

METHODOLOGY

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# What acceleration data from wildlife collars and animal body mass tell us about seed dispersal

Carsten M. Buchmann<sup>1\*</sup>, Lukas Dreyling<sup>1</sup>, Mihaela Constantin<sup>1</sup> and Frank M. Schurr<sup>1</sup>

## Abstract

**Background** The seeds of many plant species can be dispersed over long distances in animal fur (epizoochory). Quantifying epizoochory in the wild is, however, challenging, since it is difficult to measure the retention times of seeds in fur. These retention times depend on the acceleration that seeds experience and that can detach seeds from fur. Wildlife collars containing accelerometers may thus provide crucial information on epizoochorous seed dispersal. However, this is only the case if acceleration of the animal's neck (where collars are attached) is informative of acceleration of the animal's main body (where most seeds are transported).

**Methods** We used accelerometers to simultaneously measure acceleration at the neck, breast and the upper hind leg of 40 individuals of eight mammal species spanning a large range of body masses (26–867 kg). We then quantified maximum acceleration as the 95%-quantile of the resultant acceleration (of all measured values in data intervals of 5 s).

**Results** Maximum acceleration was comparable between the neck and breast but substantially higher at the hind leg. Maximum acceleration measured by neck collars and body mass jointly explained 81% of the variance in maximum acceleration of the breast and 62% of the variance in maximum acceleration of the leg.

**Conclusions** Acceleration measured by neck collars is informative of the acceleration experienced by seeds attached to other body parts (breast and leg). When combined with animal movement data and lab measurements of how fur acceleration affects seed release and retention times, widely used collar accelerometers can thus be used to assess distances of epizoochorous seed dispersal.

**Keywords** Body acceleration, Contact separation force, Epizoochorous seed dispersal, Wildlife collar, Mammals

## Background

Animals are among the most important vectors for long distance dispersal of plant seeds [14, 22, 30]. They disperse seeds via endozoochory (passage through their digestive system, e.g., [16, 26]). However, many animals

(notably mammals) also transport large numbers of seeds of many plant species via attachment to the exterior of the body (epizoochory). A major challenge in the understanding and prediction of epizoochorous seed dispersal is the quantification of seed detachment from the animal. Consequently, we lack information on the retention time of seeds in animal fur, a crucial parameter for quantifying seed dispersal and dispersal distances [30]. This study aims at quantifying and explaining shaking movements, relevant for seed detachment from different parts of mammal bodies. In particular, it evaluates whether wildlife collars fitted with accelerometers, that are now widely

\*Correspondence:

Carsten M. Buchmann

carsten.buchmann@uni-hohenheim.de

<sup>1</sup> Institute of Landscape and Plant Ecology, University of Hohenheim, Ottilie-Zeller-Weg 2, D-70599 Stuttgart, Germany



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used on wild animals, can inform us on the process of seed detachment.

Two aspects of epizoochorous seed dispersal, namely, seed attachment to the fur and animal movement are comparatively well-studied by moving animal furs through/along vegetation [13], combing furs of wild animals (e.g., [20]) and recording animal movement with modern tracking technology (e.g., [18, 40]). However, the quantification of seed detachment, which determines seed retention time and hence dispersal distance, is more challenging, since epizoochorously dispersed seeds are typically small, hidden in animal fur and cannot be observed without altering animal behaviour [29].

Since it is difficult to investigate seed detachment in the wild, previous studies have resorted to lab measurements of the forces needed to detach seeds from fur or the time needed to shake seeds out of the fur. They found that detachment is controlled by the interplay of the animal surface (e.g., fur properties) and seed morphology (e.g., appendages like hooks), which determines the ‘contact separation force’ that is needed to detach the seed from the fur [10, 11, 17, 37]. On an animal body forces to release seeds can be created via shaking of the body. According to Newton’s second law of motion, the force experienced by a seed is the product of seed mass and fur acceleration. It has been shown that seed release can be induced by fur acceleration [35] and that the strength of fur shaking determines the proportion of seeds released (see Additional file 1: Figure S1).

Accelerometers, that measure acceleration at high frequency can quantify the force that seeds of a given mass experience in animal furs (according to Newton’s second law of motion, see above). Hence, accelerometers on bodies of wild animals may provide information on seed detachment from and seed retention in fur. Thanks to rapid advances in GPS telemetry in the last decade [6, 19] more and more studies measure animal acceleration in the wild, since nowadays many commercially available GPS tracking collars (e.g., Eobs, Vectronic aerospace, Biotrack) are equipped with three-dimensional accelerometers and the recording of acceleration data does not cause much additional effort and costs (apart from battery life and storage space). These data can be used to infer animal activity, energy budgets or even specific behavioural patterns or syndromes [4, 15, 25, 34].

Acceleration measurements on wild animals are mostly taken at the neck [8, 38], whereas most seeds are attached to lower parts of the animal torso and the legs (compare [1, 27, 32]). However, it is largely unclear how acceleration of animal necks is related to acceleration of other body parts. Moreover, such relationships may depend on properties of the animals, notably their body mass. In general, smaller animals show faster (limb) movements

which should result in higher acceleration of their body and hence larger forces acting on seeds in their fur (compare [7, 9, 24]). In contrast, higher inertia of the torso of larger animals could possibly result in a weaker link between the acceleration of the limbs and the neck.

To assess the value of collar accelerometers for assessing epizoochorous seed dispersal by wild animals, we measured acceleration simultaneously at different body parts of mammals ranging in body mass from 26 to 867 kg. We then quantified (i) how acceleration at the breast/torso and the leg of mammals is related to acceleration at the neck of animals, and (ii) how this relationship depends on animal body mass.

## Methods

We measured three-dimensional acceleration on different sections of the animal body for 40 individuals of 13 breeds of 8 mammal species kept at the Agricultural Science Faculty of the University of Hohenheim and Wilhelma Zoological Garden, Stuttgart (Table 1, Fig. 1). To this end, accelerometers were attached with nylon straps (2.3 cm wide, metal buckles) to the neck, breast and hind leg (shank, between knee and heel) of the animals. Deployment of sensors to the breast and leg was easily feasible and caused minimal distress for the animals. Where necessary (e.g., for goats with short fur and thin legs), sensors were additionally fixed to the upper leg of the animals with adhesive elastic bandages. Animals were then left to move for at least 5 min in their enclosures (indoors and outdoors) with the aim of recording a minimum of three time segments of at least 5 s with (i) walking-like movement and (ii) running movement. If necessary and possible animals were tempted to move by leading them on a leash (camel, horse) or gently chasing them (sheep, goat). This research was approved by the animal welfare officer of the University of Hohenheim (Nr. S 476/18 LÖ).

Sensors used were two MSR 165 (MSR Electronics GmbH, Seuzach, Switzerland), recording continuously, and e-obs GPS and acceleration neck collars (e-obs GmbH, Grünwald, Germany), recording acceleration in so-called “bursts” of 330 values (3.3 s) followed by a (technically inevitable) gap of approx. 1.4 s. Positions of the different sensors were randomly alternated. Still, a large e-obs sensor (tag 1653) was only used with four individuals, a smaller e-obs sensor (tag 4462) was more often used at the leg, since it was less disturbing for the animal and could be attached more easily and stable at the leg compared to the slightly heavier MSR sensors. Before use all four sensors were tested for comparability by simultaneously measuring the movement of a laboratory shaker. This showed negligible variation between sensors (max. 3.5% variation in maximum acceleration

**Table 1** List of species and individuals used for the study including additional information on the animals and study conditions. Locations were all in Baden-Württemberg, Germany; Wilhelma Zoological Garden and research facility Hohenheim “Meiereihof” are in Stuttgart, the research station Hohenheim “Unterer Lindenhof” is located in Eningen unter Achalm

Species	Breed	Individuals	Individuals with leg acceleration measurement	Body mass range (kg)	Range of the length of hind leg (cm)	Location	Ground surface
Camel ( <i>Camelus ferus</i> )	Bactrian Camel	3	3	580–800	94–103	Wilhelma Zoological Garden	Soil (outdoors)
Cow ( <i>Bos Taurus</i> )	Holstein–Friesian Cattle	3	3	715–867	97–100	Hohenheim (“Meierei-hof”)	Concrete, plastic (indoors)
Cow ( <i>Bos taurus</i> )	Jersey Cattle	3	1	169–465	76–83	Hohenheim (“Meierei-hof”)	Concrete (outdoors)
Donkey ( <i>Equus asinus</i> )	Poitou	3	3	470–530	83–90	Wilhelma Zoological Garden	Soil (outdoors)
Goat ( <i>Capra aegagrus</i> )	Bunte Deutsche Edelziege	5	4	39–86	43–53	Hohenheim (“Meierei-hof”)	Concrete with straw cover (indoors)
Goat ( <i>Capra aegagrus</i> )	West African Dwarf	2	1	26–28	30–34	Wilhelma Zoological Garden	Concrete (outdoors)
Horse ( <i>Equus ferus caballus</i> )	Dülmener Horse	2	2	246–293	74–77	Wilhelma Zoological Garden	Soil (outdoors)
Horse ( <i>Equus ferus caballus</i> )	Shetland Pony	2	2	157–178	57–64	Wilhelma Zoological Garden	Soil (outdoors)
Mule ( <i>Equus mulus</i> )	–	1	1	292	72	Wilhelma Zoological Garden	Soil (outdoors)
Sheep ( <i>Ovis aries</i> )	Cameroon Sheep	4	4	27.5–50	38–43	Wilhelma Zoological Garden	Concrete (outdoors)
Sheep ( <i>Ovis aries</i> )	Merino	5	3	76–122	48–60	Hohenheim (“Meierei-hof”)	Concrete with straw cover (indoors), concrete and soil (outdoors)
Pig ( <i>Sus scrofa domesticus</i> )	Deutsche Landrasse x Pietrain	5	5	32–275	28–52	Hohenheim (“Unterer Lindenhof”)	Concrete (indoors)
Pig ( <i>Sus scrofa domesticus</i> )	Kunekune	2	0	90–120	26–28	Wilhelma Zoological Garden	Soil (outdoors)

Locations were all in Baden-Württemberg, Germany; Wilhelma Zoological Garden and research facility Hohenheim “Meiereihof” are in Stuttgart, the research station Hohenheim “Unterer Lindenhof” is located in Eningen unter Achalm

of any single sensor from the mean of all sensors). All sensors were set to record at 100 Hz (i.e., each of the three axes would record at 33.3 Hz). Temporal synchronization of all collars/sensors was achieved by starting a 0.1 s resolution stop watch at the same time as manually shaking all three sensors for approx. 15 s. This “extreme acceleration event” could later easily be recognized at the beginning of the data series of all sensors and defined the beginning of the specific measurement session. The time of the stop watch was used as reference for any observation during the animal trials that could be linked to the data series (start and end of valid recording period for any animal). Body mass of each individual was obtained from the respective zookeepers (last weighing).

Acceleration data series were calibrated (raw measurement values transformed to  $m/s^2$ ) according to manufacturer instructions and visually checked for synchronism between neck breast and leg. For each animal

the acceleration timeseries were cut into 5 s intervals on which analyses were performed. We chose an interval length of 5 s, since this was short enough to cover only a single type of behaviour but long enough to minimize the impact of recording gaps of the e-obs sensors (see above). We did, however, repeat all analyses with 10 s intervals and found that this did not notably change results.

From acceleration measurements in three dimensions, we calculated body acceleration by calculating the resultant acceleration vector (resultant acceleration =  $\sqrt{\text{acceleration}_X^2 + \text{acceleration}_Y^2 + \text{acceleration}_Z^2}$ ) and subtracting gravitational acceleration ( $9.81 m/s^2$ ). We then calculated the 95%-quantile of body acceleration per 5 s interval as a measure of maximum acceleration (Fig. 2). Intervals with maximum neck acceleration  $< 0.1 m/s^2$  were excluded from further analyses, since they represent phases when the animals did not move.



**Fig. 1** Examples of animals [top left: donkey (*Equus asinus*), top right: camel (*Camelus ferus*), bottom: goat (*Capra aegagrus*)] carrying accelerometers (green arrows: MSR 165 and yellow arrows: e-obs sensor, tag 4462) around the neck, the breast and the upper hind leg. Photos taken in Wilhelma Zoological Garden in Stuttgart, Germany

To investigate how well maximum acceleration of other body parts can be explained by maximum acceleration of the neck and by an animal's body mass we fitted linear mixed-effects models (packages `lme4`, [2] in R version 4.0.2 [33]). The response variables of these models were maximum acceleration at the breast and the leg, respectively. As fixed-effect predictor variables both models included maximum acceleration at the neck and individual body mass plus the interaction of these two variables. The models also included random effects of individual nested within species on the intercept and the slope for neck acceleration (Additional file 1: Eqs. 1, 2). These random effects capture variation not accounted for by body mass (resulting from other animal traits or measurement conditions). All variables were log-transformed and scaled, to yield power-law scaling relationships.

## Results

Maximum acceleration (the 95% quantile of body acceleration per 5 s interval) varied considerably between species and individuals (Fig. 3, Additional file 1: Figure S2). Acceleration values and their variability (within an between species) were much larger at the hind leg than at the neck or breast.

Acceleration at the breast of animals is well-explained by acceleration at the neck of animals. Body mass slightly weakens the positive effect of neck acceleration on breast acceleration (negative interaction term with neck

acceleration, Fig. 4, left panel). The marginal  $R^2$  (variance explained by fixed effects only, i.e., neck acceleration and body mass) is 0.81. In addition, the acceleration at the hind leg is well-explained by neck acceleration and body mass (marginal  $R^2=0.62$ ), but here body mass increases the effect of neck acceleration on leg acceleration (Fig. 4, right panel). Coefficients of fitted models, likelihood-ratio tests and AIC values are given in the Additional file materials (Additional file 1: Tables S1, S2). Besides neck acceleration and body mass, some variability in body shaking is also explained by individuals and species (conditional  $R^2$  including fixed effects and random effect of individual nested within species was 0.89 and 0.71 for breast and leg acceleration, respectively). By back-transforming the fixed-effect components of the fitted (full) models, we obtain the following equations for acceleration A at the breast (Eq. 1) and leg (Eq. 2):

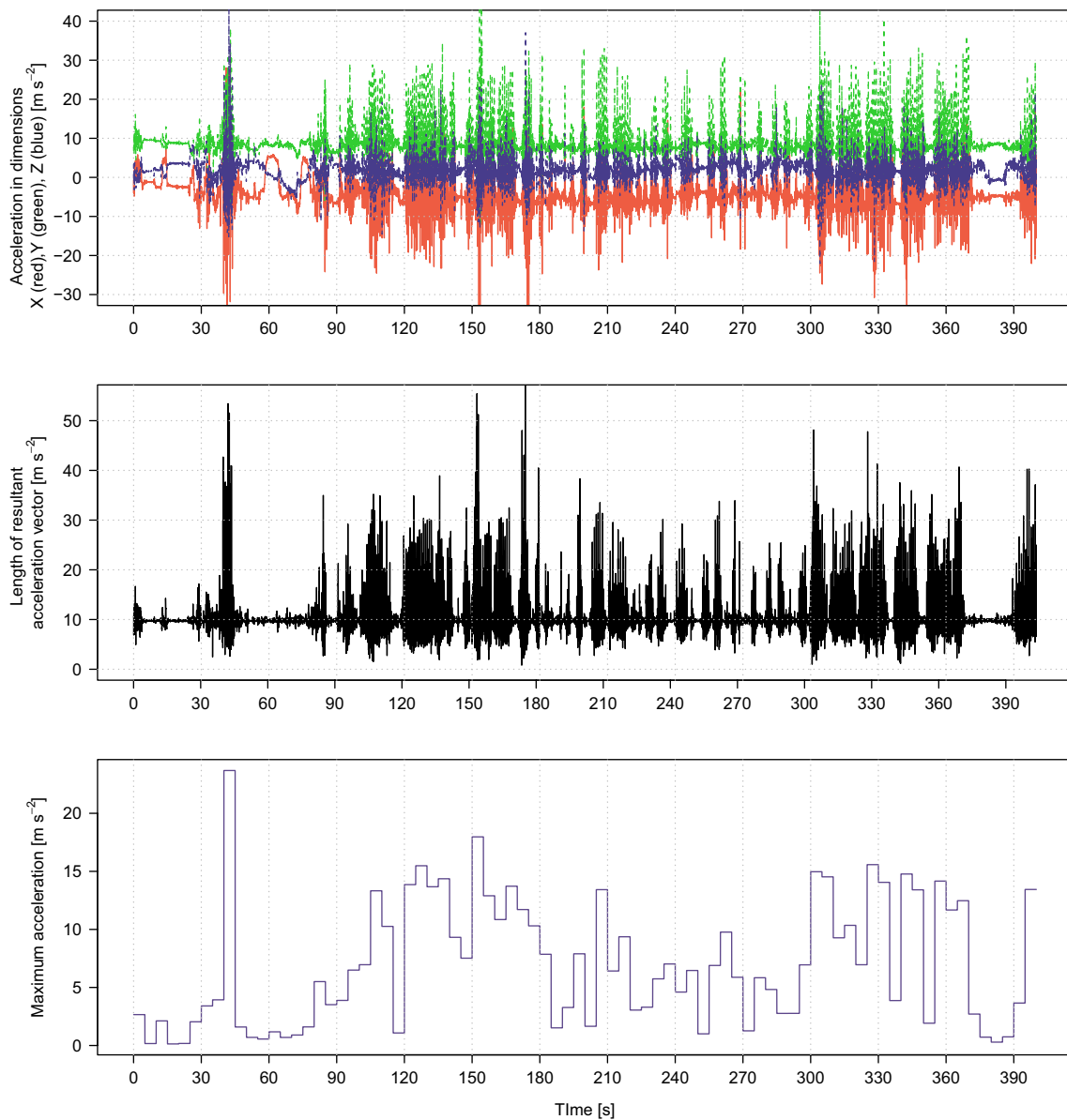
$$A_{breast} = 0.534 * A_{neck}^{1.547} * mass^{0.094} * A_{neck}^{-0.107*mass} \quad (1)$$

$$A_{leg} = 4.222 * A_{neck}^{0.922} * mass^{-0.170} * A_{neck}^{0.044*mass} \quad (2)$$

## Discussion

This study shows that maximum acceleration of the breast and leg of mammals can be predicted well from two variables that are widely available for wild mammals: body mass (the most frequently used trait in animal ecology; [5, 7, 39] and acceleration of the neck (now routinely measured by many wildlife collars). This makes it possible to translate acceleration measurements at the neck into the forces experienced by plant seeds attached to other body parts, a crucial step for assessing epizoochorous seed dispersal by wild mammals. The predictive capacity of maximum neck acceleration and body mass was somewhat higher for maximum acceleration of the breast than for maximum acceleration of the hind leg. This could be explained by the larger spatial separation of neck and hind legs. Moreover, different behaviours, walking modes, gaits or movement speeds in the moment of measurement should more directly affect leg movement and hence, cause partial independence of leg and neck acceleration. The fact that individual and species did not explain more variance of leg acceleration than of breast acceleration (both less than 10%) supports this interpretation, namely, that such behavioural aspects play an important role, especially compared to other species-specific characteristics like body composition, geometry, leg length etc.

The weaker positive effect of neck acceleration on breast acceleration for larger animals is likely to result from greater torso inertia in large-bodied animals



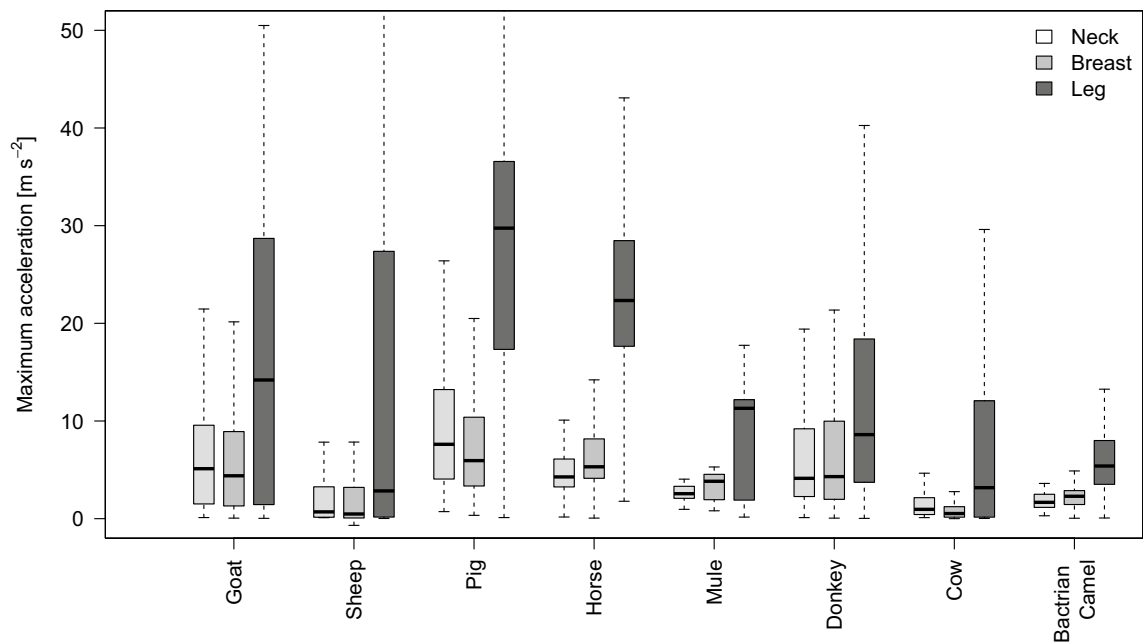
**Fig. 2** Timeseries (covering 400 s) of the acceleration measured on the neck of a goat in each of the three axes (upper panel), the length of the resultant acceleration vector (middle panel) and the maximum acceleration (lower panel). Maximum acceleration is calculated as the 95th quantile of resultant acceleration minus gravitational acceleration per 5 s interval

(compare [28]). To some extent, it may also reflect greater neck length in large animals (notably camels) which may cause weaker translation of head movements into torso movement.

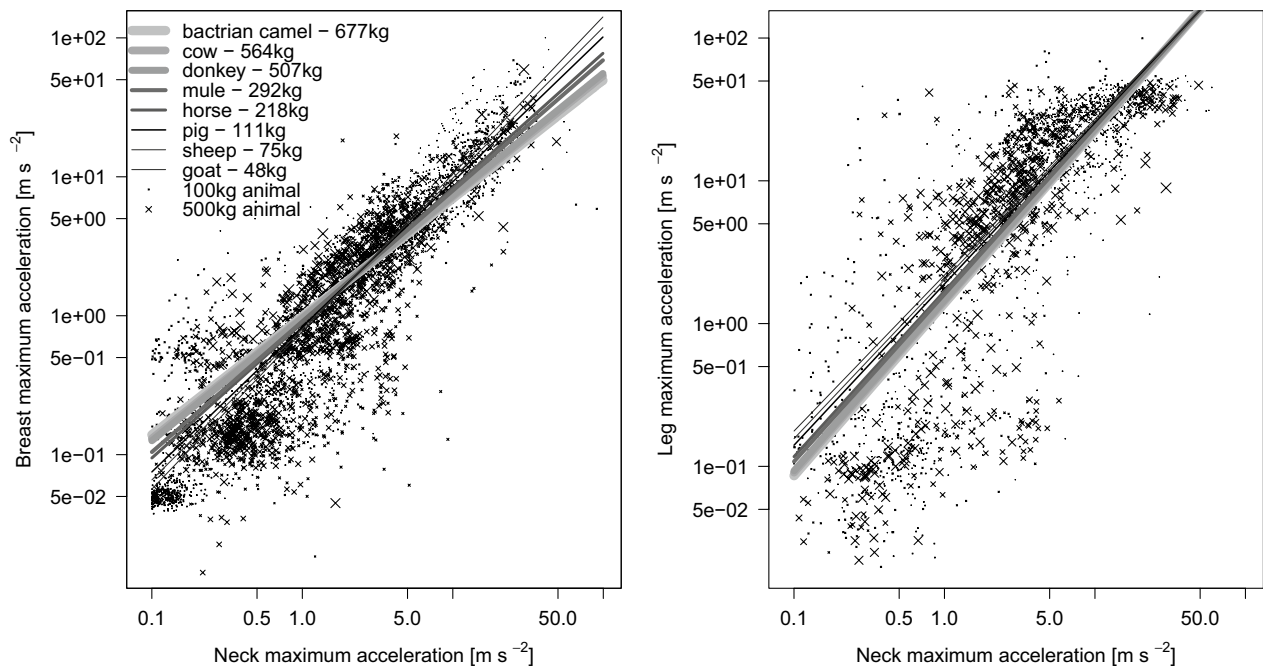
Quantification of acceleration at the body of mammals is of crucial importance for epizoochorous seed dispersal (compare [35]). For the removal of seeds with strongly attaching appendages (e.g., hooks) intentional shaking, grooming behaviour or rubbing against objects [27] are obviously very relevant. Among these at least intentional

shaking can still be recorded with acceleration measurements. However, numerous vascular plant species without obvious morphological adaptations to epizoochory, such as hooked appendages, are transported in animal furs [13]. Particularly for these seeds body acceleration while walking and running can be expected to be a very important factor causing seed release (compare Additional file 1: FigureS1).

To mechanistically predict distance of epizoochorous seed dispersal, acceleration measurements have to be



**Fig. 3** Boxplots showing maximum acceleration at the neck, breast and leg of eight mammal species (ordered by increasing mean body mass). Maximum acceleration is calculated as the 95% quantile of resultant acceleration minus gravitational acceleration per 5 s interval. Outliers are omitted for clarity



**Fig. 4** Prediction plots of linear mixed-effects models for maximum acceleration at the breast (left panel) and the hind leg (right panel). Predictions are only shown for fixed effects, namely neck acceleration and body mass; line thickness and symbol size indicate mean species body mass and individual body mass, respectively, see legend. Maximum acceleration is calculated as the 95% quantile of resultant acceleration minus gravitational acceleration per 5 s interval

integrated with other types of data. First, estimates of the acceleration and resulting force experienced by seeds need to be combined with either direct measures of the contact separation force of seeds in a particular fur [17] or with measurements of the distribution of seed retention times for given fur acceleration [35]. This will yield distributions of retention times for a specific seed-fur combination. Secondly, by combining these retention time distributions with measures of animal speed or spatially explicit movement trajectories, one can obtain distances of epizoochorous seed dispersal (analogous to [36, 40] for endozoochorous seed dispersal).

Knowledge of variation in acceleration across animal bodies may also be relevant for ecological fields other than the study of seed dispersal. Body acceleration determines the forces experienced not only by seeds but also by animals such as grasshoppers that are dispersed in fur [13]. Moreover, ecto-parasites have to spend more energy when experiencing strong and repeated acceleration, while they crawl through the fur until they reach their targeted feeding location [31]. Once an ecto-parasite started feeding, the acceleration it experiences should become even more relevant, since it determines how strongly attachment force has to increase as the parasite's mass increases [23]. Such variation in energy expenditure is likely to affect the fitness of ecto-parasites and their hosts.

## Outlook and conclusions

Acceleration measurements at animal necks contain valuable information on epizoochorous seed dispersal by wild mammals. Since such measurements are now widely available, there is considerable potential for 'recycling' them [21] to assess the dispersal services provided by wild animals [12].

### Abbreviations

Aneck	Maximum acceleration at animals' necks ( $m/s^2$ ) Quantified as the 95%-quantile of resultant acceleration
Abreast	Maximum acceleration at animals' breasts ( $m/s^2$ ) Quantified as the 95%-quantile of resultant acceleration
Aleg	Maximum acceleration at animals' hind legs ( $m/s^2$ ) Quantified as the 95%-quantile of resultant acceleration
mass	Individual body mass (kg)

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-023-00331-4>.

**Additional file 1: Figure S1.** Acceleration measured on a laboratory shaker running at three different intensities for 25 s, and maximum acceleration, quantified as the 95% quantile of the resultant acceleration in subsections of 5 s. The acceleration created by this laboratory shaker is comparable to the acceleration measured on the animal bodies. Symbols show the proportion of three herb seeds that were separated from a rabbit fur after running in each intensity for 450 s (mean  $\pm$  S.E. of three

runs, each with 15 seeds of any species placed on the fur). Note: some noise is added to the x-coordinates of the symbols to improve readability. **Figure S2.** Boxplots showing maximum acceleration (as well as acceleration) determined for 5 s subsections of acceleration data measured at the neck, breast and leg of 40 individuals of 13 breeds of 8 mammal species; ordered after individual body mass. Outliers are omitted for clarity. **Table S1.** Summary of fitted linear mixed-effects models for breast and leg acceleration. Model coefficients are for models with log-transformed and scaled variables. Likelihood-ratio tests were performed between full model and additive model for the interaction term, and for Aneck and mass they were performed between the additive model and the model containing only mass and Aneck, respectively. **Table S2.** AIC values of the full linear mixed-effects models for breast and leg acceleration and reduced simplified model versions.

### Acknowledgements

The authors thank many scientists and technicians that helped in data collection: the Biomove team at the University of Potsdam, specifically F. Jeltsch and W. Ullmann, the working groups Behavioral Physiology of Livestock and of Animal Nutrition at the University of Hohenheim and the teams at Meiereihof and Unterer Lindenhof, specifically M. Rodehutsord, V. Stefanski, B. Pfaffinger, J. Krieg, H. Trapp, W. Dunne and M. Ganser, and the team of Wilhelma Zoological Garden, specifically B. Schäfer and G. Schleussner.

### Author contributions

CMB and FMS conceived the idea. CMB organized and led data collection, analysed the data and wrote the manuscript. LD and MC assisted data collection. FMS, LD and MC assisted analysis. All authors contributed critically to the manuscript drafts and gave final approval for publication. All authors read and approved the final manuscript.

### Funding

Open Access funding enabled and organized by Projekt DEAL.

### Availability of data and materials

All data, specifically measured acceleration of all animals, are published at figshare.com: <https://doi.org/10.6084/m9.figshare.20182100.v1>

## Declarations

### Ethics approval and consent to participate

This research was approved by the animal welfare officer of the University of Hohenheim (Nr. S 476/18 LÖ).

### Consent for publication

Not applicable.

### Competing interests

The authors declare that they have no competing interests.

Received: 8 November 2022 Accepted: 20 April 2023

Published online: 18 May 2023

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