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MEASURING BITE FORCE IN SMALL MAMMALS WITH A PIEZO-RESISTIVE SENSOR

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We tested the use of piezo-resistive force sensors to measure bite force in small mammals. These force sensors are thin (less than 1 mm) and can be used to measure forces up to 4,500 N. A battery-operated unit, ideal for field research, can be built easily and inexpensively. We tested this sensor in the laboratory and in the field on a variety of small mammals. Although our results indicate that the sensor is somewhat less accurate (coefficient of variation = 4%) than a conventional load cell, the small size and ease of use of the piezo-resistive detector is highly desirable. We also investigated the problem of performance and physiological condition of animals. We found the problem of lack of effort by test animals can enter a significant bias into estimates of maximal bite force.

Key words: bite force, bite performance, biting, dental sensor, field sensor, piezo-resistive sensor, thin sensor

Measuring bite force is a common practice in vertebrate biology (Aguirre et al. 2002; Meers 2003, and references therein). Maximum bite force is seen as an important factor in the ability of a species to kill and process prey (Aguirre et al. 2002; Freeman 1984, 1992; Meers 2003) or open hard foods (Smith 1970). The force sensor used to measure bite force in larger animals is typically (e.g., DeChow and Carlson 1983; Oyen and Tsay 1991; Thomasen et al. 1990) a load cell based on a wheatstone bridge of 4 strain gauges and is highly accurate with a coefficient of variation (*CV*) < 1%. Although these load cells have seen great miniaturization, commercially available models remain too large to fit easily into the mouths of mammals weighing <1 kg. Aguirre et al. (2002) and Herrel et al. (1999) have worked with reptiles and small mammals by using a scissors-like attachment to an external piezo-sensor. The attachment is bitten and not the piezo-sensor directly (Aguirre et al. 2002:figure 1). The thickness of this device occupied a considerable portion of the animal's gape. Researchers studying human bite forces have used piezo-resistive force sensors even though they are somewhat less accurate than load cells. However, these sensors can be very small and thin, which is a clear advantage when working with small mammals. Here we describe the construction of a device using a piezo-resistive sensor to measure bite force. We calibrated this unit in the laboratory and tested its accuracy under a variety of loads. Further, we field-tested the device to see how animals responded to the sensor and how different protective coatings might affect how hard the animals bite.

We also investigated the problem of determining bite force for a species. Anytime a researcher measures the force of a bite, no matter how accurate the force sensor, there is the issue of how much effort the test animal expended (i.e., whether the animal exerted the maximum force it could) and what was its physiological state (Garland and Losos 1994). The use of the best, fastest, or strongest trial as an index of maximal performance of an individual is typical (Garland and Losos 1994, and references therein; however, see Jayne and Bennett 1990a, 1990b). The hope is that an adequate sample of trials will measure performance close to the maximum for that individual. Once individual ''maximal'' performance has been obtained, the intraspecific mean can be calculated for interspecific testing (Garland and Losos 1994). However, examination of our data forces us to question the uncritical use of the mean of bite force because of the bias that may be created by intraspecific or interspecific differences in effort.

Materials and Methods

Our bite force detector contained 2 parts, a piezo-resistive sensor and an electronic device to track changes in the resistance of the sensor. The piezo-resistive sensor we used was a strip of thin plastic 10 mm wide, 150 mm long, and only 0.2 mm thick and relatively inexpensive (4-pack for under $100; Fig. 1A). It is a Flexiforce sensor from Tekscan (Tekscan, Inc., South Boston, Massachusetts), which can manufacture smaller or larger units. The sensor functions as a variable

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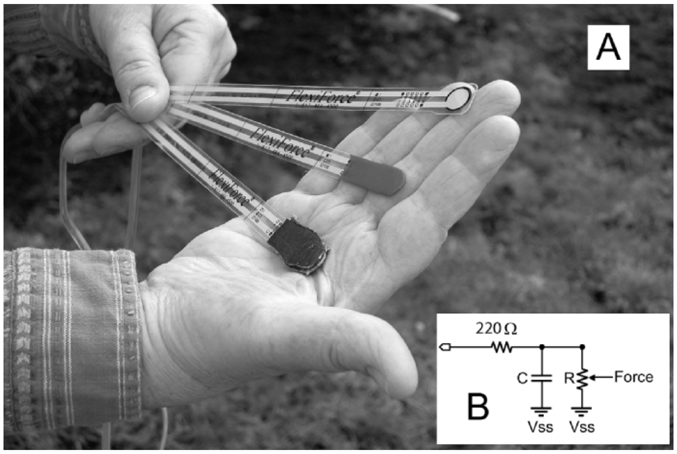

Fig. 1.—A) Photograph of Flexiforce sensors from Tekscan. The piezo-resistive material is the circular area at the tip of the sensor, which is really between a flexible sandwich of thin plastic (uncovered sensor at top). Middle sensor has a covering of liquid plastic and bottom sensor has thick leather pads to protect it from powerful bites. B) The circuit we used to measure resistance changes in the Flexiforce (marked as R). In parallel with the Flexiforce is a small ceramic capacitor, C (approximately 0.01 μF, but it can be adjusted to alter sensitivity of detection). The circuit is connected to a microcontroller that charges the capacitor and then measures the time required to discharge the capacitor through the Flexiforce. The lower the resistance, the quicker the capacitor discharges. At 10 N of force the discharge time for the 1-pound sensor in this circuit is about 0.5 ms.

resistor where the more force applied, the lower the electrical resistance. The Flexiforce sensor we used can be obtained in 1-, 25-, and 100-pound (roughly 5-, 110-, and 450-N) versions. Also, by changing the sensitivity of the electronic device measuring resistance, the range of a sensor can be increased by a factor of 10. Because of failure of the piezo-resistive material, 4,500 N is the upper limit of force detection. The 2nd part, the electronic device we constructed to detect the resistance in the sensor, was a circuit using a B2pe microcontroller from Parallax (Parallax, Inc., Rocklin, California). A simplified version of the circuit is shown in Fig. 1B; those interested in a complete description of design, construction, and programming can contact the senior author (PWF). Our detector is designed to keep track of and display the lowest resistance until the unit is reset. This allowed the animal to bite the sensor several times in quick succession and record the hardest bite. With little change in software the device can be connected to a computer and record resistance readings continuously. For our study, emphasizing field conditions, we preferred to avoid a computer interface and used a small, battery-powered detector.

We protected the thin piezo-resistive strip from the sharp teeth of our test subjects with a variety of coatings. Many methods work and a well-protected sensor can be constructed easily. In one method we coated the tip of the sensor by dipping it into liquid plastic that dries to a tough coating. This product is designed to coat tool handles and is available in hardware stores (Plasti Dip; Plasti Dip International, Blaine, Minnesota). We like this approach because multiple coats can be applied uniformly to increase thickness and protection. The end result is an extremely tough covering that resists bites of small mammals easily. Our most-used sensor had 2 coats of plastic totaling 1.3 mm thick. We were concerned with the feel of the sensor to the biting animal. The plastic coating was fairly hard, and we worried that this might inhibit stronger bites. From experience we knew that small mammals are very willing to bite leather gloves. Therefore, we also covered sensors with leather of a variety of thicknesses to match the gape of test animals. We attached the leather with rubber cement so that when the leather deteriorated we could strip it off easily and replace it. Finally, to protect the sensor from the stronger bites, we applied 2 thin stainless steel disks (0.012 inches = 0.3048 mm thick) to cover the top and bottom surfaces of the sensor exactly. The steel was applied with rubber cement and then coated with the dipping plastic. We also added leather to this design to make a sandwich of leather–plastic–steel sensor. This resulted in a total thickness up to 4.5 mm (we used thick leather). The thickness meant it was not appropriate for testing smaller animals; however, it was bitten with ease by larger rodents such as a fox squirrel (*Sciurus niger*, 520 g) and a plains pocket gopher (*Geomys bursarius*, 275 g).

Each sensor must be calibrated separately to determine the relationship between applied force and conductance. Ideally, a uniform force would be applied to the entire surface area of the piezo-resistive sensor. Because this will not happen with biting, we calibrated the sensors using both sharp and blunt teeth of big brown bats (*Eptesicus fuscus*) and simulated rodent teeth (chisel-shaped steel indenters 4.5 mm wide). The upper and lower jaws of the bat specimens and the steel indenters were mounted in opposition to each other on a uniaxial compression device (Inspec 2200; Instron Corp., Norwood, Massachusetts) to simulate a bite. The Inspec can be set to move the indenter at a fixed speed (we used 0.1 mm/s) and to continue until a set maximum force is reached. This allowed us to calibrate the sensors against a known load. Under field conditions we made every attempt to have the animals bite the sensor in the front 40% of its surface area. During calibration we tested the sensor's response to force applied at the front edge. Teeth were not applied to 1 exact spot on the sensor. We consciously varied the position in the front area of the sensor to simulate the typical field situation where bite position cannot be entirely controlled. Most bites in field situations occurred in this front area both because of the size of the animal and natural biting tendencies of the animals and our attempts to keep bites in this area by controlling the way the sensor was presented. To understand the importance of position, we also applied force to the center 30% for a separate calibration run.

We performed our research on live animals following guidelines approved by the American Society of Mammalogists (Gannon et al. 2007), and approved by the University of Nebraska's committee on animal care and use. Our standard protocol for testing bite force was 1st, no pain stimulation would be used, and 2nd, the testing could only last about 1 min. We presented the sensor to the mouth of the animal and if the animal bit once, the force of the single bite would be measured. If the animal bit several times in rapid succession, our data

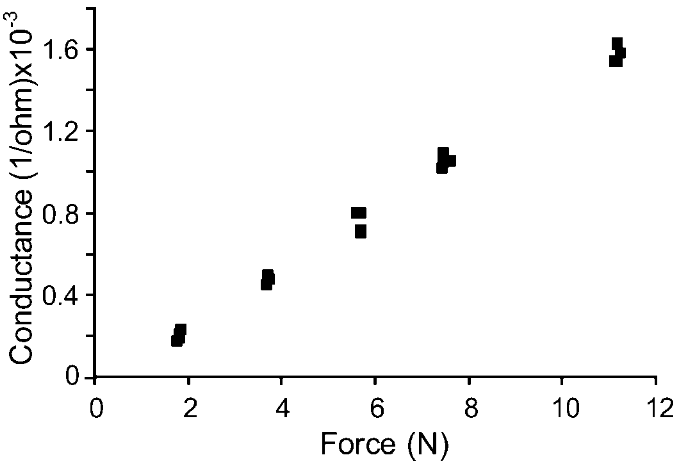

Fig. 2.—Calibration curve showing the relationship between force in newtons (N) applied to the front 40% of the circular piezo-resistive material and the conductance (1/ohm) of the sensor. Conductance is used to make the relationship linear.

recorder preserved only the strongest bite of the series. This procedure was repeated up to 5 times and the strongest reading used. During the testing, the animal was held as loosely as possible. Subjectively, we believed that animals tend to bite when they sense an opening for escape. Conversely, when animals are held securely they often offer little resistance and refuse to bite.

All bite forces were measured in the field. Rodents were trapped overnight and bite force was measured when the traps were checked in the morning. Species of rodents tested and sample sizes are: white-footed mouse, *Peromyscus leucopus* (19); deer mouse, *P. maniculatus* (4); northern grasshopper mouse, *Onychomys leucogaster* (2); western harvest mouse, *Reithrodontomys megalotis* (3); prairie vole, *Microtus ochrogaster* (2); meadow jumping mouse, *Zapus hudsonius* (1); fox squirrel, *S. niger* (1); plains pocket gopher, *G. bursarius* (1); plains pocket mouse, *Perognathus flavescens* (1); and Ord's kangaroo rat, *Dipodomys ordii* (11). Bats were captured from roosts or with mist nets. Species and sample sizes are: fringe-tailed myotis, *Myotis thysanodes* (1); hoary bat, *Lasiurus cinereus* (1); and big brown bat, *E. fuscus* (5).

Results

The relationship between force applied to the piezo-resistive sensor and the conductance (1/ohm) for 1 of our sensors is shown in Fig. 2 ($r = 0.99$, $P < 10^{-19}$). This high correlation was typical of all the sensors. We used a linear regression to quantify the relationship between conductance and force by calibrating the sensor against known loads. Each sensor was calibrated separately because there were statistically significant differences in their relationships between force and conductance. Our results indicated that all of our methods of protecting the sensor (plastic, leather, and steel) had little impact on the linearity or sensitivity of the sensors.

Samples at 1 load showed that accuracy yields a *CV* of about 3.6% for these sensors if the load was applied to the front 40% of the sensor's surface (Table 1). The results were significantly different between the bites in the middle and at the front areas. Differences in force averaged 7.8%, but the direction of difference was not consistent. If results are combined the *CV*s across samples increase to an average of about 5.6% (Table 1).

Table 1.—Results of a series of tests to measure the impact of bite placement and tooth sharpness on load readings. The first 3 entries are for 3 different sensors (labeled 1–3), all loaded at 10 N with the *Eptesicus* that had duller teeth. The last entry is with sensor 3, but loaded with an *Eptesicus* with sharp teeth. Positions of loading are marked as Front (front 40% of sensor), Middle (middle 30% of sensor), and Combined (found by combining Front and Middle values). The *t*-values and *P*-values are for comparison of force readings from the front and middle of sensor.

Indent/sensor	Statistic	Front	Middle	Combined
Dull/1 ($t = 2.54$, $P < 0.02$)	$\bar{X}$	10.17	9.66	9.91
	CV	3.92	2.99	4.29
	n	6	6	12
Dull/2 ($t = 5.57$, $P < 0.001$)	$\bar{X}$	9.21	9.99	9.57
	CV	3.64	4.32	5.71
	n	17	17	34
Dull/3 ($t = 6.71$, $P < 0.001$)	$\bar{X}$	10.1	9.27	9.69
	CV	3.01	5.49	6.11
	n	7	7	14
Sharp/3 ($t = 4.98$, $P < 0.001$)	$\bar{X}$	9.95	8.97	9.46
	CV	3.74	3.62	6.21
	n	7	7	14
Mean *CV*		3.5775	4.105	5.58

The relationship between tooth sharpness and force is shown in Table 1. Using *t*-tests, we compared force readings from the front of a sensor with sharp and dull teeth and found no significant difference ($t = 1.1$, $d.f. = 12$, $P < 0.28$). This test was repeated in the middle of the sensor and again there was no significant difference between sharp and dull teeth ($t = 1.3$, $d.f. = 12$, $P < 0.1$).

We considered that coverings such as the disks of thin steel might distribute the force more evenly and thus have lower variances than sensors with rubber only. However, when a test was run between a sensor covered in rubber only and one with steel and rubber, the rubber-only sensor had a slightly but not significantly lower variance (variance ratio test $n_1 = n_2 = 17$, $F = 1.2$, $P < 0.5$).

In an attempt to create a sensor that was animal friendly, we covered sensors with leather in a range of thicknesses. All sensors calibrated equally well and we found no evidence that these coverings stimulated stronger bites than those with the simpler plastic covering. The main variability in strength of bite seemed to be the behavior of the individual animal as it was taken from the trap or net. Some animals acted very aggressively and freely supplied strong bites and others did not.

We field-tested our sensor on 13 species of small mammals (Fig. 3). Given small sample sizes for several species, we do not attempt to make much of this graph. An allometric relationship can be fit to these data ($\ln(\text{force}) = 0.77 \times \ln(\text{mass}) - 0.23$, $F = 173$, $P < 0.0001$). This relationship is roughly consistent with published relationships (line A in Fig. 3) for bats by Aguirre et al. (2002).

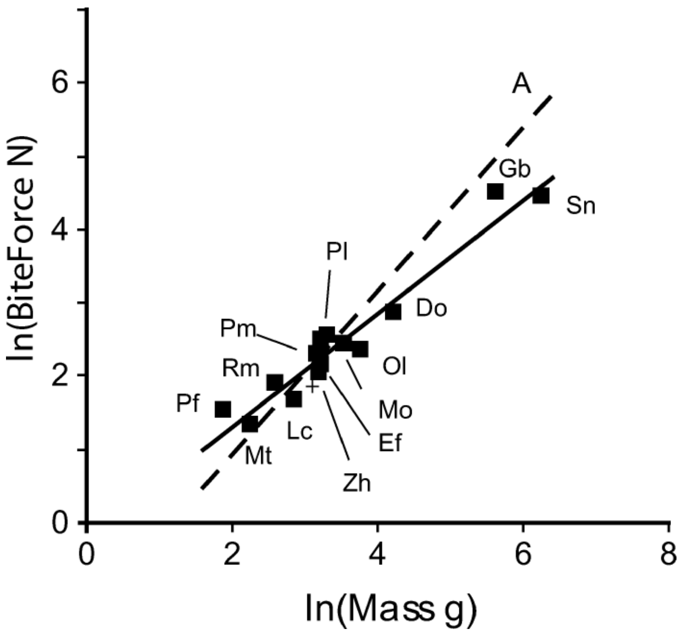

Fig. 3.—The relationship between body mass and bite force for 13 species of small mammals listed in "Materials and Methods" (solid line). Also plotted is the linear regression line (marked A) from Aguirre et al. (2002). The mean for the cold-stressed *Peromyscus leucopus* is plotted as a plus symbol (+) but was not used in the calculation of the regression line.

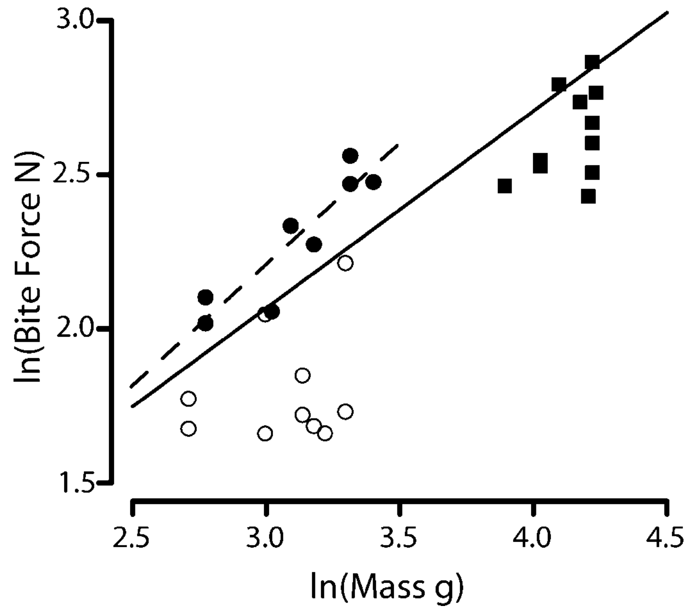

Fig. 4.—Plot of body mass to bite force for *Peromyscus leucopus* and *Dipodomys ordii*. The solid circles are the initial sample of *P. leucopus*, and there is a significant relationship between mass and bite force. The open circles are the 2nd sample of *P. leucopus* that may have been affected by the cold and are included only for comparison. There is a significant difference in the mean bite force for these 2 samples. The bite forces of *D. ordii* are plotted as solid squares. Two regression lines also are plotted; the solid line is for the regression of all 13 species used in this study and the dashed line is just for the non–cold-stressed *P. leucopus*.

A concern about measuring bite force is the issue of performance versus behavior raised by Garland and Losos (1994). Are animals biting at or near their maximum capacity? Our experience in handling thousands of small mammals of many species is that individuals within species and among species show differences in willingness to bite. The role of effort was emphasized by our data from *P. leucopus*. We accidentally conducted an experiment on cold stress in this species that showed how performance could vary from day to day. Mice were caught in the same field 14 days apart. The 1st night was cool and dry (7°C). The next morning when traps were checked, all animals were apparently in excellent condition, and they were tested for bite force immediately (Fig. 4, solid circles). When we retrapped the field 2 weeks later, the overnight low was still cool (6°C) but with misting rain. Of the 37 *P. leucopus* caught, 1 animal was dead in the trap and 5 others were suffering from obvious hypothermia (slow movement, "sleepy" eyes, or both). The rest of the animals showed no apparent ill effects and behaved normally as they were handled. However, their behavior was clearly different when it came to bite force (Fig. 4, open circles), and this difference was statistically significant ($t = 4.7$, $P < 0.0005$). Until the bite force experiment, we detected no indication that the animals were stressed (beyond the fact that other animals had suffered hypothermia). However, the mean value for bite force was 31% lower in this sample. Because of the circumstances of this sample it was not used in our interspecific analysis.

To demonstrate how issues of effort might impact an analysis, we tested the hypothesis that *D. ordii* has a relatively weak bite in comparison to *P. leucopus*. Using the interspecific regression for all species, we found the residuals for *D. ordii* and *P. leucopus* and determined that the residuals for *P. leucopus* were significantly larger than those for *D. ordii* ($t = 4.44$, $P < 0.0005$). This result can be seen graphically in Fig. 4. Note that data for *P. leucopus* (solid circles) cluster slightly above the regression line and values for *D. ordii* (solid squares) tend to be below it. However, if the *P. leucopus* we surmised were cold-stressed (open circles in Fig. 4) are included in the *t*-test, there is not a statistical difference between these species ($t = 0.65$, $P > 0.5$). Therefore, using data from cold-stressed animals could be misleading.

Discussion

The accuracy of the piezo-resistive sensor was good, with a *CV* around 5.6%. This is less accurate than a conventional load cell ($CV < 1\%$), but probably accurate enough for a study of bite force. The piezo-resistive sensor is small, thin, and easy to bite. This may stimulate stronger bites than a larger, more intrusive sensor.

On different days, *P. leucopus* from the same study area had different bite forces, perhaps caused by cold stress. This issue was easily dealt with; we simply ignored the sample on the rainy day because of the overwhelming difference between the samples. More subtly, animals may bite with different effort.

In our data on *P. leucopus*, the intraspecific regression was significant and there was close agreement between the scatter of points (Fig. 4, solid circles) and the interspecific regression line. The regression of body mass to bite force for *P. leucopus* indicated about 82% of the variation in bite force was explained by body mass. These facts lead us to believe that we have a good estimate of maximal bite force in *P. leucopus* with the proviso that our sample size was small. Of course, all these animals could be biting at a consistent below-maximum effort. We are much less confident in the data from *D. ordii*, where there was no significant relationship between body mass and bite force. The range of bite forces produced by the larger *D. ordii* was considerable (Fig. 4), suggesting that some variation was caused by lack of effort.

Variation in the stress levels or the amount of effort an animal puts into its bite may be a severe problem in the testing of bite force. Aguirre et al. (2002) made the assumption that a mean value of bite force was a reasonable measure of bite force for a species. The assumption is that either animals tend to bite sensors about as hard as they can (Herrel et al. 1999), or at least all species use about the same effort. This assumption appears to be vindicated by the strong correlation of body mass and bite force. However, when dealing with species that span orders of magnitude in mass, even relatively large differences in effort may not appear important. For example, the cold-stressed *P. leucopus* (plus symbol [+] in Fig. 3) would not appear unusual if we had not known that these results were much lower than an earlier sample from the same field. If the goal was to quantify the relationship of mass and bite force across mammals in a mouse-to-elephant regression, the differences in effort may not be important. However, when testing hypotheses about the relative strength of the bite between 2 species, differences in stress or effort can be a major problem.

Because of the problem of stress and performance, we preliminarily suggest every effort should be made to reduce stress on animals, to increase sample size, and to use multiple localities or nights of capture to reduce spurious results. Although beyond the scope of this paper, it is possible that the average of bite force will not be the most useful statistic for quantifying bite force and a more aggressive statistical method for the elimination of low performance outliers may be needed.

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