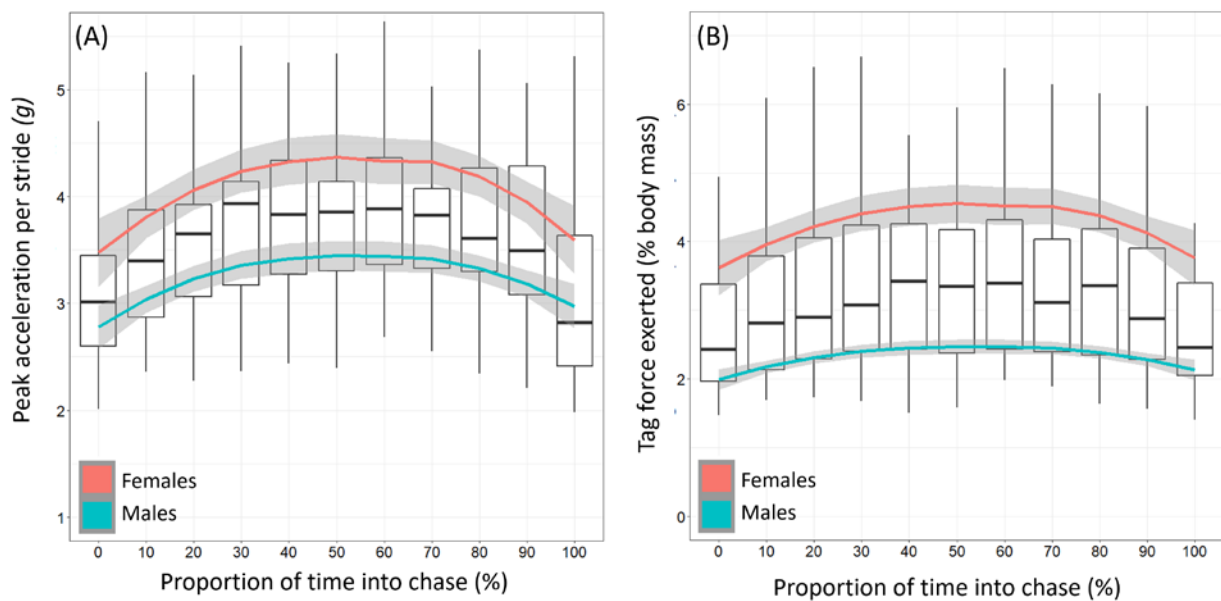


**FIGURE 3  Hunting lions experience maximum tag forces mid-chase and show substantial inter-sex differences.** Box and whisker plots [bold horizontal bars show means, boxes inter-quartile ranges and whiskers 1.5 X IQR] of the; (A) vectorial sum of the acceleration peaks per bound [cf. Fig. 1] and (B) the tag-based forces exerted as a percentage of the gravitational force exerted on the animal's body (because our tag constituted 1.02% and 0.72% of the female and male body weights, respectively – see Table S1) for lions chasing prey as a function of the percentage progression into the chase (considered to have started when bounding began). Red and blue lines show grand means for 5 females and 5 males, respectively. The maximum

301     acceleration was 15.1 $g$, which would equate to a 3% tag exerting a force equivalent to 45.3% of

302     the gravitational force exerted on the animal's body.

303

304     In dogs, stride peak accelerations increased linearly with travel speed (Fig. 4), but at greater rates

305     with increasing relative tag mass (there was a significant interaction effect between travel speed

306     and tag % body mass: $F_{1,\,500.77} = 4.44$, $P$=0.004, Table S6).  There was also a significant

307     interaction effect between gait and tag % body mass on stride peak accelerations ($F_{1,\,498.57} = 4.33$,

308     $P$=0.0002, Table S4). Peak accelerations ranged from 4-18 $g$ during bounding with collar tags

309     equivalent to 3% of the carrier body mass (Fig S2). In this scenario, movement of the tag relative

310     to the body (flapping/ swinging) was exacerbated and, as a consequence, the force exerted by the

311     tags ranged from 20-50% of the gravitational force exerted on the carrier animal's body mass

312     (Fig S3).

313

314     Stride peak accelerations were largely invariant with body mass ($F_{1,10.12} = 3.51, P$=0.090, Table

315     S6) across dog breeds for any given gait (Fig. S2). Consequently, the peak forces exerted by the

316     tags were directly proportional to tag mass and body mass. Accordingly, relative forces (force as

317     a percentage of normal carrier body mass) were independent of carrier body mass (Table S6, Fig.

318     S3).

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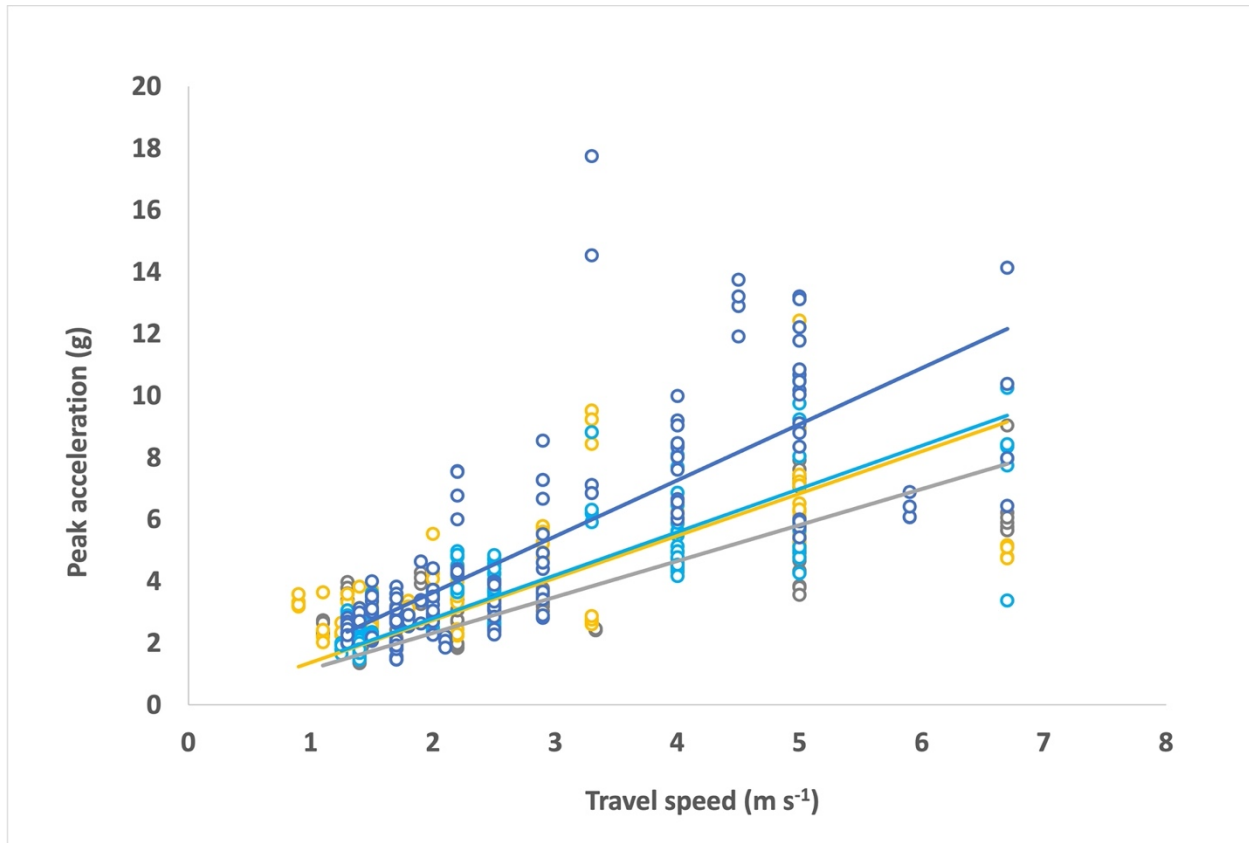
**FIGURE 4 Travel speed and tag mass influence tag peak acceleration.** The relationship

between peak accelerations and travel speed for 12 individual dogs (masses 2-45 kg), colored

according to the percentage mass of the tag relative to the carrier; 0% (grey, $y = 1.16x$, $R^2$=0.93),

1% (yellow, $y = 1.37x$, $R^2$=0.86), 2% (light blue, $y = 1.40x$, $R^2$=0.92), 3% (dark blue, y = 1.81x,

$R^2$=0.87). Data points are the four greatest peaks in acceleration per 20 m per gait and dog.

**3.2 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. Fig. 1) for all

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10 study species for periods when animals were considered active and these all showed a characteristic sigmoid pattern (Fig. 5a). These relationships were displaced further to the right as higher acceleration activities accounted for an increasing proportion of any animal's time (Fig. 5a). 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 (TbAM); 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 (Fig. 5b). We note, however, that even these corrected tag masses would effectively exceed the 3% rule conditions for 1/20th 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 (Fig. 5b). 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%.
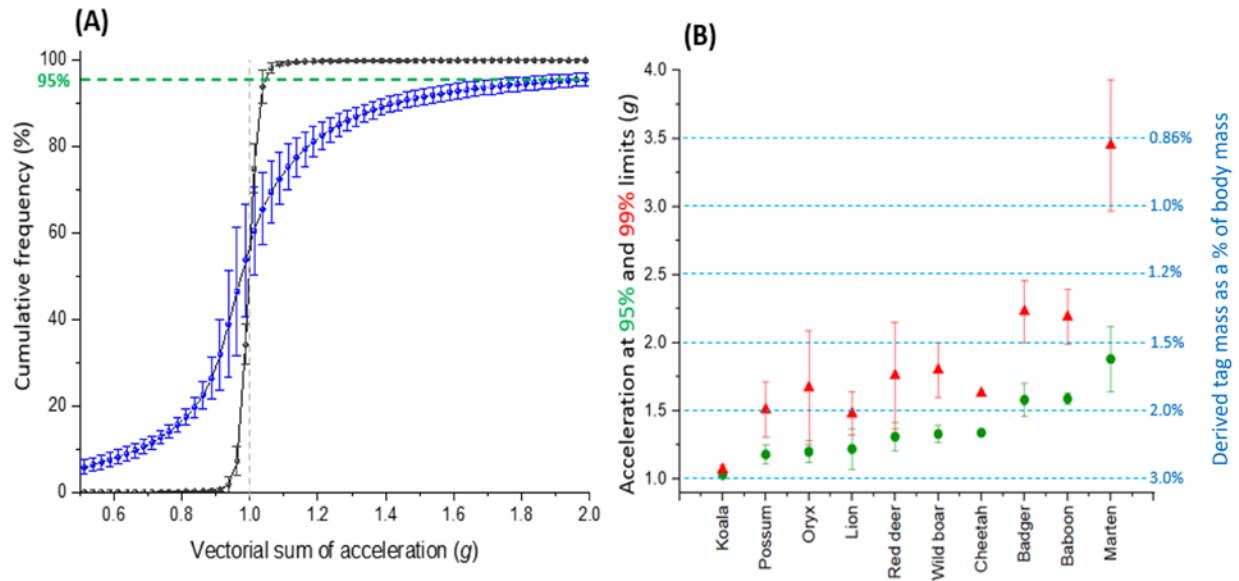
**FIGURE 5 Defining tag mass limits based on cumulative time spent experiencing tag forces.** (A) shows the mean cumulative frequency (bars = SD) of the vectorial sum of the acceleration for two arboreal animals with very different athleticisms: 5 koalas (black line) and 5 pine martens (blue line). The 95% limit is shown by the dashed green line. (B) shows these two species points (and the 99% limits in red) 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).

## 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

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367 to the device. One direct aspect that exemplifies this is, for example, measurable physical harm

368 to the animal, such as pressure sores [12], the severity of which might be expected to depend on

369 movement patterns. However, physical harm can also effectively occur if tagged animals or their

370 offspring cannot balance energy budgets due to compromised foraging stemming from tag

371 interference  [6, 30, 31]. Often, this is simply a result of higher movement costs or reduced

372 performance in tagged animals as they travel [18]. This also means though, that precise limb

373 kinematics may be different in travelling tagged animals, and this will affect acceleration signals

374 recorded by animal-attached tags, which is relevant to a study such as ours. So, measurement

375 affects performance [32] and we must bear this caveat in mind when we advocate that our tag

376 data represent the norm of untagged animals. Against this, however, we can and should use

377 proper physical frameworks to assess tag detriment because this is precisely what our tagged

378 animals experience, whether their movement is 'normal' or not, because we have specifically

379 equipped them with the source of detriment. Indeed, this is the fundamental premise behind our

380 work although the issue of what untagged animals may experience remains problematic [5].

381

382 A rigid vehicle accelerating in a straight-line only experiences acceleration in the longitudinal

383 axis. In contrast, the multiple limb-propelled motion of an animal with a flexible body produces

384 complex three-dimensional trunk accelerations owing to the changing limb accelerations [23]

385 caused by multiple muscle groups that ultimately transfer mechanical energy and affect shock

386 absorption [33], and the mechanical work conducted within each stride [34]. Ultimately, the

387 magnitude of trunk accelerations depends on the combined acceleration of the limbs, and the

388 masses of those limbs  (cf [23]). Thus, animals engaging in high performance activities are

389 expected to produce high body accelerations, and have physiological and anatomical adaptations

390 to enhance performance, such as fast twitch muscles [35], and tendons designed for greater

391 storage and release [36], which will increase this. Through all these complexities, tags mounted

392 on the trunk of an animal result in greater forces being imposed that scale linearly with the

393 acceleration of the tag and its mass. Consideration of animal lifestyle then, can already inform

394 prospective tag users of the likely scale-up of the tag forces beyond the 1 $g$ normally considered

395 for tag detriment because force = mass X acceleration, the repercussions of which are discussed

396 below in terms of potential detriment. Consequently, the 3-5% mass limits for slow-moving

397 animals, such as sloths (Bradipodidae) or koalas (Phascolarctidae) (Fig. 5), seem most

398 appropriate, though this does not mean that tags will not affect the animals. Against this, the 3-

399 5% mass limits may be less appropriate for pursuit predators, such as wild dogs (*Lycaon pictus*),

400 regularly jumping animals like kangaroos (Macropodidae) or martens (Mustelidae) (Fig. 5) and

401 rutting ungulates (Ungulata). Beyond that, in our small sample of carnivores at least, which

402 nonetheless covers about two orders of magnitude in mass, it seems that peak acceleration

403 associated with gait varies little with mass, although larger animals have longer stride periods

404 (Fig. 2 – cf. [37]). If these animals were to carry tags constituting 3% of their normal body mass,

405 mean peak forces imposed by the tags would constitute *ca*. 4.5%, 6% and 12% of the

406 gravitational forces exerted on the animals' bodies for walking, trotting and bounding gaits at

407 frequencies of between 1.6 and 4 times per second (for walking lions and trotting badgers,

408 respectively - Fig. 2, Table S2). We also note how minor differences in sex-dependent tag

409 masses coupled with differences in performance affect the forces imposed by the tags, as

410 exemplified by the lions (Fig. 3) and how, were the tags in this study to constitute 3% of the

411 animals' masses, the tag-based forces would scale up accordingly. Against all this, we recognize

412 two important trends; (i) that as animals get larger, deployed tags on them are likely to be a

413    smaller fraction of their mass anyway but that (ii) despite miniaturization advances in tag

414    technology, researchers continue to deploy systems that are around the 3-5% mass limit on

415    smaller animals [21].

416

417    Importantly, tag attachment is relevant in translating the acceleration experienced by the

418    animal's trunk into tag-dependent forces acting on the animal, with collars predicted to be

419    particularly problematic. A tag that couples tightly with its carrier's trunk, such as one attached

420    with tape to a bird [38] or glue to a marine mammal [39], experiences acceleration that closely

421    matches that of its substrate, so it exerts forces at a site where most of the animal's mass lies. In

422    contrast, a device on a looser-fitting collar of a moving tetrapod not only exerts forces on the

423    (less massive) head and neck areas, rather than the animal's trunk, but the tag also oscillates

424    between essentially two states: One is analogous to 'freefall', which occurs between pulses of

425    animal trunk acceleration in the stride cycle which project the collar in a particular direction

426    owing to its inertia and lack of a tight couple with the neck. The collar is therefore subject to

427    peaks in acceleration when it interacts with the animal's neck, causing greater collar acceleration

428    than would be the case if it were tightly attached to the animal's body (cf. peaks in Fig. 1). This

429    explains why Dickinson et al. [40] reported that acceleration signatures from collar-mounted tags

430    deployed on (speed-controlled) goats *Capra aegagrus* became increasingly variable with

431    increasing collar looseness, and is analogous to the concerns related to injuries sustained by

432    people in vehicles depending on seatbelt tightness [41]. Partial answers to minimizing such

433    problems may involve having padded collars that should reduce acceleration peaks, making sure

434    that the tags themselves project minimally beyond the outer surface of the collar and having

435    wider collars to reduce the pressure.

436

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 X 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 (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]). But

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].

453

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

459    body mass, and therefore experiencing an additional force equivalent to up to 16 kg during every

460    bound of a prey pursuit, might have its hunting capacity compromised. We note that the survival

461    of such animals is believed to be especially sensitive to the proportion of successful hunts (cf.

462    [47]), which calls for critical evaluation of performance between tag-wearing and unequipped

463    animals, or animals equipped with tags of different masses (cf.[32]).

464

465    In the meantime, our suggested approach of setting tag mass limits based on the overall

466    (corrected) forces being less than 3% of the gravitational force exerted on the animal's body for

467    95% of the active time should go some way to getting a more realistic assessment of the potential

468    for detriment. Where researchers adopting this approach do not have appropriate acceleration

469    data for their study animal, they could use a surrogate species, perhaps from an online database.

470    Such a resource should define the length of time that study animals were equipped to derive the

471    acceleration frequency distribution because animal activities (and therefore the acceleration

472    signals associated with them) occur variously over time. For this, longer periods are obviously

473    better, but a pragmatic approach might be to plot cumulative frequencies of the vectorial sum of

474    the acceleration as a function of recording time to see how they change or tend towards a stable

475    value as the monitoring period increases. In this, we note that seasonal variation in animal

476    behaviours, such as occurs in rutting ungulates, have potential to affect the distribution

477    substantially, emphasizing the importance of considering the context under which the data were

478    gathered.

479

480    Importantly, we do not advocate the 3% rule as such, but recognize that it has been widely

481    adopted and could serve as a useful starting point with which to consider tag detriment if

482  calculated as we have suggested here. In this, cognizance should also be given to the extent of

483  tag forces for periods above the 95% threshold because, where these are excessive, it may be

484  appropriate to use a 99% threshold or higher to derive appropriate tag masses. Notably though,

485  even 99% limits do not highlight the high tag forces developed during prey pursuits exhibited by

486  the cheetah. We suggest that the solution to this lies in more detailed consideration of the

487  animal's lifestyle; in particular, identifying survival-critical behaviours with exceptionally high

488  accelerations. Such periods may persuade ethics bodies to raise their thresholds still further.

489  Underpinning this will be ongoing miniaturization, where tags benefit from the sensor revolution

490  in human wearables, which will undoubtedly percolate through to animal applications: Advanced

491  smart phones have >10 sensors, along with significant memory and data transmission

492  capabilities, and typically weigh 150 - 200 g or about 0.2 % of average human body mass,

493  although human wearables benefit from regular contact with charging systems while many

494  wildlife tag applications are projected for long-term deployments (e.g.[48] that either necessitate

495  correspondingly large batteries or autonomous charging systems, both of which increase the

496  mass of tags [49].

497

498  Finally, consideration of the acceleration-based forces generated by animal-attached tags does

499  not cover all forms of detriment because other forces are at play, such as greater drag in

500  swimming- and flying species (cf.[6]), and more esoteric elements, such as device colour, that

501  affect animal behaviour [50]. However, our framework should take the current 'one-size-fits-all'

502  basic 3% rule into an arena where quantitative assessment of acceleration can be compared to the

503  myriad of tag-influenced behaviours recognized by the community to link animal lifestyle to

504  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.

**DATA AVAILABILITY STATEMENT:** Data pertaining to this study are available on dryad

XXXXX

**AUTHORS' CONTRIBUTIONS**

Conceptualization: RPW, KARR

Methodology: RPW, KARR

Investigation: RG, SHB, NM, JPT, JH, JA, BMA, DAW, NCB, MCC, RH, VS, MP, MJ, AA,

DMS

Software development: MH

Visualization: RPW, RG, MH, KARR

Supervision: RPW, KARR

Writing—original draft: RPW, KARR, DMS

Writing—review & editing: All authors

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**SUPPORTING INFORMATION**

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661 Additional supporting information may be found online in the Supporting Information section