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METHODS & TECHNIQUES

Measurement of voluntary bite forces in large carnivores using a semi-automated reward-driven system

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ABSTRACT

Bite force is a key performance trait of the feeding system, but maximal *in vivo* bite force has been measured in few large mammals. The alternative, modelling of bite force from anatomy, cannot be validated without *in vivo* measurements. To overcome existing limitations of ethics, safety and animal well-being, we propose a semi-automated method to obtain voluntary maximum bite forces from large mammals using bite plates that automatically dispense a food reward if an incrementally increasing threshold force value is reached. We validated our method using two Malayan sun bears, two Andean spectacled bears and a lioness. We show that voluntary bite force measurement using positive reinforcement is a non-invasive and reliable method to record maximum voluntary bite force performance in large mammals. Our results further show that *in vivo* data are critical as modeling efforts from osteology have greatly underestimated bite forces in Andean spectacled bears.

KEY WORDS: Biting, Carnivora, Environmental enrichment, Feeding

INTRODUCTION

Feeding is among the most essential interactions of an animal with its environment (Schwenk, 2000). Specializations of the feeding apparatus allow specific trophic niches to be exploited, often at the expense of taking advantage of others owing to biomechanical trade-offs (Aguirre et al., 2002; Herrel et al., 2009; Konuma and Chiba, 2007; Van Valkenburgh, 2007). The biomechanics and comparative functional ecology of the feeding apparatus has therefore been studied extensively to understand the relative roles of adaptation and functional trade-offs in driving the diversity of the feeding system (Aguirre et al., 2002; Christiansen and Wroe, 2007; Grossnickle, 2020; Herrel et al., 2002; Wroe and Milne, 2007; Wroe et al., 2005). The performance of the feeding apparatus in vertebrates includes a variety of traits such as processing rate, gape and bite force. The latter has been shown to be a limiting factor in the feeding performance of many vertebrates (Aguirre et al., 2003; Maestri et al., 2016). Beyond feeding and prey capture, the jaw–cranial system is an essential functional complex in defensive and reproductive behavior. Quantifying the performance of this complex is therefore necessary to understand the ecological role and evolution of the whole organism (Anderson et al., 2008), and can be informative in terms of conservation biology (Erickson et al., 2004; Fleming et al., 2020).

Maximum bite force is a key performance metric of the jaw–cranial system, determining dietary diversity and defensive ability in a wide range of taxa (Dumont and Herrel, 2003). Despite its importance, bite force has been measured in surprisingly few large vertebrates with the exception of crocodilians (Erickson et al., 2003). Large, and sometimes dangerous, mammals are notoriously difficult to measure the bite force of, likely owing to limited access and the inability to manipulate these animals easily. There are understandable limitations to the handling and coercion necessary to produce strong defensive bites in these animals, as such provoked defensive bites involve considerable risk to the experimenter and the animal. Furthermore, it may negatively affect the association the animal has with humans, sometimes permanently. Thus, considerations of animal well-being, ethics, conservation and safety have severely limited the availability of larger mammals for the measurement of bite forces.

To fill this gap, many researchers have used a modeling approach, yet these models cannot be validated if no actual bite force measurements exist (Christiansen, 2007; Heethoff and Norton, 2009; Thomason, 1991; Westneat, 2003; Wroe et al., 2005). Any ecologically relevant comparative study of the feeding apparatus of larger mammals therefore requires measurement of bite force *in vivo* to obtain a direct estimate of maximum bite force to validate existing models. Once the principles are better understood and modelled in extant species, inferences can be then made on the performance and trophic niche of fossil species, allowing better insights into the evolution of the ecomorphological characters of extinct species. To measure *in vivo* bite force, several methods have thus far been employed. Bite force can be measured by either making an animal bite a device and recording the force, or by implanting a sensor in the teeth. The latter method requires anesthesia, dental surgery and tethering the animals with wires, and is highly invasive. It has been used to measure the bite force of domestic dogs (Brunski and Hipp, 1984), domestic pigs (Bousdras et al., 2006) and macaques (Hylander and Bays, 1979). A less invasive method is to induce the animal to bite on a device and record the force. The bite on the device can be enticed behaviorally or through electrostimulation of the jaw muscles in various anesthetized animals: domestic dogs (Ellis et al., 2008), domestic pigs (Ström and Holm, 1992), possums (Thomason et al., 1990) and rhesus monkeys (Dechow and Carlson, 1983).

Animals can be behaviorally enticed to bite a force-sensing device through defensive behavior, feeding, play or by training. Defensive bites are the easiest to elicit, particularly in wild animals. This method has been used on mammals ranging from bats (Aguirre et al., 2003; Dumont and Herrel, 2003) and rodents (Becerra et al., 2014) to ferrets (Dessem and Druzinsky, 1992), wild pigs (Sicuro

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et al., 2021) and canids including foxes and dogs (Brassard et al., 2020, 2021). Utilizing feeding and/or play behavior, Lindner et al. (1995) measured bite forces of domestic dogs with a rawhide covered force sensor, but could only elicit six to nine bites of even the most enthusiastic participating dogs. A combination of training and play was used to measure bite forces in spotted hyenas (Binder and Valkenburgh, 2000), and manual training was also used to measure the bite forces of dogs (Brassard et al., 2020). Manual training with a food reward was used to train restrained macaques and galagos to bite a force sensor (Hylander, 1979). However, most of the above-mentioned studies were invasive or time-consuming, and bites were part of an interaction with humans in non-feeding contexts. To overcome limitations of ethics, safety and animal well-being, we propose an automated method to obtain voluntary maximum bite forces from large mammals, and validate it as part of environmental enrichment in a zoo setting. We validated our method using two bear species and a lion, and show that *in vivo* data are critical as current modeling efforts may underestimate bite forces.

MATERIALS AND METHODS

Description of the bite force device

To record bite forces in bears, we designed sturdy bite plates that have less than 2.5 mm bending deflection under the maximum expected loads. In order to reduce bending by increasing the second moment of area of the bite plate beams, the plates were attached to stainless steel U-beams. These were further stiffened, where possible, with square steel tubing (see Fig. 1). The force is transmitted from the bite plates to a piezo sensor with a range of 20 kN (Kistler model 9331B). In voluntary biting, the position of the teeth on the plates cannot be precisely controlled (Lappin and Jones, 2014). This may result in variation in the effective in-lever length of the plates. To minimize this source of variation, we exposed only the first 45 mm of the plates to the animals, and lengthened the in-lever arms to 435 mm, resulting in a mechanical advantage of 1.37 in the middle of the plates ±0.083 to the front and rear extremes. This design has the added advantage of lowering the fulcrum reaction forces. See Fig. S1 for details of the parts.

The charge signal of the piezo sensor was transformed to a voltage using a Kistler 5018a charge amplifier, which was then sampled using a LabJack U3 I/O board at a frequency of approximately 2 kHz. This high sampling rate is necessary, as we did not know the loading and unloading rates and bite durations of bear bites. Under-sampling may unnecessarily increase the variance in measured bite forces, and can lead to an underestimation of the bite force. The samples were converted to Newtons, corrected for the mechanical advantage of the middle of the plates, and recorded using a laptop computer.

The exposed bite plates were sanded to reduce sharp corners. Then, to protect the teeth of the animals from the stainless-steel plates, we covered the plates with three layers of 'Aramid Armor' Kevlar mesh tubing (bears) or two layers of fire hose material (lion). We chose these materials for their high tensile strength to withstand pulling, and their high wear resistance. We found the latter to be more resistant to attempts at destruction.

To provide a reward for each bite, we placed a thin flexible plastic hose between the bite plates through which honey, diluted with lukewarm water for fluidity, could be delivered directly into the mouth of the bears. The lioness was rewarded with cow blood. The delivery of the liquid reward was controlled with a solenoid valve, which could be controlled from the laptop through the output of the LabJack I/O board, and by hand using a remote-control button. When the solenoid valve was activated, the liquid reward was forced through the tube by gravity, as the reward container was placed higher above the ground than the bite plates.

To record which side of the jaw was used, how the jaws were applied to the plates, and which individual was doing the biting, a video of each bite with a force above the trigger threshold was recorded using a USB camera (ELP, Ailipu, Shenzhen, China; see Fig. 2).

To achieve maximal bite forces, we programmed the reward to be triggered above an incrementally increasing threshold, initially set at 20 N. The peak bite force was then stored only if it was above the threshold. The reward threshold was then increased to be the mean of the previous bites, with a maximum of 20 previous bites. In this manner, the reward threshold increased a little with each subsequent bite above the previous threshold, as the mean of a sliding window of the last 20 measurements. This was intended to mimic the natural slow depletion of a hard object with a desired food, such as chewing on a piece of wood with a honeycomb, or on an animal bone.

Testing and validation of the method

To test, improve and validate our method, we introduced the setup to captive specimens of two bear species: the Malayan sun bear [*Helarctos malayanus* (Raffles 1821)] and the Andean spectacled bear [*Tremarctos ornatus* (Cuvier 1825)]. To show the method also works for felids, we tested the device on a lion [*Panthera leo* (Linnaeus 1758)].

We started with two female specimens of the Malayan sun bear named Linh (born 8 April 2011) and Cindy (born 16 July 2000) at the Ouwehands Dierenpark Rhenen in The Netherlands. Both bears were born in captivity, and are estimated to weigh approximately 50 kg. Initially, the bears were separated in order to avoid any competition. The device was attached to the bars of the indoor part of the enclosure, with only the bite plates protruding beyond the bars (see Fig. S2). The bears were introduced to the device by their daily

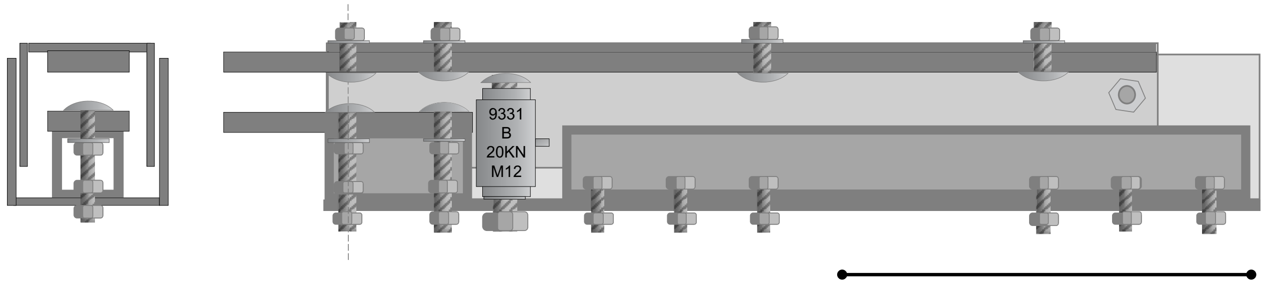

Fig. 1. Schematic drawing of the bite plates. On the left is a cross-section of the device at the dashed line. The reward tube (not shown) opens between the bite plates on the left side of the device. Scale bar: 20 cm.

Journal of Experimental Biology

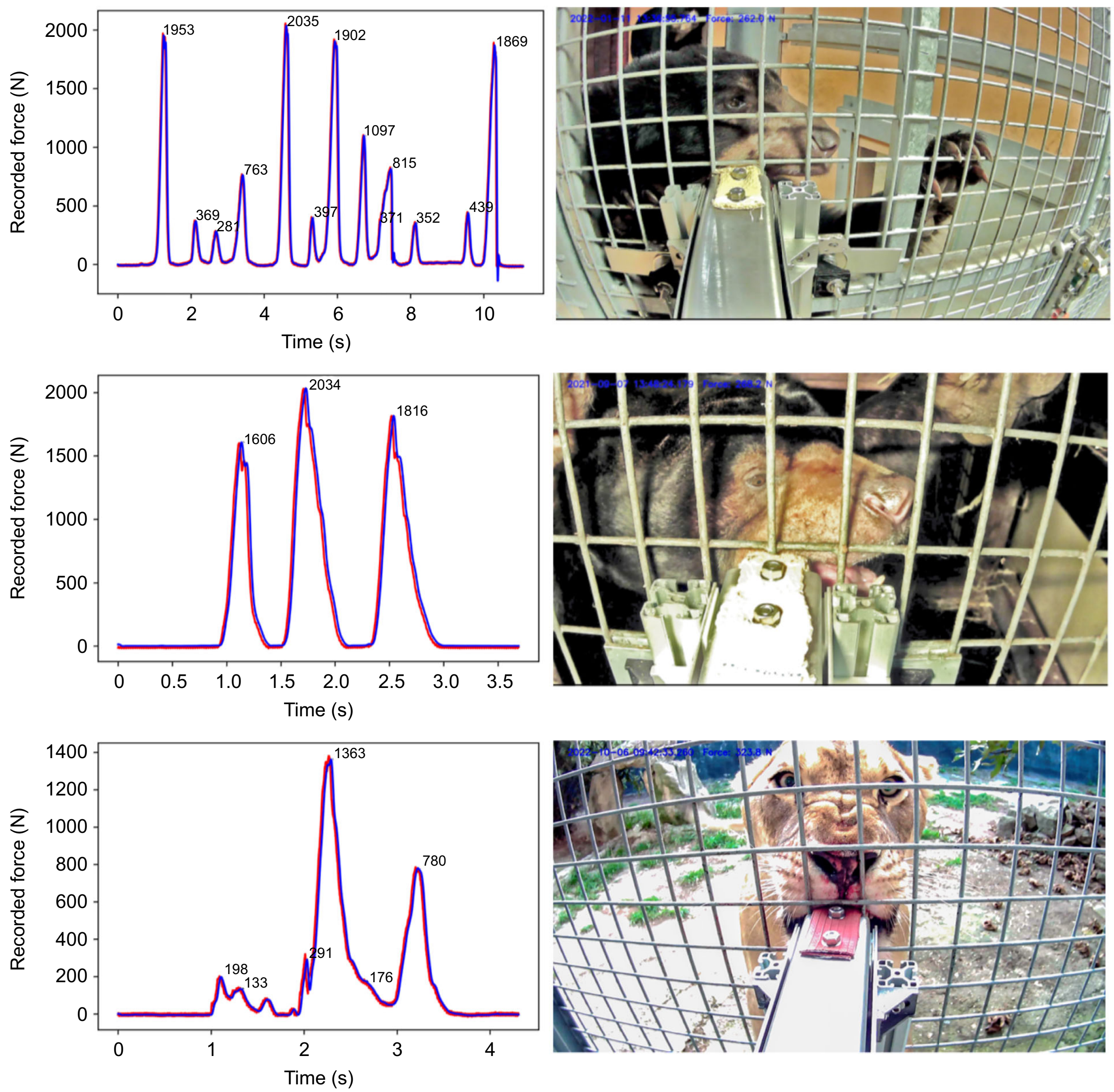

Fig. 2. Exemplary bite force events for each species. Left column shows the recorded forces, the right column shows video stills of the corresponding event. From top to bottom: Andean spectacled bear Teju, Malayan sun bear Cindy, and lioness Savannah. The red line shows the unfiltered data, the blue line represents the filtered data. Values represent peak values.

caretakers. Interest in the device was rewarded with peanuts and walnuts as external rewards. Linh rapidly learned to bite the plates, and was rewarded with the diluted honey automatically dispensed from the device, as well as the external rewards. After this initial training, the bears were left with the device available in their enclosure without supervision. Linh regularly used the bite-force plates correctly to obtain the reward over a period of several days, but Cindy had to be re-trained multiple times. This allowed us to test different training approaches, including using dummy plates and external rewards. We found that training by rewarding desired behavior using manual control of the internal reward system only was most effective. This training method was therefore used subsequently.

At the DierenPark Amersfoort in The Netherlands, we measured bite forces of two young male specimens of the Andean spectacled bear, two brothers named Ariba (91 kg) and Teju (80 kg; both born in captivity 24 December 2017). Both bears were trained exclusively using manual control of the internal reward system, and each learned to bite the plates correctly, using only the molars, within a single session of less than 20 min. The bears were then allowed access to the device in their enclosure for several hours per day in the subsequent days, with the reward being triggered automatically. Re-training with manual control of the internal reward system was done only when necessary.

The lioness Savannah at Maia Zoo in Portugal was trained over three to four sessions of 20–30 min. Savannah is estimated to weigh 100–120 kg and was born 13 May 2014 in captivity.

Because the animals can choose how they reach forces high enough to trigger a reward, there was a potential for them to use their body mass to achieve a higher downward force on the upper plate. To check whether the recorded bite forces were unintentionally inflated in this manner, we mounted the device upside down in the

Journal of Experimental Biology

last session with the spectacled bears. In this manner, the lower plate is recording the force, and any body mass force exerted on the upper plate is not transferred to the transducer.

This research did not require ethical approval under Portuguese law (Decreto-Lei no. 113/2013, 7 August).

Analysis of bite force data

For each bite event, the force data, time and accompanying video were recorded on the laptop computer using a custom Python script (available from the corresponding author upon request). After each day of trials, the videos were reviewed to identify the bear that was biting, and bites were classified as valid (unilateral bites using molars) or invalid (anything else). For valid bites, we noted which side of the jaw the bear used. This allowed us to test for fatigue and left–right preferences. The lioness only used the canines or incisors to bite the device.

Before analysis, the bite force traces were filtered using a fourth-order low-pass Butterworth filter with a cut-off frequency of 20 Hz. To quantify the duration of the bites, we used the find_peaks function in the Scripy python package to determine the peak widths with a relative height setting of 0.1 and a minimum peak height of 100 N.

To analyze the bear data, we used linear models and ANOVAs on the $\log_{10}$-transformed data in R version 21.09.1 (https://www.r-project.org/) using the lmer function of the lme4 package (Kuznetsova et al., 2017). We performed an ANOVA to test for differences in force using the left and the right jaw while controlling for species and specimen [model: logforce_N∼side+species/(1|individual)]. To test for fatigue, we ran a linear model of bite force against the time since the previous bite in seconds, controlling for individual and species as nested factors [model: logforce_N∼logtimeDiff+species/(1|individual)]. Finally, we tested for any effect of the orientation of the bite plates while controlling for the individual bear [model: logforce_N∼plateUD+(1|individual)].

To compare our *in vivo* measurements at the rear molar with the estimated values of bite force at the carnassials and the canines by Christiansen (2007), we measured the distances of the molar, carnassial and canine tip to the joint axis from 3D scans of a skull of *T. ornatus* (MNHN specimen CG1990-696_F) and *H. malayanus* (MNHN specimen GC1914-360). To calculate the force estimated at the rear molar, we multiplied the force at the carnassial by the ratio of the distances from the joint axis to the carnassial and the rear molar, and similarly with the ration of out-lever distances of the canine and rear molar. Because the lioness used only the canines and incisors to bite, these values could be compared with modeled values directly.

RESULTS

We recorded 4068 valid bites in four recording sessions/days for the Andean bears, 1937 bites in five recording sessions/days for the Malayan bears, and 852 bites over seven recording days for the lioness (see Table 1).

Behavioral observations

We found that the animals approached and used the device repeatedly, despite being fed their normal diet and having access to their complete indoor and outdoor enclosures. Wear marks and video recordings indicate that most bites were in the middle of the plates. Bears quickly favored unilateral bites with the rear molars, whereas the lioness mostly used the incisors. Bites were usually concentrated in bouts of many repeated bites until the force necessary to trigger a reward became very high. We noted large individual differences in the necessity for re-training between the individuals in both species. In the Malayan sun bears, Linh was able to keep using the device correctly over a period of several days. However, Cindy had to be re-trained several times to use the device correctly. Similarly, in the Andean spectacled bears, Teju consistently used the device correctly, whereas Ariba had to be re-trained after a hiatus of a day or two. In both bear species, the bear that retained the training best was also the bear that most frequently used the device. The lioness Savannah was slower to learn to use the device, but did not require re-training.

Statistical analysis

There was no difference in force between left and right in the bears, even when taking species and specimen into account (species F=0.0040, P=0.96, side F=0.026, P=0.87).

We also found no evidence for fatigue. The relationship between bite force and time since the previous bite was significant (F=153, P<2e-16), but negative, suggesting that the higher forces were recorded as part of a burst of repeated bites (as in Fig. 2).

We found no evidence for influence of the bite plate orientation, suggesting that bears do not use their body mass to increase downward force (F=0.87, P=0.35). In fact, the single highest bite force (2196.8 N) was recorded with the plates inverted.

Across all bear specimens, we found that of the valid bites, 13.6% were over 80% of the maximal recorded bite force, reducing to 2.8% and 0.47% for bites over 90% and 95% of maximal bite force, respectively (but note the large individual variation in Table 1). The lioness had a lower percentage of peak forces. For the bears, at an average rate of one valid bite every 3.3 s during a biting bout (here defined as a string of bites with a hiatus between bites of less than 100 s), a bite>95% of the maximum force occurred on average every 12 min, and a bite of >90% of the maximum on average every 2 min.

Correspondence to models

We found that the recorded maximal bite forces at the rear molar for the Malayan sun bears was close to the estimated maximal force of

Table 1. Overview of results per individual

Species/individual	Bites	Maximal force (N)	Mean force (N)	Peak width (ms)	No. of bites over 80% of maximal	No. of bites			Maximal force (N)		
						Left	Right	Invalid	Left	Right	Invalid
Andean spectacled bear											
Ariba	352	2196.8	692.1	69	35 (9.9%)	151	137	64	2128	2197	1857
Teju	3962	2167.4	996.0	62	767 (19.4%)	2640	1140	182	2133	2167	1966
Malayan sun bear											
Linh	1696	1907.3	539.8	48	34 (2%)	724	872	100	1907	1811	1706
Cindy	602	2020.6	1057.7	48	62 (10.3%)	310	249	43	1944	2021	1689
Lion											
Savannah	852	1593.8	378.9	51	4 (0.47%)						

The lioness only used canines or incisors to bite. 'Invalid' indicates invalid bites and other force-generating events, such as paw presses.

1722±423 N, based on the model of Christiansen (2007). The canine bite force of lions is estimated at 1104–1483 N, based on the dry skull method and regression analysis, respectively (Thomason, 1991), and at 1768 N by Wroe et al. (2005), which is in line with the maximal incisor bite force of 1594 N we recorded. The recorded maximum *in vivo* force for the Andean spectacled bears of 2197 N was much higher than the estimated force for this species at 1236 ±296 N, even when corrected for the better mechanical advantage of the rear molar.

Bite force is one of the key performance variables of the feeding system and may constrain dietary diversity, prey size and type, and the capacity of an animal to defend itself in intraspecific or interspecific contexts. Understanding bite force variation and how it relates to diet may be particularly important in rare or endangered species, especially species involved in head-start programs or re-released into the wild. Our method seems to have overcome the ethical and safety limitations that have hitherto largely precluded the measurement of bite forces in large captive carnivores, many of which are vulnerable.

We found that the maximal bite forces of the Andean spectacled bears and the lion we recorded are well above those predicted for these species based on the dry skull method (Christiansen, 2007). This underestimation is a known shortcoming of the dry skull method, in part owing to an overestimation of the physiological cross-sectional area (PCSA) of the masseter and underestimation of the PCSA of the temporalis muscle (Law and Mehta, 2019; Thomason, 1991; Wroe et al., 2005). In the case of the Malayan sun bears, when corrected for the mechanical advantage of the rear molar, the *in vivo* values of 1907–2021 N are within the upper range of the estimated maximal force of 1722±423 N. For the Andean spectacled bears, even when corrected for the mechanical advantage of the rear molar, the maximal predicted bite force at 1236±296 N remains well below the *in vivo* forces. We thus found that the one-sided bite forces we recorded are higher than the estimates reported in the literature. Such modeled bite forces may lead us to underestimate the potential diet range and defensive capability. Our results thus highlight the need for further *in vivo* measurement to validate and improve biomechanical models.

To train the bears to use the bite plates correctly, rather than using their paws, pulling or biting at ineffective orientations (see Movie 1), we found that using only the manual control of the internal reward system of the device was most effective. We found our initial training regime using both internal and external rewards focused the attention of the bears on the trainers rather than their interaction with the device, leading to a longer training time. By concealing the manual reward trigger button in a pocket and observing the interaction of the animals with the device from a distance, we were able to train the correct bite orientation rapidly without the animals associating the reward with humans. Once trained, two of the bears and the lioness were able to use the device correctly for several subsequent days without any human presence, whereas the other two required a brief daily re-training. We found the fraction of incorrect bites to be relatively low (5–18%), and these were generally of a much lower force than valid bites. Because the device provided novelty and stimulated exploration, zoos regarded its use as habitat enrichment.

To be able to use these data for biomechanical modeling, it is necessary to know which teeth were used during the biting. Our videos show that once trained, the bears quickly favored using the rear molars to achieve the high bite forces necessary to receive a reward. Thus, by rewarding increasing force, our reward protocol naturally led to the use of the rear molars, which have the best mechanical advantage to achieve high forces. A session of an hour is sufficient to record several bites near the maximum bite force in a well-trained and sufficiently motivated animal. Overall, we found the duration of the force peaks to be short, with mean peak widths of 48–69 ms per bite, and peak force plateaus of ∼10 ms. Such rapid bite peaks make the measurement of bite forces using slower sampling rates difficult. It also suggests that previously recorded bite forces in mammals using lower sampling rates may be underestimates of the maximal forces.

This method may not produce bite forces as may be produced during aggressive or defensive behavior, as the motivation is of a different nature. Individual differences in motivation by the reward or ability to learn may also lead to underestimates of the maximal bite force. We therefore recommend measuring multiple specimens of the same species to obtain better estimates of the maximal capacity.

Our reward protocol is an attempt to mimic a natural situation where a hard or tough food item requires increasing chewing force to extract food. The biting behavior is driven by the desire to obtain the food reward. The recorded bite forces are therefore relevant in a feeding context, rather than the defensive bites often measured using coercion methods. To measure voluntary bite forces, we left the device present in the animals' normal enclosures without human presence. By simultaneously recording force and video, we were able to identify the individual and assess the validity and orientation of each bite. Our camera angle did not allow us to measure the jaw opening angle, but we would recommend recording this for detailed biomechanical modelling. Although we did not record the body mass of the individuals in this pilot study, placing a force plate near the bite device would allow the body mass to be measured quickly and unobtrusively. We expect this method to be applicable to other large carnivores and omnivores. Herbivores, with their lower gape angle and narrower mouth opening, may require a different design of the bite plates and reward system.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: A.v.d.M., J.C.G.-G., M.D.P.-O.; Methodology: A.v.d.M.; Software: A.v.d.M.; Validation: A.v.d.M.; Formal analysis: A.v.d.M.; Resources: A.H.; Data curation: A.v.d.M.; Writing - original draft: A.v.d.M.; Writing - review & editing: A.v.d.M., J.C.G.-G., M.D.P.-O., A.H.; Visualization: A.v.d.M.; Supervision: A.v.d.M.; Project administration: A.v.d.M.

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Data availability
All data are included in the manuscript and the supplementary information. The custom Python script is available from the corresponding author upon request.

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