Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure

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Measurements of whole-organism performance traits have been useful in studies of adaptation and phenotype–environment correlations. Bite force capacities may be tightly linked to both the type and magnitude of the ecological challenges of food acquisition, mate acquisition, and antipredation in vertebrates. In the present study, we present technical details on bite meters and on measuring bite forces. The ability to take reliable measurements depends on specific features of the measuring device and on where in the mouth the bite is applied. Using both previously available and original data, we demonstrate several ecologically and evolutionarily relevant features of bite force measurements. First, maximal bite forces are repeatable among individuals across all vertebrates studied to date. Second, in ectotherms such as lizards, maximal bite forces are affected by body temperature and motivational states. Third, bite forces are strongly correlated with head size and shape. Fourth, bite forces correlate with features of prey of vertebrates. Finally, bite forces are linked to male dominance and correlated with social-display structures. Thus, bite force performance measures can be used as 'traits', and thus be used in integrative studies at multiple levels of organismal biology. Accordingly, bite force data will help our understanding of the functions, capacities, and evolution of jaw–cranial musculoskeletal systems. Moreover, a plethora of opportunities exist for the use of bite force measurements, and if methods are carefully applied, several levels of organismal and ecological organization can be integrated to aid our understanding of the ecology and evolution of vertebrate taxa. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **93**, 709–720.

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INTRODUCTION

Multicellular organisms are the sum of integrated form–function complexes (Bock & von Wahlert, 1965). Comparisons among animals varying in form–function complexes for their relative abilities to perform ecologically relevant tasks (e.g. evading predators and capturing prey, *sensu* Huey & Stevenson, 1979) enhance our understanding of the evolution of the enormous morphological diversity of animals (Arnold, 1983; Wainwright, 1991). Locomotor performance traits, for example, have been useful tools for analysing the design, function, and evolution of locomotor systems in vertebrates (Irschick & Garland, 2001). Furthermore, analyses of locomotor performance traits have provided insights into our understanding of evolutionary and functional trade-offs and their roles in the evolution of phenotypic variation (Vanhooydonck, Van Damme & Aerts, 2001; Van Damme *et al.*, 2002).

Similarly, performance measures associated with the vertebrate jaw system provide insights with respect to vertebrate ecology and evolution. The jaw–cranial musculoskeletal system is a hallmark form–function complex of vertebrates, used to capture, subdue, and orally process prey, and to obtain mates (Motta & Kotrschal, 1992; Korf & Wainwright, 2004; Lappin & Husak, 2005) and, presumably, to defend against predators. Bite forces explicitly can be assumed to be tightly linked to design features of the jaw–cranial system, and thus bite forces could be used as performance measures at the whole-animal level. If bite force is an ecologically relevant performance measure, then variation among taxa in bite

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forces should be linked to variation among taxa in the intensity of ecological challenges (e.g. prey, predator, or sexual competitor) that they encounter. For many species, maximal bite force may be an infrequently used, but exceedingly important factor in the outcome of agonistic and mating encounters (Schoener, 1966; Cooper & Vitt, 1993; Lailvaux *et al*., 2004; Huyghe *et al*., 2005), resource use (Hernandez & Motta, 1997; Herrel *et al*., 1999b; Herrel *et al*., 2001a, Herrel, De Grauw & Lemos-Espinal, 2001b; Grubich, 2003), and breadth of the resource niche (Herrel, Van Damme & DeVree, 1996; Herrel *et al*., 1999a).

Variation among individuals in bite performance may be linked to variation in fitness (Wainwright, 1991). If bite force is a reliable whole-animal performance trait within a population, however, several conditions must be met. First, maximal bite forces must be repeatable for individuals under similar conditions; significant changes in maximal bite force may relate to ontogenetic or seasonal changes in response to hormones (Herrel & O'Reilly, 2006; Herrel *et al*., 2006; Irschick *et al*., 2006). Second, variation among individuals must correlate with measurable morphological features. Individuals with the largest heads will presumably possess larger adductor muscle masses (Herrel *et al*., 1996, 1999a; Herrel, McBrayer & Larson, 2007); thus, these individuals should also be able to bite harder. Third, variation in bite force among individuals must correlate with a measure more directly related to fitness, such as the net rate of energy intake when foraging (Anderson & Karasov, 1988), number and quality of mates acquired (Anderson & Vitt, 1990; Lappin & Husak, 2005), or success in antipredation (Marquez & Cejudo, 2000).

The present study examines the collection, use, and efficacy of bite force as a whole-animal performance measure and reviews the relevant data collected previously. We describe two experimental procedures for measuring bite force *in vivo*. We present new data demonstrating how transducers can be tested for accuracy and precision. We then show how bite force data from a variety of vertebrates that face different sets of ecological challenges help to answer a variety of questions. The study foci are to present caveats in collecting and interpreting bite force data (e.g. motivation to bite) and to explore how bite force data could be used to test ecological and evolutionary hypotheses.

MATERIAL AND METHODS

BITE FORCE METERS AND THEIR CALIBRATION

One bite force meter (i.e. that of R. A. Anderson) was modelled after the detailed specifications of Sinclair (1983). The bite plates consist of two alloy steel plates (each 1.5 mm thick) clamped onto a solid metal block. Foil strain gauges are bonded to both the upper and lower plates. The gauges convert the amount of deformation (strain) of the plates to a change in resistance in a wheatstone bridge circuit. This change in resistance is calibrated to be directly proportional to the compressive force in Newtons (see below). The meter is equipped with an analogue output connection so that the data may be displayed, stored, and analysed directly on a computer. Depending on the size of the mouth of the study species, transducers of various dimensions (total length, width, or height), or adjustable transducers (see below) may be constructed. Similar transducers have been used to measure bite forces in mammals (Binder & Van Valkenburgh, 2000; Thompson, Biknevicius & German, 2003), lizards (McBrayer, 2002, 2004; McBrayer & White, 2002), and small alligators (Erickson, Lappin & Van Vliet, 2003).

This style of transducer must be calibrated prior to use. The linearity of the relationship between the output (mV or N) should be quantified for both a mass applied to the plates and the location of this force along the length of the plates. For novel data presented herein on the lizards *Tupinambis teguixin* and *Gekko gecko*, the meter was standardized at 9.8 N kg^{-1} force at 10 mm from the tip of the plates. The placement of these bites at this calibrated location was confirmed for each bite session, or that session was excluded. Eight different masses were applied at this location and the output was highly repeatable and linear ($R^2 = 0.99$; $y = 0.0478x + 0.0075$). The bite plates were also calibrated at each 2-mm increment along its full length. These results were also highly linear for each of four masses tested (0–26 mm, 14 locations; $P < 0.001$ for each mass; $R^2 = 0.999$ for 0.494 kg and 1.994 kg, $R^2 = 1.00$ for 0.994 kg and 4.049 kg; y intercepts for increasing masses = 6.467, 13.089, 26.529, 53.646; slopes for increasing masses = −0.169, −0.330, −0.683, −1.333) so, for any bite location, the transducer voltage (force) output was corrected for the leverage-dependent bite location. These calibration steps are essential to ensure that the force values reported are actual values and thus will be comparable among individuals and/or species. Biting on catheter-type pressure transducers or on two always-parallel plates would not require such careful calibration to compensate for bite location on the device (Huber & Motta, 2004).

The second bite force meter (i.e. that of A. Herrel) is based on a piezo-electric force transducer [Kistler, types 9203 (±500 N) and 9207 (±5000 N)], mounted into a custom-built holder. Attached to the transducer is a screw that is connected to a top plate. The top plate pivots across a fulcrum (Mitutoyo 150–802 micrometer head) mounted onto the holder and

adjustable in height. Bite plates of varying thickness and dimensions are mounted on the top plate and holder and provide a surface for the animal to bite on. The point of application of the bite forces on the plates is standardized by the length of the bite plates. Detailed descriptions and illustrations of the set-up are provide elsewhere (http://webhost.ua.ac.be/ funmorph/bite force transducers.html). The transducer is connected by means of a high impedance cable (Kistler type 1631C) to a 9-V battery operated, handheld charge amplifier (Kistler type 5995A) with hold function. This piezo-electric transducer is precalibrated and shows a linear response throughout its entire range. Thus, transducer output needs to be corrected for the lever system (fulcrum-to-bite distance) of the bite plates only. Transducers of this style have been used to measure bite forces in birds (Herrel *et al.*, 2005a, b), sharks (Huber *et al.*, 2005), caecilians (Measey & Herrel, 2006), large alligators (Erickson *et al.*, 2003), lizards (Herrel *et al.*, 2001a; Lappin & Husak, 2005), bats (Aguirre *et al.*, 2002; Dumont & Herrel, 2003), mice (Byron *et al.*, 2004), and turtles (Herrel, O'Reilly & Richmond, 2002; Herrel & O'Reilly, 2006).

THE BITE SESSIONS

For the methods-testing data presented herein on lizards (*T. teguixin* and *G. gecko*), individuals were tested in five to ten bite force sessions, each session involving multiple bites and with typically at least 30 min of rest between sessions. Between sessions, lizards were maintained at their field active body temperatures, which are close to the optimal performance temperature for bite force (Bennett, 1985; A. Herrel, unpubl. data). These and most other vertebrates tested for bite force readily open their jaws in response to being hand-held, regardless of whether in recent (weeks for *G. gecko*) or long-term captivity (months for *T. teguixin*). Putatively vigorous bites also were reported for long-term captive mammals (Binder & Van Valkenburgh, 2000; Thompson *et al.*, 2003) and alligators (Erickson *et al.*, 2003). Bite plates were positioned symmetrically under the upper tooth rows. The typical subject's response was to bite quickly and vigorously as soon as one of the bite plates touched a tooth row. More vigorous bites from individuals with anomalously weak bites were induced to bite harder when light taps were applied to the side of the jaws.

Bite plates were covered with a thin layer of material (chamois) to prevent tooth damage and slipping. Moreover, the bite location of the anterior teeth could be marked and checked to ensure that the teeth did not fully pierce the covering and encounter metal. The combination of a thin pliable covering, the gape distances required to bite, and the movement of the bite

plates whereas biting mimics the texture, size, and resistance of a conspecific or animal prey item.

Given the biomechanics of the jaw lever system, forces measured closer to the angle of the jaw will be greater than those measured closer to the jaw tips. Thus, we explored the feasibility of measuring bite forces along (anteriorly posteriorly) the tooth row in some smaller lizards. Rubber-coated metal rods were glued transversely on the plates and the rods were placed precisely against the teeth at a given distance along the tooth row. These narrow rods could be placed at pre-calibrated locations along the bite plates so that maximal bite forces at varying positions along the jaw (front to back) could be obtained. Most bite force studies have measured force in the front of the jaws because it is relatively easy to get animals to bite at a standard location nearer the front (but see also Dumont & Herrel, 2003), and it is more difficult to fit the bite bars between teeth in the rear of the mouth, particularly in fish (Grubich, 2005). Investigators must report where along the length of the jaw (e.g. distance anterior to the angle of the jaw) so that maximal bite force values can be compared among studies.

RESULTS AND DISCUSSION

BITE POSITION AND GAPE ANGLE

Effects of bite position are typically strong for the lizards we tested herein and in other vertebrates tested to date. In a moderate-sized lizard [adult *G. gecko*, 149 ± 18 mm snout–vent length (SVL)], bite force near the tip, just posterior to the nostrils, averages $78.5 + 1.6\%$ ($N = 7$, range 73–84%) of the bite force midway towards the joint. Likewise, in several species of bats, the bite force approximately doubles when moving from the anterior canine posteriorly to the molars (Dumont & Herrel, 2003). Thus, the standardization of bite position, and the accurate recording and reporting of the point of application of bite force (e.g. by video; Erickson *et al.*, 2003; Thompson *et al.*, 2003; Lappin *et al.*, 2006a) or tooth-mark locations (McBrayer & White, 2002), are essential results to be included in analyses. Moreover, documenting bite positions will help focus research on where the forces are applied and the function of the bite. Indeed, the high bite force in the rear of the jaw may be an epiphenomenon for some vertebrates, whereas the rear bite forces may be the primary selected feature in others. The morphotype of the jaw–cranial complex and magnitude of bite force, for example, may vary with bite function, such as would be associated with killing or capture bites at the front of the mouth (e.g. the ambush and subduing of prey) or crushing bites near the back of the mouth (e.g. crushing the skull or

exoskeleton of prey; McBrayer & White, 2002; Korff & Wainwright, 2004), or shearing bites from mid-mouth to the back (e.g. herbivores processing fruit or plant matter or breaking bones along the carnassials in mammals).

Another consideration is that the jaw–cranial complex may show unique adaptations to proficiently exert bite force along only one side of the jaw as might be needed in prehension of evasive prey or crushing or shearing small hard-bodied prey. For example, Summers (2000) showed that myliobatid stingray bite asynchronously, have a unique jaw muscle lever system, and rigid symphyses. Each of these modifications are presumed to permit the great bite forces needed for crushing hard prey (mollusks). For animals specialized for such tactics, the consequences for bite force capacity may differ from animals that typically bite bilaterally (i.e. equally across both rami of the jaw). The adaptive features of unilateral forceful biting may comprise more than just flexibility of the symphysis (Herrel, Aerts & De Vree, 2000; Lieberman & Crompton, 2000). Moreover, cranial kinesis, which is common birds and lizards (Frazetta, 1962; Bock, 1964; Arnold, 1998), may also influence bite force. Bite forces in taxa with cranial kinesis may vary differently with sustained bites, bite locations, or gape sizes, compared to bite forces in taxa without kinetic skulls (Herrel *et al.*, 1999c, 2000).

If the influence of bite position, gape, body temperature (see below) and motivational state (see below) of study taxa are known, then portable force transducers are effective tools for measuring bite force in vertebrates. Their simple design delivers accurate and precise force values, as well as a rapid, real time responses to subtle changes in bite force (McBrayer & White, 2002). These bite force meter designs have been successfully used to measure bite forces of species in most major vertebrate taxa (mammals: Binder & Van Valkenburgh, 2000; Dumont & Herrel, 2003; Thompson *et al.*, 2003; squamates: Herrel *et al.*, 1999a, b, 2001a, b, Herrel, Vanhooydonck & Van Damme, 2004; McBrayer, 2002, 2004; birds: van der Meij & Bout, 2004a; Herrel *et al.*, 2005a, b; turtles: Herrel *et al.*, 2002; crocodiles: Erickson *et al.*, 2003; sharks: Huber & Motta, 2004; Huber *et al.*, 2005). The various transducer designs allow for flexibility; animals from the size of hatchling lizards (0.3 g) to adult hyena (*Crocuta crocuta*, Binder & Van Valkenburgh, 2000) and adult American alligators (*Alligator mississippiensis*, Erickson *et al.*, 2003) can be tested. Moreover, the same system can easily be used to measure grasping force of claws of crabs (Levinton & Judge, 1993; Schenk & Wainwright, 2001) and scorpions (A. Herrel & A. P. Summers, unpubl. data).

Alternative, indirect methods have been used to predict and estimate maximal bite forces that conscious, motivated animals would attain. Measuring muscle lever mechanics or the physiological cross section of a muscle or bone strain have been used as presumably reliable estimates of the maximal bite force (Herrel *et al.*, 1996; Herrel, Aerts & De Vree, 1998a, b; Herrel *et al.*, 1999a, 2005c; Taylor, 2000, 2001; Ross *et al.*, 2007). Another useful approach is to measure the force necessary to crush prey, and to compare that force with the force generated by muscle stimulation or EMG-based estimates of crushing forces (Wilga & Motta, 2000; Huber & Motta, 2004; Korff & Wainwright, 2004; Huber *et al.*, 2005). Stimulating muscles to tetany with a force transducer positioned along the tooth row is a viable approach to test taxa in which individuals are typically unwilling to bite a transducer. For example, Huber & Motta (2004) directly tested four different morphological and physiological methods (none measured bite force of conscious individuals) and showed that the methods yielded statistically equivalent results. These authors, however, presented caveats for the use of each method. Given that the precision, accuracy, and repeatability of any method used for measuring bite force should be considered, the present study aims to demonstrate the utility, reliability, and caveats in measuring bite force of animals performing voluntary bites.

Bite velocity, in addition to bite force (strength), may be an important feature for prehension of prey. For simple lever systems with all other factors being equal, velocity and force represent biomechanical trade-offs (Levinton & Allen, 2005): long jaws produce higher angular velocity, whereas shorter jaws produce higher force outputs. Alternatively, bite force could be an epiphenomenal result of high bite velocity. Thus, high-speed video would be useful for documenting the capture (prehension) phase of predator-and-prey interactions; the predator's bite velocities can be compared with similarly documented bite velocities and concurrent bite forces on the bite bars. In the context of vector mechanics analyses, however, the statics of bite force should be much easier to reliably measure than the dynamics of bite forces associated with rapidly moving jaws (Beer *et al.*, 2006). Moreover, the dynamic process of biting to establish mouth contact with the prey and to begin the act of prey prehension may grade or switch into a more static (and typical) measure of maximal bite force when the mouth is closed and pressing on the prey in the completion of prehension and as prey are subdued.

Sustained bites may be necessary for holding struggling prey or mates. The variation among animals in force and duration of the holding bite could be compared with variation among individuals in maximal bite force. We examined holding forces during 1-min bite sessions of our largest seven tegu lizards (*T. teguixin*). Between the 6.4 ± 0.5 bites per minute,

holding bites of 11.9 ± 1.4 N (range 9–20, 263–313 mm SVL, three males, four females) occurred between the brief, strong bites (mean $\pm$ SE maximal bites = 106 ± 12 N). Thus, conspecifics varying in size and maximal bite force had remarkably similar sustained bite forces. Sustained bites in some species may be performed with a relatively closed mouth, whereas, for other species, the gape size when biting may be considerable; hence, musculoskeletal design may differ for such species. Notably, variation in the relative abundance of muscle fibre types, as well as cross-sectional area of adductors, patterns of pennation, and origin-and-insertion, all may be features of fine tuning for sustained bites, and may represent trade-offs for bite force.

The maximum bite force also should be compared with the ability to maintain a sustained, full mouth grip, particularly if the gape angle is large. The full mouth grip is seen not only in prey capture, such as when the long-nosed leopard lizard, *Gambelia wislizenii*, or the flapfooted lizard, *Lialis burtoni* grip and apparently asphyxiate lizard prey (R. A. Anderson & A. Herrl, pers. observ.), but also when male broadheaded skinks *Eumeces laticeps* trade bites during intrasexual combat (Cooper & Vitt, 1993) or when male western whiptail lizards, *Aspidoscelis tigris* hold females during copulation (Anderson & Vitt, 1990). The foregoing animals represent an opportunity to investigate how bite force relates both to gape size when biting and bite duration. Moreover, the mechanistic, musculoskeletal correlates (e.g. adductor muscle pennation, cross-sectional area, and fibre types, and the stretching of adductor muscle during gape) can be compared among age classes, sexes, and taxa as well.

The relationship of gape size to bite force has been tested explicitly only in bats, wherein a four-fold increase in gape angle decreased bite forces by as much as 40% in some species (Dumont & Herrel, 2003). Musculoskeletal adjustments, however, can compensate for large gape. The grasshopper mouse *Onychomys leucogaster* kills rodent prey similar to its own body size by biting their skulls with the incisors. The grasshopper mouse has a much greater gape than related, seed-eating rodents, and it has an increased mechanical advantage in the masseters, despite their relatively smaller size (Satoh & Iwaku, 2006). Although some preliminary evidence permits the inference that gape effects vary among lizards and that these differences may relate to differences in musculoskeletal patterns of adductors (A. Herrel, unpubl. data), explicit comparisons of bite force among designs of vertebrate jaw adductors have not been performed previously.

Open mouth threat displays in most vertebrates are presumed to be 'truth-in-advertising', as in sharks (Barlow, 1974), crocodiles (Kofron, 1993), some lizards (Hertz, Huey & Nevo, 1982; Greene, 1988; Marquez & Cejudo, 2000; Lappin *et al.*, 2006a), and many mammals (Szamado, 2003). If the proclivity to perform a threat display varies within conspecifics and congenerics, then it would be propitious to compare variation in that proclivity with variation in willingness to bite and maximal bite force (Lappin *et al.*, 2006a).

REPEATABILITY OF MAXIMAL BITES

Among vertebrates, whether it is individuals varying in body size or among taxa with different hardness of prey, maximal bite forces of vertebrates are repeatable, both as measures of tetanic bite force in anaesthetized fish (Huber & Motta, 2004) and in voluntary bites on force transducers by birds, turtles, and bats (intraclass correlation coefficients on regressions with body size were > 0.95; Aguirre *et al.*, 2002; Herrel *et al.*, 2002, 2005a). We tested for repeatability within adult individuals of the lizard *T. teguixin*. Maximum bite force on cantilevered bite bars within a single trial showed repeatability (Fig. 1). Moreover, their maximal bites were repeatable among trials (Fig. 2); the second strongest bites were always within 10% of the strongest bite even on trials separated by many weeks. Hence, we infer that bite force measurements by individuals that are presumably motivated to bite can be reliable indicators of maximal bite force capacity.

EFFECTS OF TEMPERATURE AND MOTIVATIONAL STATE ON BITE PERFORMANCE

In ectotherms such as lizards, temperature may have strong effects on whole-organism performance traits. Force generation at the muscular level has been suggested to be less sensitive to changes in temperature (Bennett, 1985). Bite force of the nocturnal lizards *G. gecko*, however, is significantly higher at 30° body temperature than at 20° (Fig. 3). Similarly, in agamid lizards, a 10° decrease of the body temperature results in an approximately 50% decrease in bite force (Herrel *et al.*, 1999b). Similarly, temperature-related changes were documented in the feeding kinematics of bluegill sunfish *Lepomis macrochirus* (Wintzer & Motta, 2004).

Intrinsic factors affecting the motivational state of the animals may also affect bite force measurements. For example, we measured bite force of the aforementioned *G. gecko* during their activity period (night) and outside of it (day); they consistently bit harder at night (i.e. during their natural activity period) than during the day ($t = 3.9$, d.f. = 9, $P = 0.004$), despite being at the same body temperature (Fig. 4). Moreover, for each of four individual *T. teguixin* that we
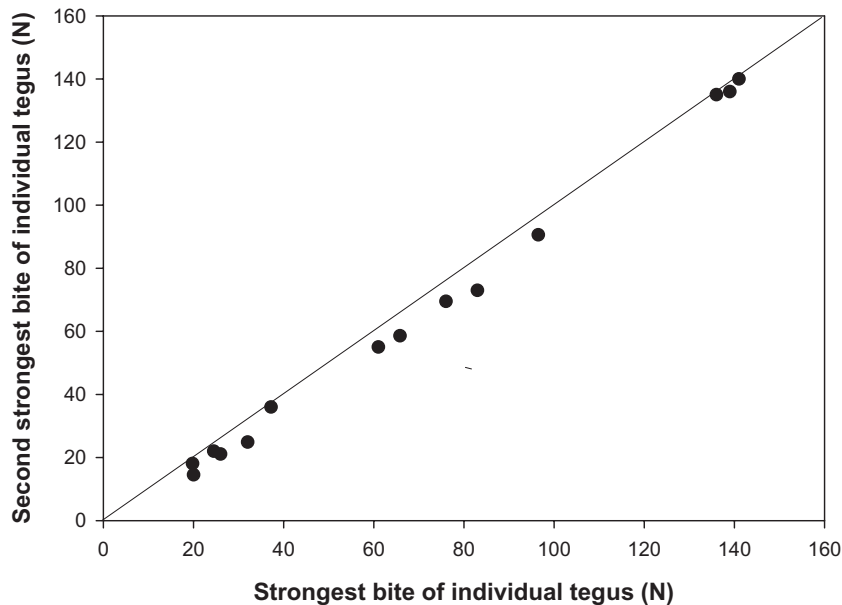
Figure 1. Repeatability of bite forces within a trial of bite force measurements for *Tupinambis teguixin* ($R^2 = 0.99$, $P < 0.001$).
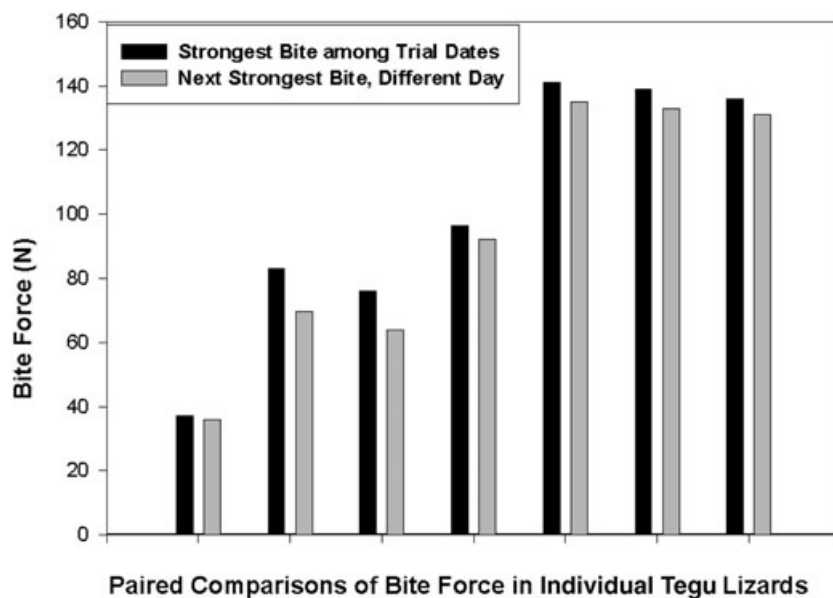

Figure 2. Repeatability of bite forces among trials (different days) of bite force measurements for *Tupinambis teguixin* ($R^2 = 0.99$, $P < 0.001$).

had fed versus post-absorptive bite force comparisons, the bite forces when the lizards were post-absorptive and presumably hungry were $46 \pm 1.9\%$ higher on average than the bite forces when they still had food in their stomachs. This sample even included one unfed individual with a body temperature at 10 °C less than when it was fed and at the likely field-active body temperature of 35 °C. For four other individuals,

the maximal bite forces when unfed and at 25 °C were 73, 91, 95, and 96% of the maximal bite forces than when they were unfed and at 35 °C. In a similar vein, satiation-related changes were seen in the feeding kinematics of the fish *Micropterus salmoides* (Sass & Motta, 2002).

Seasonal variation in bite force has been reported for the lizard *Anolis carolinensis* (Irschick *et al*.,
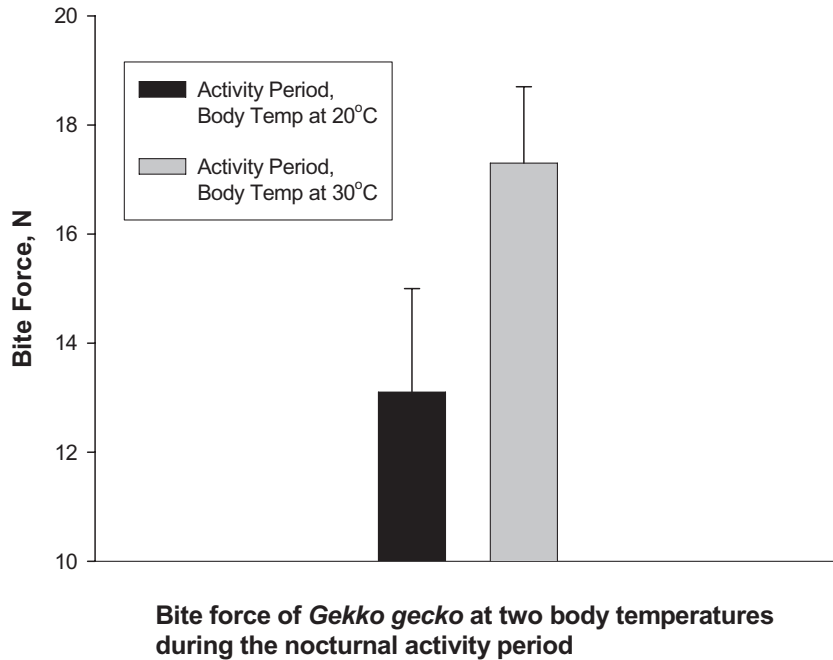
Bite force of *Gekko gecko* at two body temperatures during the nocturnal activity period

Figure 3. *Gekko gecko* bite forces compared: cool versus warm body temperatures ($N = 10$, mean bite force = 17.7 ± 1.4 N at 30 °C versus 12.0 ± 1.9 N at 20 °C; paired t-test: $t = 3.17$, $P = 0.01$).
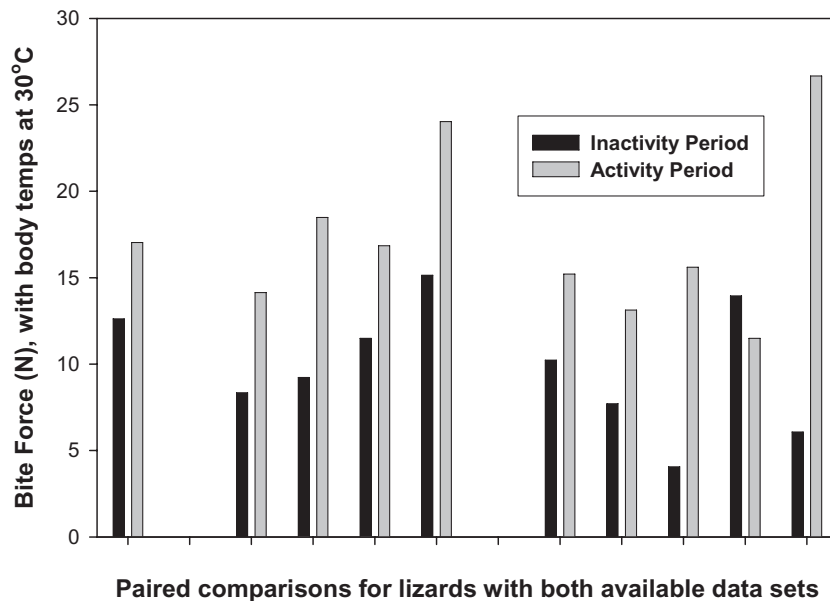

Paired comparisons for lizards with both available data sets

Figure 4. *Gekko gecko* bite forces at 30 °C compared: inactivity period versus activity period. ($N = 10$, paired t-test; $t = 3.915$, $P = 0.004$).

2006). The seasonal patterns in hormone titre and male aggression correlate with seasonality in male head form in the broad-headed skink *Eumeces laticeps* (Cooper & Vitt, 1993). It would be propitious to test these lizards for maximal bite force and relate it to motivation (Irschick *et al*., 2006) or actual seasonal hypertophy of adductor muscles.

Motivation to bite also appears to be higher earlier in a bite session, as was the case for *T. teguixin*. The strongest bites among all sessions for *T. teguixin* were the first bite in a session for ten of 13 individuals and the second bite in a session for the other three individuals. Similarly, the strongest bite happened in the first 30 s for ten of 14 adult *G. gecko* and, in seven of

the 14 individuals, the first bite was the strongest. It is doubtful that fatigue is a factor in the reduced bite force later in the trials because bites that are almost as strong as the first bites do happen much later in the same bite trial. Thus, attention to the methods used, as well as the aforementioned temperature-related impairment, temperature-related motivation, and temporal variation (e.g. hormonal) in motivation to bite forcefully, should be assiduously compared with the actual ability to bite and the musculoskeletal correlates of bite force.

MORPHOLOGICAL CORRELATES OF MAXIMAL BITE FORCE

Maximal bite force is strongly correlated to body and head sizes for all taxa studied. Animals that are larger (Meyers, Herrel & Birch, 2002; Erickson *et al.*, 2003; Herrel & O'Reilly, 2006) or with larger heads (Herrel *et al.*, 1999a, 2001a, b, 2002; Verwaijen, Van Damme & Herrel, 2002; Husak *et al.*, 2006a; present study), bite harder. Among the different shape components of the head that could affect bite force, head width and height are usually the best predictors of maximal bite force capacity within and across species (Herrel *et al.*, 1999a, 2001a, b, 2002, 2004). Despite the relatively low head height of the crevice-dwelling herbivorous lizard *Sauromalus ater*, its bite forces are considerable, especially in males (Lappin, Hamilton & Sullivan, 2006b). Hence, beyond the simple indicators of head size, little is known about the proximate determinants of bite force in vertebrates.

Cross-sectional areas of the adductor muscles, muscle masses, and distribution of muscle fibre types, as well as extent of pennation and positions of the origin-and-insertion of muscles, in concert with the sizes, shapes (e.g. length, width, height, robustness, curvature) of the jaw and cranium, along with cranial kinesis (Frazetta, 1962; Arnold, 1998) and flexibility of the mandibular symphysis (Lieberman & Crompton, 2000; Summers, 2000), should all be examined to understand how bite forces vary within and among species. Furthermore, there are many opportunities to study the effects of maturation on the form and function of the jaw–cranial complex and tooth morphotypes for species of vertebrates that ontogenetically shift prey (Erickson *et al.*, 2003; Christiansen & Adolfssen, 2005; Herrel & O'Reilly, 2006; Irschick & Lailvaux, 2006). These ontogenetic shifts can be compared with similar ecological 'shifts' among species. Moreover, these kinds of functional data may allow us to determine how much of the variation in bite performance is directly related to which musculoskeletal design components, thus revealing musculoskeletal structural constraints and opportunities in evolution of bite force in vertebrates.

ECOLOGICAL SIGNIFICANCE OF MAXIMAL BITE FORCE

If bite force is to be an effective whole-organism performance measure, then it must not only be correlated with morphotype and be repeatable within individuals, but also be commensurate with differences among individuals in an ecological outcome that is likely to have fitness consequences. For example, in laboratory studies of lizards, bite forces were correlated to handling times; individuals with higher bite forces needed less time to consume a given prey item (Herrel *et al.*, 2001a; Verwaijen *et al.*, 2002). Differences among species of bats and birds in the size and hardness of prey (i.e. prey types) eaten, directly correlated with differences in bite forces (Aguirre *et al.*, 2002, 2003; Herrel *et al.*, 2002, 2004; Van der Meij, Griekspoor & Bout, 2004b). The increase in bite force with growth and maturation of individuals also may be related to changes in the prey spectrum or prey types consumed (Erickson *et al.*, 2003; Herrel & O'Reilly, 2006). That is, a greater bite force may increase proficiency in handling prey (i.e. the ability to capture, subdue, break, crush, and swallow prey in general, and harder and larger prey, in particular), thereby increasing the net rate of energy intake when foraging, and presumably enhancing fitness. Alternatively, just the presence of a hypertrophied jaw–cranial complex or other direct correlate of body size (sizes of mouth gape, teeth, or claws) may be enough to defeat conspecific competitors, thus avoiding the battle that could cause direct harm or attract predators (Vanhooydonck *et al.*, 2005a). It is expected that the need for maximal bite force must occur at least once over an individual's lifetime or at least often enough in a particular lineage for the maximum bite to be maintained or hypertrophied within that lineage. The challenge for biologists is to obtain evidence that tightly links variation in whole animal performance such as maximal bite force with variation in fitness (Husak *et al.*, 2006b).

SEXUAL DIMORPHISM AND BITE FORCE

The hypothesis that the differences in head size and body size between male and female teiid lizards should be mirrored by greater bite force of males than in females of the same body size (Anderson & Vitt, 1990) is supported over a range of adult body sizes for *T. teguixin* (analysis of variance, $F = 9.788$, $P < 0.008$. $N = 10$ females, 151–300 mm SVL, female regression: adjusted $R^2 = 0.97$, slope = 0.45, intercept = −49.9; $N = 6$ males, 146–312 mm SVL, male regression: adjusted $R^2 = 0.8$, slope = 0.58, intercept = −66.6). In several other taxonomic families, the sex and age class with the larger head also bit with significantly more force (Herrel *et al.*, 1999a, 2001a, b; Lailvaux *et al.*, 2004; Lappin & Husak, 2005; Husak *et al.*,

2006a; Lappin *et al*., 2006b; McBrayer & Anderson, 2007). Thus, sexual dimorphism in head size is mirrored by a commensurate difference in bite force and, for at least one species, has been directly related to increases in cross sectional area and muscle volume (Herrel *et al*., 2007). This sexual difference in bite force may be a consequence of natural selection for reduced trophic competition (e.g. eating prey of different size or hardness) between the sexes (Herrel *et al*., 2001a; Verwaijen *et al*., 2002; Radford & du Plessis, 2003) or could be the result of sexual selection for male bite performance or head size (Anderson & Vitt, 1990; Herrel *et al*., 1996, 1999a; Lappin & Husak, 2005; Lappin *et al*., 2006b; McBrayer & Anderson, 2007).

Whereas support is scant for the hypothesis that fitness is conferred on individuals that exhibit greater differences in trophic structures (e.g. head and jaw size) from the opposite sex, there is support for the hypothesis that bite force is correlated with male–male combat in lizards. In staged contests between similarly sized males, the winning males typically have higher bite forces, at least among males in the larger size classes (Lailvaux *et al*., 2004; Huyghe *et al*., 2005). In lizards, bite forces may correlate with the size of sexual ornaments such as the dewlap in *Anolis* (Vanhooydonck *et al*., 2005b) and mouth patches in *Crotaphytus* (Lappin *et al*., 2006a). Moreover, dewlap size appears to be an honest indicator of male bite force (and thus fighting capacity) in territorial species but not others (Vanhooydonck *et al*., 2005b). Males of many lizard species also use their jaws to hold females prior to and during copulation (Anderson & Vitt, 1990; Herrel *et al*., 1996). Biting performance in male lizards also may improve their chances of copulations with females (Lappin & Husak, 2005). Even in species with females-larger sexual dimorphism in body size, males may have more robust jaw–cranial complexes than females of similar size, and thus may have greater bite force per unit body size than females (McBrayer & Anderson, 2007).

CONCLUSION

We present evidence that maximal bite force is a useful performance trait that can be compared within and among species of organisms. That is, maximal bite force is repeatable for individuals within and among trials, and differences among individuals and between sexes in bite force are related to body size and the size and functional morphology of the jaw–cranial complex. Moreover, bite force is sensitive to temperature effects and motivation to bite. Because ethotypic, physiotypic, and morphotypic features are all involved and in play, bite force is a nonpareil whole-animal performance measure that has ecological and evolutionary relevance. Bite force is expected to affect the animal's fitness in the contexts of food acquisition, mate acquisition, and antipredation.

Future studies should investigate: (1) how bite force capacities vary among morphotypes of the jaw–cranial musculoskeletal complex; (2) field evidence of ecological significance of bite force; (3) effects of hormones and other proximal influences on bite force generation; (4) whether practice and experience in biting influences an individual's bite force capacities; (5) the heritability and fitness-conferring benefits of bite force, bite velocity, and bite duration; and (6) the ecologically relevant trade-offs in design features of the jaw–cranial musculoskeletal complex within and among species.

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