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Bite Force, Behavior, and Electromyography in the Teiid Lizard, *Tupinambis teguixin*

LANCE D. MCBRAYER AND THOMAS D. WHITE

We used electromyography (EMG) to investigate bite force production and feeding behavior in five individuals of the teiid lizard, *Tupinambis teguixin.* Three jaw adductor muscles were tested: pseudotemporalis superficialis (PST), adductor mandibulae externus superficialis (AMES) and pterygoideus (PTY). Force transducer tests determined that mean peak bite force in males ($n = 3$) was 79 N (22–105 N; $n = 24$). In females ($n = 2$), mean peak bite force was 60 N (14–90 N; $n = 19$). During high-intensity bites, the three muscles tested exhibited synchronous activation patterns, and these activities began before the onset of measured bite forces. Motor activities typically ceased at one-half of the total bite force duration. During natural feeding trials, initial capture bites and crushing bites exhibited motor activity patterns in all three muscles and were similar to those observed during high bite force development. In bites in which the lizards were picking up or moving prey, only the AMES exhibited motor activity. During prey processing, bites were observed that served to position the prey within the jaws and transport it to the esophagus. These bites were accompanied by activity in the AMES and PTY. In some cases, the latter bites were accompanied by activity in the PST. We concluded the AMES is active in all jaw closures. The PTY and PST are sequentially recruited to increase bite forces.

MAXIMUM bite force is a measure of whole animal performance that has been predicted to be an important factor in determining niche breadth, resource use, and winners of agonistic encounters in lizards (Schoener, 1966; Vitt and Cooper, 1985; Cooper and Vitt, 1993). Nevertheless, few studies have measured bite forces of living organisms, and none has investigated motor patterns of the muscles contributing to bite force in lizards. Most studies of the heads of lizards have been descriptions of myology, osteology, and cranial kinesis (Jollie, 1960; Haas, 1973; Iordansky, 1996). Other works have focused on feeding kinematics (Schwenk and Throckmorton, 1989; Herrel et al., 1995; Urbani and Bels, 1995). The few existing works on jaw adduction in generalized lepidosaurs are limited to *Sphenodon punctatus* (Gorniak et al., 1982) and, in lizards *Uromastix aegyptius* (Throckmorton, 1978, 1980), *Varanus exanthematicus* (Smith, 1982, 1984), *Trachydosaurus rugosus* (Gans et al., 1985; Gans and De Vree, 1986), and *Agama stellio* (Herrel et al., 1997, 1998, 1999a). These studies tested hypotheses on cranial kinesis, oral transport, swallowing, and muscle function.

Although bite force production has been considered in many studies, few have measured bite force directly or considered the importance of head size in relation to force production. Bite force modeling was used to explain dietary differences between male and female wall lizards,

Podarcis hispanica (Herrel et al., 1996), to test for differences between herbivorous and insectivorous lizards (Herrel et al., 1998), and to assess variation in head form in crotaphytid lizards (A. K. Lappin, pers. comm.). Because many lizards are sexually dimorphic in head size (e.g., Trivers, 1976; Carothers, 1984), greater potential bite forces in one sex may allow for differential resource partitioning (Schoener, 1966; Shine, 1989; Herrel et al., 1996).

Male *Tupinambis teguixin* (Teiidae) exhibit larger head and body size than females (Anderson and Vitt, 1990; Fitzgerald et al., 1991). The larger heads of males are attributed in part to a larger adductor muscle mass (Rieppel, 1980). Dietarily, *T. teguixin* is a generalist (Gudynas, 1981); it has been observed eating snails, carrion, small birds, mammals and reptiles, as well as fruit (Fitzgerald et al., 1991; Williams et al., 1993; Green et al., 1997). It is also one of the few lizard species known to undergo ontogenetic changes in tooth morphology (Dessem, 1985). A recent study revealed differences in bite force between male and female *T. teguixin* (R. A. Anderson and L. D. McBrayer, unpubl.). Thus, *T. teguixin* is a suitable species for an investigation of bite force and function of the adductor complex.

This study investigates the function of three jaw adductor muscles during bite force production and feeding in *T. teguixin* and relates activity patterns to feeding behaviors. Variation in
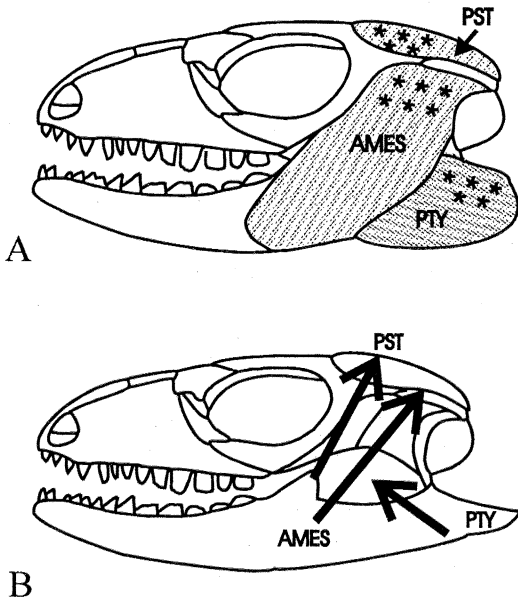
A

B

Fig. 1. (A) The external jaw adducting muscles of *Tupinambis teguixin*. The motor patterns of the adductor mandibulae externus superficialis (AMES), pseudotemporalis superficialis (PST), and pterygoideus (PTY) were investigated during bite force production and feeding. Asterisks indicate sites of electrode placement. For a detailed discussion of jaw adductors in *Tupinambis*, see Riepple (1980). (B) The skull of *T. teguixin* showing approximate lines of action of these jaw muscles.

muscular activity patterns during biting was quantified in the primary jaw adductors and bite forces were measured simultaneously. Our goal is to understand both the role(s) of these major jaw adducting muscles in producing bite force and in feeding. Finally, we discuss hypotheses to explain the possible functions of these muscles during feeding.

MATERIALS AND METHODS

Anatomy.—Two adult female *T. teguixin* (sensu Fitzgerald et al., 1999) were dissected to determine muscle size and position. Origins, insertions and fiber directions were closely noted in the large, superficial adductors: adductor mandibulae externus superficialis, pseudotemporalis superficialis, and pterygoideus (Fig. 1). Our myological assessment agreed with previous description of cranial anatomy of *Tupinambis* by Gomes (1974) and Riepple (1980).

The adductor mandibulae externus superficialis (AMES) is a thick, parallel-fibered muscle (Riepple, 1980) that originates along the temporal arch, cephalic condyle, and quadrate aponeurosis. It courses anteroventrally to insert on

the lateral surface of the lower jaw. The pseudotemporalis superficialis (PST) is a fusiform muscle that originates along the parietal and supratemporal bones and inserts on the coronoid process via a long tendon and the aponeurosis on the medial surface of the AMES. The superficial pterygoideus (PTY) originates along an aponeurosis extending ventrally from the pterygoid. It runs ventrolaterally beneath the ramus of the lower jaw to its steep insertion on the lower jaw's lateral surface. This muscle forms a large mass around the posterior portion of the lower jaw.

Electromyography (EMG).—Five adult lizards (3 males, SVL = 310, 316, 318 mm; 2 female, SVL = 296, 314 mm) were used in this study. Lizards were anesthetized with an intramuscular injection of Ketaset (up to 100 mg/kg body weight, D. Ritter, pers. comm.) Electrodes were constructed of coated stainless steel surgical wire (Cooner Wire Corp., AS 631) with 0.5 mm of bared wire at the tips. Electrode tips were separated by 1–2 mm (Loeb and Gans, 1986). Electrodes were implanted in the AMES and PST (Fig. 1) via a 20-gauge hypodermic needle through a small incision in the skin. Care was taken to place electrodes in the center of the muscle near its origin. Electrodes were placed in the posteriodorsal portion of the PTY through a small incision just below the tympanum with the wire leads running through a canulus and out of the skin via another incision at the base of the neck just cranial to the pectoral girdle.

All electrode leads were glued to the surface of the skin at the point of exit using Super-Glue®. The leads were soldered into gold connecting pins in a strip connector (Amphenol). A small length of 18-gauge galvanized steel wire was run through each end of the connecting strip creating a harness around the neck of the animal. Animals were allowed to recover from anesthesia for 2–4 days unrestrained prior to data collection.

A lightweight, shielded, and grounded cable was secured to the galvanized steel harness around the neck of each lizard. EMG signals were amplified (Analog Devices AD521 with CMR >110 dB) with a gain of 1000×, filtered (high pass, 75 Hz) and full wave rectified. Data were digitized at a sampling rate of 16 kHz and stored on a personal computer with R.C. Electronics Computerscope software (Jayne et al., 1990). Comparisons of the onset and offset of motor activities were made by measuring the duration of the rectified EMG signal from each burst. Only motor patterns that had amplitudes

of two times the baseline amplitude were included in the analysis (Jenkins and Goslow, 1983).

Bite force.—Bite forces were measured with a dual cantilever force transducer. The force transducer is made of parallel aluminum bite bars. Each aluminum bar measured 30 mm × 10 mm × 1 mm with a separation between the upper and lower bars of 4 mm. Foil strain gauges (Omega Corp. SG-3/120/LY21) were bonded at the clamped bases of the upper and lower bars. The gauges convert the amount of displacement (strain) of the bars to a change in resistance in a wheatstone bridge circuit. A deflection of the bars resulted in a change in voltage within the circuit. This change in voltage was directly proportional to the compressive force of the bite (see calibration below). Analog signals from the wheatstone bridge were digitized (sampled at 16 kHz) and collected with EMG data.

Prior to all experiments, lizards were warmed to a body temperature of 35 C and induced to bite a force transducer while EMG data were collected simultaneously. Lizards were agitated while restrained by hand, resulting in the lizard giving an open mouth threat display. When the force transducer was touched to the anterior premaxillary teeth, the lizards bit the transducer. To standardize all measurements, only the anterior premaxillary and dentary teeth bit the transducer at known locations (see below).

Calibration of bite force transducer.—The Newtons of measured bite force (N_m) were estimated using the relationship between voltage readout and the Newtons readout on the bite force transducer. By applying masses of 0.5, 1.0, 2.0, and 4.0 kg on the bite bars and recording the number of Newtons on the LCD display of the force transducer, the relationship between forces applied to the transducer and measures of force in Newtons could be calculated (N_m = 0.043887 X− 0.105181; R^2 = 0.97) and used to predict N_m for voltages generated by subjects during the trials.

To obtain accurate estimates of forces (N_r) for data collected with the bite force transducer, the transducer was calibrated with known masses at various locations between the free and clamped ends of the bite bars. Weights (0.5, 1.0, 2.0, and 4.0 kg) were hung on the bite bars at 2-mm intervals from 0 mm (free end) to 24 mm (clamped end). Regression equations were calculated for each location. Thus, by knowing N_m and the bite position (i.e., the number of millimeters from the tip of the bars), the bite force

TABLE 1. SUMMARY STATISTICS OF BITE FORCE FOR FIVE INDIVIDUAL *Tupinambis teguixin*.

Lizard SVL [sex]	# of bites	Mean bite force (Newtons)	SD	Range (Newtons)
296 [f]	14	62	17.1	14–90
314 [f]	6	54	3.1	51–57
313 [m]	5	55	7.9	44–62
318 [m]	17	86	19.2	22–105
321 [m]	6	73	2.0	72–76

in Newtons (N_r) could be determined. During each bite force experiment, the bite bars were wrapped in chamois cloth and athletic tape. The lizard's teeth punctured the athletic tape and thus gave an impression of the bite position. The bite position was measured as the distance between the most anterior tooth impressions in the athletic tape and the free end of the transducer. The bars were positioned in the center of the lizard's mouth so that compressive forces were only applied by the anterior teeth. No off-center bites were included in this analysis.

Biting behavior.—In six separate experiments, EMG data were collected while lizards were fed lab mice. Each lizard was given one to four mice (5–35g) during each trial. To correlate jaw adduction and biting behaviors with the electromyographic records, trials were recorded with standard NTSC video (30 frames/sec). Video records were synchronized with EMG data with a time base generator (TBG). The TBG assigned a time and frame record to each video frame. The TBG also generated a 5 VDC signal simultaneously with each video frame and this was recorded with the EMG data.

RESULTS

Bite force and electromyography.—Maximum bite forces occurred 50–100 ms after the subject initiated a bite as measured by the start of force production. Male lizards ($n = 3$) produced peak compressive bite forces that ranged from 22–105 N ($n = 24$; mean = 79; Table 1). Female lizards ($n = 2$) produced peak bite forces of 14–90 N ($n = 18$; mean = 60). A repeated-measures analysis of variance revealed no significant differences in mean bite force between the sexes ($F_{1,3} = 4.17$, $P < 0.13$), or among individuals ($F_{3,34} = 2.35$, $P < 0.09$).

Eighty-six percent of the bites (sexes combined) exhibited activation of the PST and AMES muscles 10 to 50 ms prior to force production (Fig. 2). The AMES fired slightly before
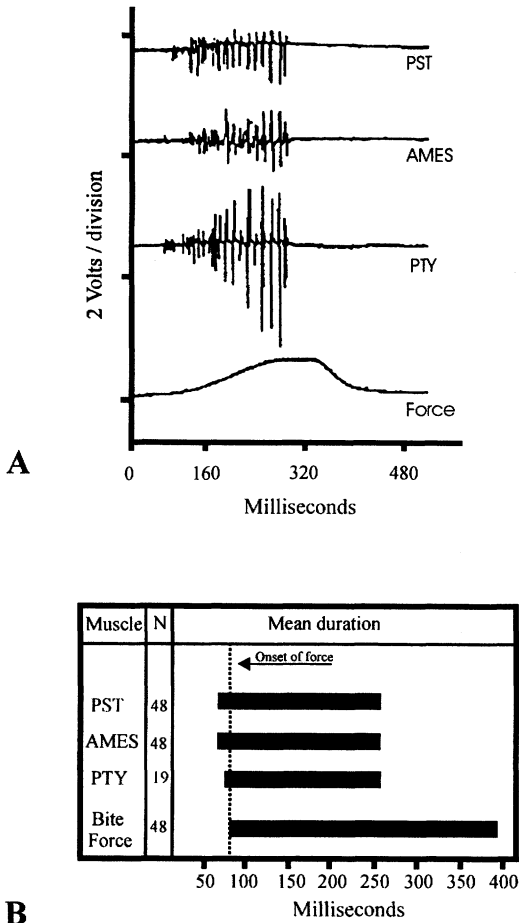
A

B

Fig. 2. (A) Representative electromyogram of the PST, AMES, PTY, and developed bite force in *Tupinambis teguixin*. (B) The mean duration of bite force production in relation to muscle activity in the PST, AMES, and PTY in five individuals of *T. teguixin*.

(10–20 ms) the PST in 48% of the bites observed. Motor patterns from the PTY were recorded on eleven bites (both females). In 45% of these bites, the PTY fired 10–30 ms after the AMES and PST. Therefore, PTY motor activity corresponded with the onset of force production (Fig. 2).

The duration of adductor muscle activity was also highly variable (30–450 ms). The duration of activity in the PST and AMES averaged 137 ± 47 ms ($n = 48$; range: 48–265) and 147 ± 58 ms ($n = 48$; range: 47–279) respectively. In the PTY, the mean duration was 200 ± 61 ms ($n = 19$; range: 94–274).

Adductor muscle motor activity ceased abruptly in all experiments. However, after motor activity ceased, lizards were able to maintain force for up to 2.5 times the duration of muscular activity (Fig. 2). The duration of motor activity during force production ranged from 30–80% of total bite duration with mean durations of 55% (± 5.6%) in females and 60% (± 3.8%) in males.

Biting behavior and electromyography.—Observed feeding behaviors were similar in all trials and revealed three distinct biting behaviors (crushing, closing and preparatory bites) that corresponded with unique patterns of adductor muscle activation. Upon detection, lizards seized the mice and oriented them to position the head between the posterior margin of the jaws. Once positioned, they crushed the skull (crushing bites). The ensuing gape cycles contained manipulations of the prey item and were divided into closing bites and preparatory biting behaviors (see below). The bite categories were defined by reviewing the video record and were easily distinguished by differential recruitment of the jaw adductors (Table 2).

Motor patterns observed during crushing

TABLE 2. BEHAVIORAL AND MOTOR PATTERN CHARACTERISTICS IN *Tupinambis teguixin* WHILE CONSUMING MICE. Muscle abbreviations: PST = pseudotemporalis superficialis, AMES = adductor mandibulae externus superficialis, PTY = pterygoideus. (n = number of bites per category).

Behavior	Bite category	n	Major feature	% bites with feature
Strikes and head bites	Crushing	23	Activation of AMES, PTY, PST;	100
			Simultaneous onset;	79
			High amplitude	100
Preparation for swallowing	Preparatory	27	Activation of AMES, PTY;	100
			Activation of PST;	26
			Low amplitude	100
Closing, pick up, turning prey	Closing	16	Motor activity in AMES only	100

Crushing

A

Closing
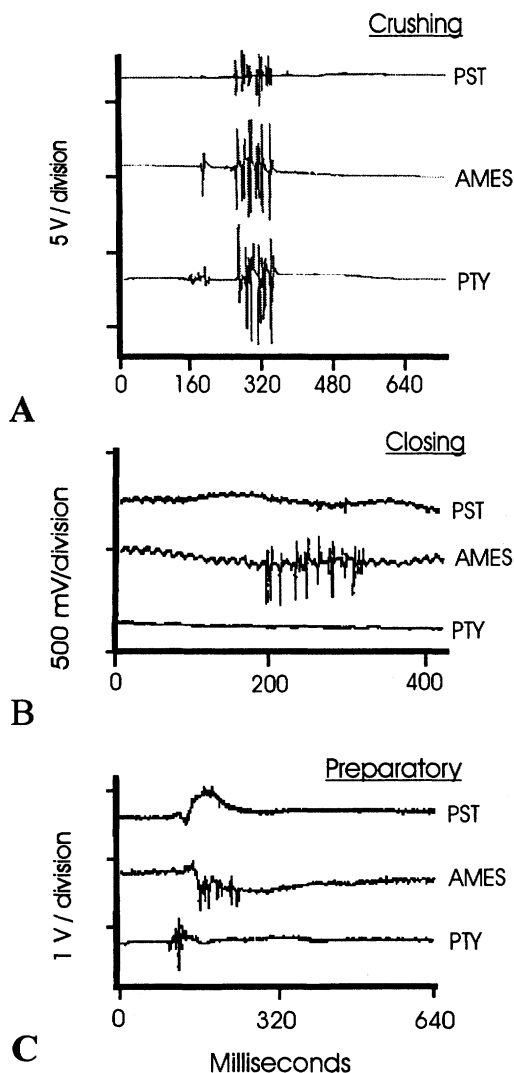

B

Preparatory

C

Milliseconds

Fig. 3. Typical raw electromyograms recorded from the PST, AMES, and PTY muscles while consuming mice. Records represent motor patterns from the crushing (A), closing (B), and preparatory (C) bite categories.

bites ($n = 23$) were characterized by the activation of the PST, AMES, and PTY muscles and high amplitude electromyograms (Fig. 3). Behaviors included in this category were bites to the head, back, or hindquarters of the mice during which the skull or back was often crushed. Activity in the PTY began between 10–40 ms after the activation of the PST and AMES in 21% of crushing bites. Two bites showed activity in the AMES prior to activity in the PST or PTY.

Duration of crushing bites was highly variable. The duration of PST activity ranged from 47–206 ms. The AMES duration ranged from 11–208 ms and the PTY ranged from 12–237

ms. The mean durations of these muscles were very similar (PST = 132 ms, AMES = 148 ms, and PTY = 121 ms).

Closing bites ($n = 16$) were bites in which the jaw closed slowly to grasp prey after it had been killed. Behaviors such as picking up or turning a prey item were included in this category. This category of bites occurred as a lizard manipulated prey prior to ingestion. Closing bites were characterized by activity only in the AMES (Fig. 3). The duration of activity in the AMES ranged from 10–347 ms with a mean duration of 151 ms.

Preparatory bites ($n = 27$) were all other bites or gape cycles where lizards prepared the mouse for swallowing. This category included both inertial feeding cycles and lingually based transport cycles where prey items were manipulated within the mouth. The combination of behaviors into this category was necessarily a result of the high variability in both behavior and motor patterns. Thus, the preparatory bite category consists of all intraoral transport behaviors.

The motor patterns of preparatory bites were the most variable of all categories; however, two distinct types of motor patterns were observed. In 20/27 preparatory bites, activity in the PTY began 10–50 ms prior to activity in the AMES (Fig. 3). No PST activity was present in these 20 bites. In the remaining seven bites, PST activity was synchronous with the AMES. Activity in the PTY was either synchronous ($n = 4$) with the AMES and PST or delayed by 50 ms ($n = 3$). Interestingly, the activation patterns of these four bites were similar to crushing bites but did not exhibit high amplitude signals.

DISCUSSION

The motor patterns obtained during force production trials and feeding suggest that activation of these adductor muscles varies between bite categories (crushing, closing, preparatory) but are consistent within them. Much of the observed variation was a result of the performance of different tasks—producing force to dispatch prey, manipulate prey, and prepare prey for swallowing. Given that prey items change shape and degree of resistance during consumption (Smith, 1982), some variability observed in our data is at least partially explained by the complex nature of prey ingestion and processing. Nevertheless, definitive, repeatable patterns of muscle activation for discrete behaviors were identified (Table 2).

Bite force.—Bite force has been estimated in several squamates (Sinclair and Alexander, 1987; Andrews and Bertram, 1997; Herrel et al., 1998) based on muscle mass, muscle fiber length, and muscle cross sectional area. However, few studies have measured bite forces in vivo. Herrel et al. (1999b) measured in vivo bite force in *Gallotia galloti*. Although this species is smaller (female SVL = 93.3, male SVL = 109.7) than *T. teguixin*, their bite forces were comparable (females = 33.5, males = 108.6 N). Bite forces in this study were higher than those observed in the ferret (up to 48.8 N; Dessem and Druzinsky, 1992) but fell within the range of those seen in domestic dogs (10–200 N; Brunski and Hipp, 1984). Thus, our bite force data on a large, omnivorous lizard are comparable to other vertebrates for which in vivo bite forces have been measured.

Previously, male *T. teguixin* (n = 6; range = 25–136 N; mean = 76.3) were found to exhibit greater bite forces than females (n = 7; range = 20–76 N; mean = 47.1; R. A. Anderson and L. D. McBrayer, unpubl.). Both the mean and range of bite forces measured in this study (Table 1) are similar to these unpublished results. Thus, it is likely that the smaller sample size and similar body sizes of the individuals used in this study contributed to the similarity in bite forces in males and females. The ecological significance of sexual differences in bite force remains to be determined. To date no thorough, quantitative analysis of the diet of male and female *T. teguixin* has been conducted. Herrel et al. (1999b) observed significantly different bite force in male and female *G. galloti*, but suggested that sexual selection, not niche differentiation, was responsible.

Results of bite force studies are greatly influenced by motivation of the subjects (Smith, 1982; R. A. Anderson and L. D. McBrayer, unpubl.). Hunger level, time of day, and the degree of habituation to handling may strongly influence a lizard's motivation to bite. In this study, individuals that were repeatedly tested during a trial exhibited the greatest force production in the first bite; subsequent bite forces decreased (pers. obs.). This observation suggests that motivation and fatigue play an important role in measuring maximal bite forces.

Bite force production in *T. teguixin* was observed following near simultaneous (within 50 ms) onsets of activities in all tests. These results are consistent with previous studies of lizards consuming prey items (Smith, 1982; Gans et al., 1985; Herrel et al., 1997). Although each of these studies found variability in motor patterns among muscles within the adductor complex, none of them found quantitative differences in the onset of activity. Therefore, activity patterns observed in *T. teguixin* while biting the force transducer are consistent with patterns observed for lizards consuming actual prey items.

Peak force production was typically attained 50–100 ms after the onset of motor activity in the jaw adductors and maintained during all motor activity. Interestingly, peak forces were maintained for intervals longer than the observed motor patterns. Maintenance of bite force after cessation of motor activity is apparently a common feature of tetrapods. Bone strains measured in the dentaries of mammals are maintained and even increased after cessation of motor activity from jaw musculature (Hiiemae and Crompton, 1985). The duration of peak bite force and rate of subsequent decline is most probably dependent on the muscle fiber-type composition (S. Herring, pers. comm.) and the rate of reabsorption of intracellular calcium by the sarcoplasmic reticulum. Although not addressed in this study, it is possible that variation in muscle fiber-type composition between individuals contributed to the observed variation in the durations of peak bite forces and rates of decline. Throckmorton and Saubert (1982) studied fiber-type composition in *T. nigropunctatus* (= *T. teguixin*). The PST and PTY consisted of glycolytic fibers. They hypothesized these fibers could contribute to high force generation for short periods of time. They showed the AMES was subdivided into a lateral region of glycolytic fibers and a medial region of oxidative fibers. Therefore, it is possible that compartmentalization of muscle fiber-types within the AMES accounts for this muscle being the only one of the three tested to be recruited in both low amplitude, slow closures (preparatory bites) and faster, higher amplitude bites (crushing bites).

Behavior and prey capture.—In the majority of high amplitude bites (crushing bites), the PST, AMES, and PTY were recruited simultaneously (within 50 ms). For those bites in which the activation of the adductors was not simultaneous, some asynchronous adductor activity may be attributed to muscle activation during jaw depression or balancing of the jaw joint (Bramble and Wake, 1985). Studies of prey ingestion in *Uromastix aegyptius* (Agamidae) showed the adductor musculature began to fire during jaw opening (Throckmorton, 1976, 1978). Gans et al. (1985) proposed that such adductor activity during jaw opening could provide tension for the jaw depressor musculature so that the adductors may continue to

fire until maximal gape is attained. The authors reason that by resisting jaw depression, the adducting muscles could undergo greater lengthening and increase both velocity of closure and the amount of tension developed. Finally, the natural variability in the position of the prey may help explain differential temporal activation of the PST, AMES, and PTY. For example, if the prey offered resistance to only one side of the jaw, adductor activity of the contralateral side may be activated differentially to help balance the force exerted on the jaw by the prey item. If this force went unbalanced, the jaw joint could potentially be disarticulated (Dessem and Druzinsky, 1992). Therefore, the functional demands on the adducting musculature are different between bites depending on the position of the prey item.

Hypotheses of muscle functions.—Our results, and its size and position, indicate that the AMES is the primary jaw adductor. This muscle was activated in all bite categories, suggesting the AMES serves multiple functions in jaw adduction. However, it was the only muscle active during closing bites. Therefore, it can be inferred the AMES was the only muscle studied that contributed to the relatively slow closure of the jaws during prey manipulation. This assertion is supported by muscle fiber-type evidence. Throckmorton and Saubert (1982) suggested the medial oxidative region could be used for manipulative and postural activities as well as joint stabilization. Our EMG data did not address compartmentalization, but the motor patterns for each bite category were explained by this hypothesis.

The PTY motor patterns indicate that it is the first muscle recruited to rapidly elevate the jaw and assist the AMES in moderate (preparatory bites) to high levels (crushing bites) of force production. Gans et al. (1985) found similar activation patterns in the PTY and AMES and pointed out the important role of the PTY in both force production and jaw stabilization. Our observation that bite force production was often simultaneous with motor activity in the PTY further supports this view. Because the PTY originates medial to the quadrate-articular joint and runs postero-ventrally to the lateral aspect of the jaw, it must play an important role in jaw stabilization especially during high force production (e.g., crushing bites). The glycolytic fibers of PTY would aid in high force production but not be as useful in generalized movements of the jaw (Throckmorton and Saubert, 1982).

Finally, the PST was activated during crushing bites and 26% of preparatory bites. As in the PTY, the PST likely served to speed up jaw adduction and bite force production. However, the intermittent activity patterns observed in the PST during preparatory bites suggest this muscle may also serve to balance forces exerted on the jaws during prey manipulation. Whether the PST acted to stabilize the contralateral jaw during unbalanced jaw closure or prevented disarticulation of the jaw joint when prey acted as an occlusal fulcrum (Sinclair and Alexander, 1987) cannot be determined from this study.

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WILLIAMS, J. D., O. E. DONADIO, AND I. RE. 1993. Notes

MCBRAYER AND WHITE—BITE FORCE, BEHAVIOR, AND EMG 119

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