BITE AND JOINT FORCE ANALYSIS
IN *CAIMAN CROCODILUS*

by

JOHAN CLEUREN, PETER AERTS and FRITS DE VREE
University of Antwerp (U.I.A.), Department of Biology
Universiteitsplein 1, B-2610 Antwerp (Belgium)

SUMMARY

The equilibrium of forces acting on the lower jaw during biting can be assessed by static modelling. Usually, no account is taken for the actual recruitment level of the involved jaw adductors and only one fixed orientation of the food reaction forces is considered. These conditions conflict with reality. Therefore, recruitment levels of eight muscles of *Caiman crocodilus* are determined by means of quantitative EMG. For 12 crushing bites and one holding bite, these levels were normalized (per muscle) to the maximal activity level ever observed in a total of 72 bites. These activity levels were used as input for a static bite model. A large numbers of simulations are run in which the orientation of the food reaction forces varies over a large range. Several bite points are considered. The model calculates the magnitude of the bite forces and the orientation and magnitude of the joint forces. The results for the individual bites are compared to a model simulation where all muscles are fully active (100 %) and to an averaged bite representing a generalized crushing bite of *Caiman*. This allows to assess the biological meaning of such simulations. It turns out that (apart from the absolute size of the forces) both the 100 % model and the generalized bite simulation result in an equilibrium condition which closely approximates the actual *in vivo* equilibria. Some functional and morphological implications are discussed.

Keywords : bite force, joint force, electromyography, biomechanics, reptiles, *Caiman*.

INTRODUCTION

For basic mechanical analysis, the lower jaw in tetrapods can safely be described as a simple lever (one rotational degree of freedom). Nevertheless, several pairs of jaw closers are always present, which makes that bite forces can theoretically be generated by a large number of combinations of muscle forces. When food particles are held or crushed, muscle forces must be in balance with all other external forces acting on the jaw. These are predominantly forces situated at the level of the jaw suspension and forces exerted by the food particle in reaction upon the biting forces themselves (*i.e.*, food reaction forces). A static force analysis allows to assess this

balance in a relatively simple way (*e.g.,* ALEXANDER, 1983 ; SINCLAIR and ALEXANDER, 1987 ; for a more elaborate 3D-example see KOOLSTRA *et al.*, 1988).

Among tetrapods, the reptilian jaw musculature must be considered as the most complex one. SINCLAIR and ALEXANDER (1987) deal in their analyses with three types of reptiles : a turtle (*Chrysemys*), a lizard (*Varanus*) and a crocodilian (*Caiman*). The simulations are based on two assumptions. (1) Muscle forces were proportional to the physiological cross-section (*i.e.,* muscle volume/mean fibre length), and all muscles are fully active simultaneously. (2) Food reaction forces or joint reaction forces have a premised fixed orientation. In case of *Caiman* and *Chrysemys* food reaction forces are oriented perpendicular to the axis interconnecting their point of application and the centre of the jaw joint. For *Varanus*, the orientation of the joint reaction force was predefined (in line with the quadrate), resulting in one fixed orientation for the food reaction force too.

Such assumptions, however, conflict with reality. The orientation of food reaction forces may well diverge from one fixed (perpendicular) condition. The actual orientation is highly unpredictable, as it depends upon shape and texture of the food particle, its position with respect to the jaws, the shape and position of the teeth, the gape angle, etc. (see also KOOLSTRA *et al.*, 1988). In addition, various papers show that patterns of co-contraction of jaw closing muscles differ between bite types (*e.g.,* prey capture, positioning, crushing, reduction, killing, *etc.* : THROCKMORTON, 1980 ; GORNIAK *et al.*, 1982 ; SMITH, 1982 ; VAN DRONGELEN and DULLEMEIJER, 1982 ; BUSBEY, 1989).

Moreover, recent quantitative analyses of electromyographic data recorded from a large number of jaw muscles during feeding in *Caiman crocodilus* (CLEUREN and DE VREE, in prep.) and in agamid lizards (A. HERREL, pers.comm.) demonstrate that even within groups of similar bites, clustered by a factor analysis (PCA ; groups coincide with bite types), the recruitment level of individual muscles changes drastically from one bite to the other. Within the group of truly static crushing bites, not only the general level of recruitment of the involved muscles varies (reflecting changing biting efforts), but also the pattern of the individual recruitment level of all muscles changes (see further).

For all these reasons, the biological significance of static bite simulations with prescribed orientation of reaction forces and full scale activity of the jaw closing muscles must be questioned. Therefore, the present study applies anew a static bite force analysis to 12 crushing bites of a young caiman, taking into account the individual recruitment level of each muscle. Calculations are performed for a wide range of orientations of food reaction forces at several biting points. Magnitude and orientation of joint forces, and the magnitude of the bite forces are computed. The results are compared to those of simulations in which all muscles are fully active (*i.e.* force level accords directly to the physiological cross section), and with simulations in which the activity level of the muscles equals the average of the actual crushing bites. This allows to assess the biological relevance and meaning of such simulation conditions. Further, one recording of another static bite type, namely holding of the prey, is included in the comparison. Morphological and functional implications will be discussed.

MATERIAL AND METHODS

Juvenile *Caiman crocodilus* were commercially purchased. The specimen used for quantitative EMG-experiments had a length of 0.74 m and a mass of 1.5 kg. Muscle masses were determined on a specimen which died a natural death (0.65 m ; 1.0 kg). EMG-signals of 8 muscles (see Table 2) were recorded by means of teflon isolated stainless steel bipolar electrodes (diameter 0.045 mm ; Leico Industries Inc.). The EMG signals were passed through Tektronix 26A2 differential amplifiers and Honeywell Accudata 117 DC amplifiers and stored on a Honeywell medium-bandpass 96 FM 14-channel tape recorder. The analogue signals were digitized afterwards at 10 kHz (Keithley DAS, series 500). The digital signal was integrated using the procedure of BEACH *et al.* (1982). In this way one value per interval of 10 milliseconds was obtained for each muscle, being a measure for the intensity of its recruitment, and thus for the force development too (BASMAJIAN and DE LUCA, 1985). Throughout two complete feeding bouts (encompassing several cycles (n = 72) of all bite types : acquisition/holding (n = 1), killing/crushing (n = 12), repositioning (n = 31), transport (n = 12) and swallowing (n = 16) (see CLEUREN and DE VREE, 1992) ; the maximal integrated value ever observed for each muscle was determined. The integrated EMG-data of all crushing and the holding bites were then normalized per muscle according to these maxima (expressed as a percentage). An extensive description of the EMG-quantification and factor analysis will be published elsewhere.

An estimate of maximal force development by each muscle was made based on the physiological cross sections (volume/mean fibre length). Muscle volume was approximated from its mass, assuming a density of 1000 kg m^{-3}. The musculus adductor mandibulae externus (MAME) consists of three parts (MAMES = superficialis, MAMEM = medialis and MAMEP = profundus ; see SCHUMACHER, 1973 ; VAN DRONGELEN and DULLEMEIJER, 1982). In the present setup, no EMG-data were available for the MAMEM, but previous experiments revealed that the activity of the pars medialis resembles this of both other parts. Therefore, half the mass of the MAMEM was added to the MAMES, the other half to the MAMEP (Table 1) in order to represent the entire MAME in the model as two separate bundles only. The total jaw muscle mass from one side was 24.95 g. Mean fibre lengths were obtained from SINCLAIR and ALEXANDER (1987 ; from a specimen of identical length and mass). The fibre lengths of the MAMES and MAMEP were taken identical, based on the evidence provided by the ranges of fibre lengths published by BUSBEY (1989). The same holds for both components of the pterygoideus. A muscle stress of 0.25 MPa was used to convert physiological cross-section to force (see for instance HERZOG, 1994). The 3D orientation of the force vectors (see Fig. 1) was determined for one specific state of jaw depression by measuring the coordinates of the centres of the origins and insertions of the considered bundles on orthogonal X-rays (Siemens Tridoros Optimatic 880, at 35 kV, 400 Mas ; positioning based on dissections). The centre of the frame of reference was situated in the mid-sagittal plane at the level of the jaw rotation centres. The X-axis ran parallel to the neurocranial base (see Fig. 2A).
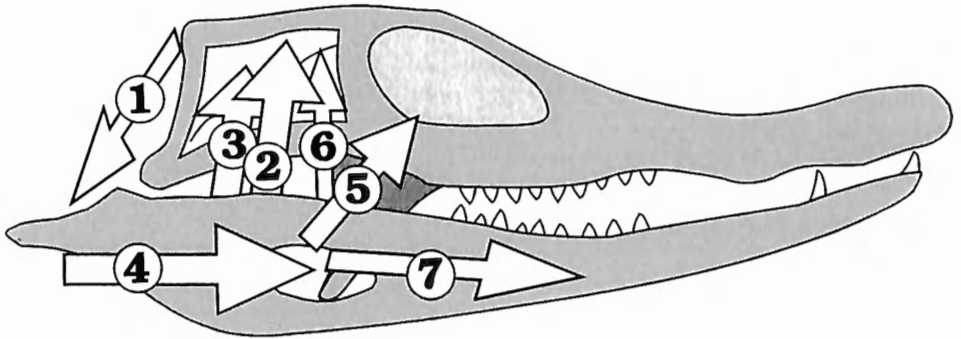
Fig. 1. — *Caiman crocodilus* : Lines of action of the jaw muscles, the width of the arrows refers to the physiological cross section. 1 = M. depressor mandibulae ; 2 = M. adductor mandibulae externus (sup., med., prof.) ; 3 = M. adductor mandibulae posterior ; 4 = M. pterygoideus posterior ; 5 = M. pterygoideus anterior ; 6 = M. pseudotemporalis ; 7 = M. intramandibularis.

The model used to calculate the static force equilibrium was planar : calculations were carried out in a sagittal plane. Nevertheless, the 3D configuration of the muscular system (which is coupled to the state of jaw depression) was taken into account. For muscles diverging from the sagittal plane, only the sagittal component of the force vector was considered. Therefore, the model can be regarded 3D in cases where biting activity is symmetrical, as any laterally directed forces cancel each other at both body sides. [Notice that in this case left + right lower jaw constitute the free body, which is reasonable because of the very strong immobile mandibular symphysis]. This holds true for crushing and holding bites of caiman (and other reptiles too), as it is evidenced by former EMG-experiments where bilateral records of jaw muscles were made. The magnitude of the sagittal component and its orientation were automatically adjusted according to the introduced gape angle. Gape angles and biting points (= point of application of the food-reaction forces) were selected on the basis of observations of feeding in unrestrained animals.

Bites were simulated by multiplying the normalized integrated EMG-level (see above and Table 2) with the maximal contraction forces (see also DE GUELDRE and DE VREE, 1990). These values were averaged per muscle to run the « averaged » (AVG) simulation. In a final simulation, all muscles were set to 100 % (« Model »). As mentioned in the introduction, « crushing » and « holding » were selected, as these are genuine static bites which furthermore show the necessary symmetrical muscle activity pattern. The model calculated the magnitude of the bite force, and the magnitude and orientation of the joint forces for every given orientation of the food reaction forces (see Fig. 2A). These were set to vary between − 50 and − 130 degrees with respect to the lower jaw (Fig. 2A). The direction of the joint forces is expressed relative to the cranium (Fig. 2A).

RESULTS

Maximal muscle forces and recruitment patterns

Masses, fibre lengths and physiological cross-sections of all muscles involved in the simulations are given in Table 1. Table 2 represents the normalized recruitment for each muscle during actual holding and crushing phases. The « model » bite (with all jaw adductors fully active) and the averaged crushing bite are added.

TABLE 1

Caiman crocodilus : *Jaw muscle masses in terms of percentage, fibre lengths (from SINCLAIR and ALEXANDER, 1987 ; also for a 1.00 kg specimen of* Caiman crocodilus) *and physiological cross sections.*
MAMP= M. adductor mandibulae posterior, MAMES= M. adductor mandibulae externus superficialis and part of pars medialis,
MAMEP= M. adductor mandibulae externus profundus and part of pars medialis, PTP= M. pterygoideus posterior,
PTA= M. pterygoideus anterior, IM= M. intramandibularis,
DM= M. depressor mandibulae

MUSCLE	MASS (%)	FIBRE LENGTH (cm)	PHYS. CROSS (g/cm)
MAMP	15	1.70	2.21
MAMES	7	0.96	1.77
MAMEP	8	0.96	2.08
PTP	34	2.00	4.25
PTA	18	2.00	2.25
PST	5	1.35	0.93
IM	5	0.47	2.65
DM	8	1.58	1.27

Bite simulations

Bite forces are given for one body side only. They have to be multiplied by two to obtain the overall bite force on the prey. They must be regarded as only a rough estimate of the forces exerted by a young caiman with a skull length of about 10 cm. Data are only presented for the extreme ($-50°$ and $-130°$) and the perpendicular ($-90°$) orientations of the food reaction force. All variables change gradually from the one extreme to the perpendicular, and then to the other extreme condition again.

TABLE 2

Caiman crocodilus : *Normalized recruitment level of the jaw muscles during holding and crushing phases.*
Model : hypothetical model with all jaw adductors fully (100 %) active simultaneously ; Hold : in vivo level during holding ;
AVG : mathematical average of all crushing bites ; 1-12 : in vivo recruitment level of all crushing bites
from two complete feeding sequences. For abbreviations of the muscles see Table 1

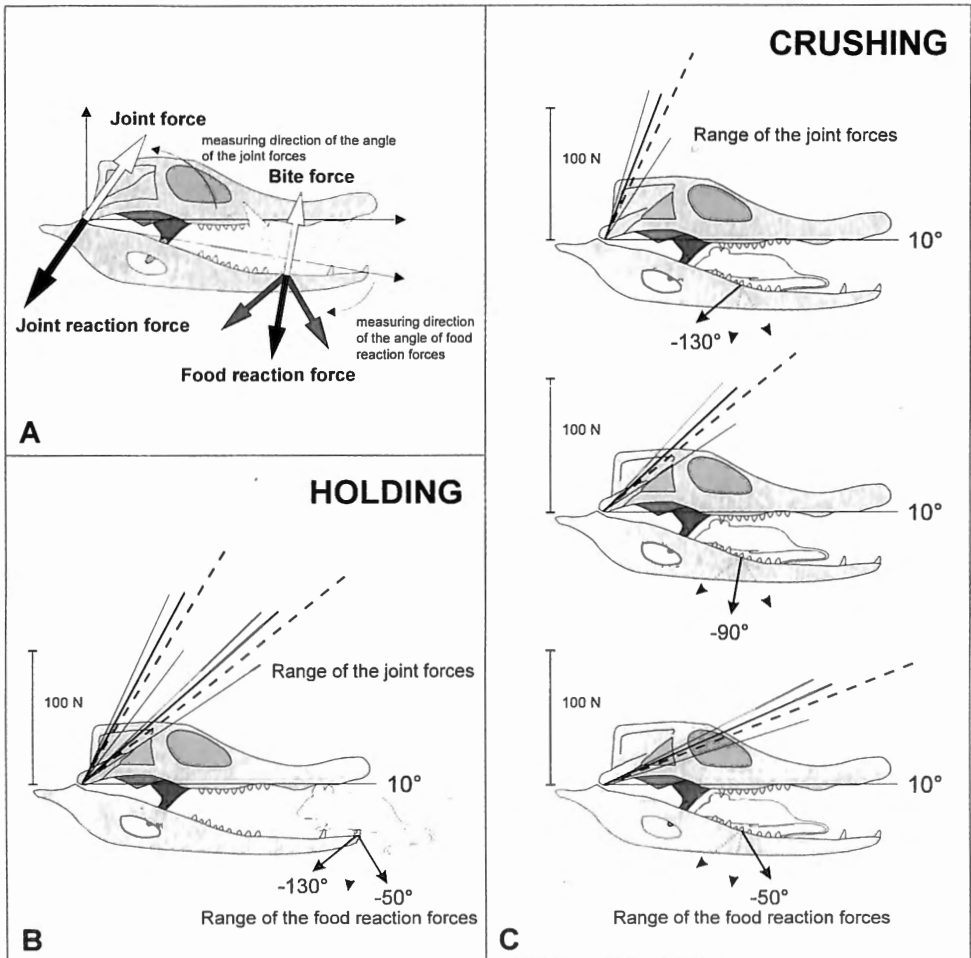|	Model	Hold	AVG	1	2	3	4	5	6	7	8	9	10	11	12
MAMP	100	97	69	43	58	59	69	76	100	60	61	62	88	78	72
MAMES	100	80	67	27	63	55	65	63	100	57	87	56	74	72	82
MAMEP	100	75	78	70	41	56	84	97	89	92	100	85	67	77	80
PTP	100	75	69	49	66	60	69	69	100	68	62	78	79	65	67
PTA	100	48	70	56	73	61	69	62	100	76	64	93	71	52	63
PST	100	100	67	31	61	55	61	77	83	80	70	66	84	65	75
IM	100	71	79	64	49	53	95	72	100	86	87	89	99	93	66
DM	0	4	5	0	3	0	0	5	3	19	6	12	2	10	1

Fig. 2. — *Caiman crocodilus* — **A**. Action (white arrows) and reaction forces (black arrows) at the jaw joint and at the bite point. The direction of the joint force is measured relative to the line interconnecting the jaw joint and the anterior tip of the upper jaw, bite forces are measured relative to the lower jaw. — **B**. Holding at bite point 4 with a gape of 10° and with food reaction force angles of − 50° and − 130°. The magnitude of the FRF is not scaled, see Fig. 3A for absolute values. Presented are the concordant joint forces of the actual holding phase (bold solid line) and the 100 % model (dashed line). Although joint forces resulting from the recruitment levels as observed during the actual crushing phases do not reflect natural conditions, caused by the artificial forward shift of the bite point, this range is also presented as thin solid lines. — **C**. Crushing in the middle of the crushing range with a gape angle of 10° and for a food reaction force angle of − 130°, − 90° and − 50°. The magnitude of the FRF is not scaled, see Fig. 3A for absolute values. Presented are the scaled joint forces when introducing the recruitment levels of the model conditions (100 %, dashed line), the averaged crushing values (bold solid line), and the *in vivo* recruitment levels (range presented between the thin solid lines).

Holding

Catching and holding occurs in the region of the anterior canine (bite point 4 in Fig. 3) and with a gape angle of 10° to 20° (Fig. 2B). The recruitment levels in terms of percentage presented in the second column of Table 2 are fed into the model. The latter predicts bite forces (BF) of 42 N for a 10° gape (Figs 2B, 3A) when food reaction forces (FRF) are perpendicular to the occlusal plane. A shift from the FRF in either direction results in an increase of the bite force : 56 N for FRF at −50° and 54 N for FRF at −130° (Figs 2B, 3A). Joint forces (JF), however, increase from 173 N (FRF at −90°) to 193 N (Figs 2B, 3B) when food reaction forces (FRF) point forward (−50°), but decrease to 160 N when the prey pushes backward on the lower jaw (−130°). This is accompanied by a change in slope from 41° to 62° relative to the cranium (Fig. 3C).

In Fig. 2B, the orientation and magnitude of the joint force of the actual holding phase (bold solid line) are compared for both extreme FRF orientations to those of the model bite (fully active jaw adductors ; dashed line) and with the range of joint forces generated by the observed recruitment levels of crushing phases when biting at the most anterior canine (thin solid lines). Notwithstanding the relatively large difference in jaw muscle recruitment level (see Table 2), both the joint force angle of the holding bite and the model bite (with all jaw muscles maximally active) fit into the envelope formed by the minimal and maximal values of the crushing bites.

Crushing

For these simulations the normalized recruitment values of the third (AVG ; averaged values of all actual crushing bites), and the fourth to last column (observed recruitment levels) of Table 2 are used. Crushing occurs in the posterior molar region *cf.* KIESER *et al.*, 1993 (biting points 1, 2 and 3 in Fig. 3), with a gape angle of 0° to 10°. The crushing region is situated near the insertions of the jaw adductors to minimize the load arm. The following numerical values refer to observed crushing phases at biting point 2 (Fig. 3) for a gape angle of 10° (Fig. 2C). During crushing, bite forces of 49 to 101 N (AVG = 78 N) are generated when the bite force is perpendicular (90°) to the tooth row. Analogous to holding, a shift from the FRF away from the perpendicular axis causes an increase in bite forces. The bite forces increase to 70 N − 144 N (AVG = 112 N) for FRF at −50°, and 59 N − 121 N (AVG = 94 N) for FRF at −130° (Figs 2C, 3A). Joint forces range from 90 N to 181 N (AVG = 138 N) with FRF at −90° at gape 10° (Fig. 3B). The range of joint angles is 33 to 47°. When food reaction forces are no longer perpendicular to the occlusal plane, but pointing forward (−50°), joint forces increase, ranging from 121 N to 248 N (AVG = 186 N) (Figs 2C, 3B), joint angles range from 17 to 26° (Fig. 3C). If the FRF slopes backward from −90° toward −130°, JF decrease to 74 N − 150 N (AVG = 118 N) (Figs 2C, 3), joint angles range from 58 to 74° (Fig. 3C). Apart from the relation between the direction of the food reaction forces and the magnitude of the bite forces and joint forces, also a clear relation with the direction of the joint forces exists : larger joint forces, resulting from a forward shift
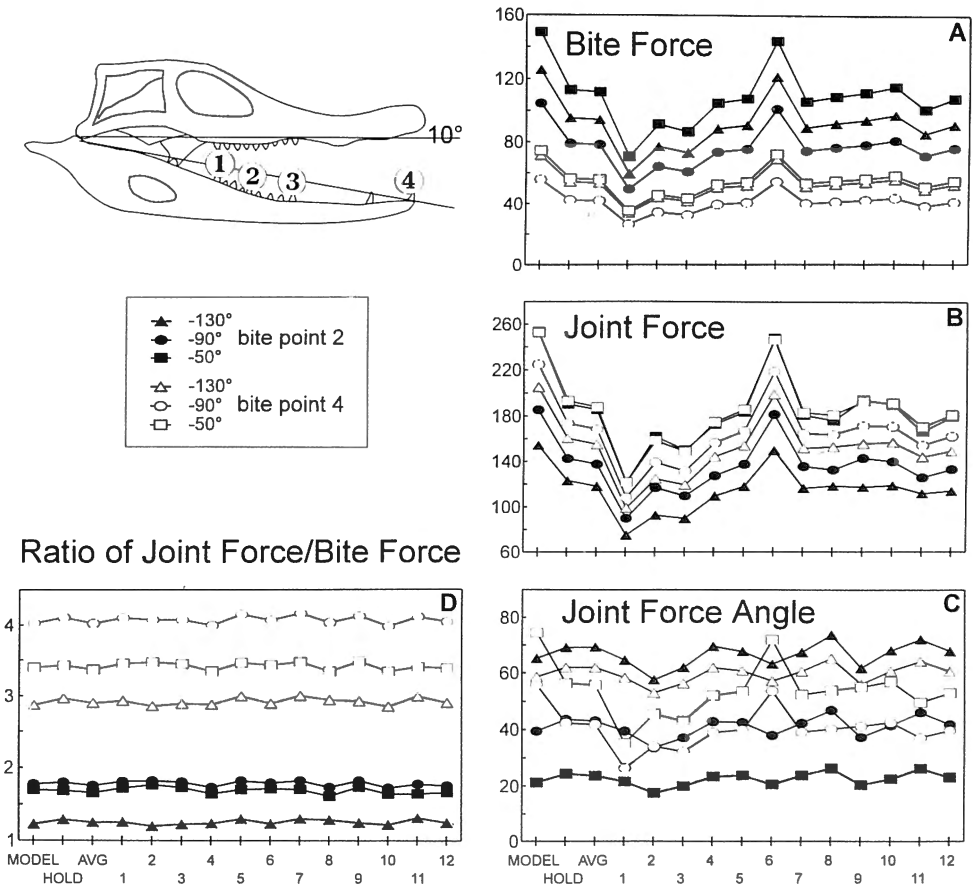
Fig. 3. — *Caiman crocodilus* — **A** : Magnitude of the bite force (values refer to one side only) — **B, C** : magnitude and orientation of the joint force at gape 10° and for food reaction forces (FRF) ranging from −130° to −50° (see legend) in function of the recruitment level (see X-axis and Table 2) and of the position of the bite point (open symbols : Holding at bite point 4 ; solid symbols : Crushing at bite point 2). — **D** : Ratio of joint force and bite force in function of the position of the bite point.

of the food reaction forces, show smaller angles. Thus, an increase of the magnitude of the joint forces coincides with a decrease of the angle this force makes with the cranium (Fig 2C, 3).

Fig. 2C demonstrates that, for the entire range of the FRF, the angle of the joint force of the averaged crushing phase (bold solid line) and the model bite (dashed line) always fits in the actual observed range of joint force angles during crushing (thin solid lines).

General

When the bite point moves from the posterior molars to the anterior incisors the magnitude of the bite forces logically decreases (see bite point 2 versus bite point 4 in Fig. 3A). This forward shift also results in a narrower range of the angle of the joint forces (compare range open symbols with closed symbols in figure 3C), and in an increase of their magnitude the more the FRF points backwards (Fig. 3B). Biting in the region of the anterior canine (during holding, Figs 3A, 3B) tends to load the joint to a larger extent than an equally sized bite force in the molar region (during crushing, Fig. 3), as also illustrated by the ratio of joint force and bite force for bite point 2 and bite point 4 (Fig. 3). This statement remains valid within the crushing region (shift from bite point 3 to 1 ; see Fig. 3).

The ratio of the joint force to the bite force is remarkably constant for a given bite point and FRF-orientation, notwithstanding the large variation in the recruitment pattern of the muscles (Fig. 3D). This factor is maximal when FRF equals 90°. The smallest factor results from biting in the molar region with an FRF pointing backwards (joint and bite forces have about the same magnitude).

DISCUSSION

DE VREE and GANS (1994) argued that modelling of muscle functions starting from its architecture only is often based on several questionable assumptions. Two of these assumptions are that all muscles act simultaneously, and that muscles are fully active. To date, it is still impossible to determine the relative recruitment level of a muscle *in vivo*. Only quantitative electromyography can give an indication of the activity level and it has been shown that the link with force output exists (BASMAJIAN and DE LUCA, 1985 ; LOEB and GANS, 1986 ; GANS, 1992). On the other hand, it is unpredictable what portion of the contracting muscle is sampled by the electrodes. Moreover, physiological cross section as a measure for *in vivo* maximal force is ambivalent too, because in most EMG studies it is unknown whether the motor units are ever active all together. For all these reasons, it remains uncertain whether the maximal activities used in this study to normalize the recruitment levels of the jaw closers (Table 2) indeed correspond to fully active muscles.

Figs 2B and 2C reveal no obvious difference between the model simulation (all adductor activities set to 100 % ; *i.e.* conditions as used by SINCLAIR and ALEXANDER, 1987) and simulations with the *in vivo* and averaged distributions for holding and crushing presented in Table 2. In case of maximally active adductors, bite for-

ces are logically larger, ranging from 104 N to 149 N at the middle of the crushing region and from 56 N to 74 N at the level of the most anterior canine for an orientation of the food reaction forces ranging from -50 to -130 degrees. Concordant joint forces for these conditions range from 154 N to 253 N (*i.e.*, dashed lines in Fig. 2C) and from 204 N to 252 N (*i.e.*, dashed lines in Fig. 2B). These force levels have to be compared to the simulations with the adjusted recruitment levels during crushing : 50 N to 144 N, and 74 N to 248 N for the bite and joint forces respectively (Figs 2C, 3A,B), and during holding : 42 N $-$ 56 N bite force and 160 N $-$ 193 N joint force. For crushing bites, *Caiman crocodilus* uses between 47 and 96 % (AVG $=$ 70 %) of its theoretical maximal bite force, but also retains between 48 and 98 % (AVG $=$ 70 %) of the theoretical maximal joint force. This variation, resulting from the shifts in recruitment level of the individual muscles (see Table 2), is likely dictated by instantaneous feedback from the jaw system. As mentioned, magnitude and orientation of food reaction forces are unpredictable from one bite to the next, especially when the food item is inhomogeneous in texture and shape. Moreover, the position of the food particle with respect to the jaws changes during the course of a feeding sequence too. Even for the bites six to 11, which represent six consecutive crushing bites of the same sequence, table 2 shows considerable variation in the recruitment pattern, resulting in the fluctuations of forces and angles exemplified in Fig. 3.

In the middle of the crushing region, the ratio of joint force and bite force ranges from 1.2 to 1.83 for gape 10° for FRF ranging from $-130°$ to $-50°$. During the holding of prey items, 75 % of the theoretical maximal bite force is retained, which equals to the retained portion (75 %) of the theoretical maximal joint force (Figs 2B, 3A, 3B). However, absolute values differ significantly, as the ratio of joint force and bite force ranges from 2.87 to 4.04 (gape 10°) at the level of the most anterior canine (Fig. 3). In other words, biting more forcefully (in absolute terms) involves a disproportional increase in joint force with a factor one to four. Therefore, it seems to make sense to adjust muscular effort to the actually required level, as in this way joint forces are kept minimal. Figures 2B, 2C and 3 further illustrate that the angular ranges of the joint forces are only slightly affected by raising all recruitment levels to 100 % and fit into the envelope of the *in vivo* crushing bites. The same findings apply to the averaged crushing bite. Apparently, the magnitude and orientation of the bite and joint forces generated by the model and average simulations perfectly fit into the observed range of *in vivo* forces (see Figs 2 and 3). Therefore, it must be concluded that both the maximal model and averaged model simulations give biologically meaningful results, especially when only relative force levels are considered. This means that static biting models are also applicable when no detailed information on the muscular recruitment level is available.

Thus, the present results for *Caiman* can be compared to those of SINCLAIR and ALEXANDER (1987). In order to do so several differences must be taken into account : the intramandibularis muscle is not included in their analyses, the musculus pterygoideus and the MAME are each represented by one force vector only, and all forces apply on the axis interconnecting the bite points with the jaw joint. A perpendicular orientation of the food reaction forces and a 100 % activity

level of all muscles is premised. First, as a test, input data gathered from Fig. 3C in SINCLAIR and ALEXANDER (1987) are fed in our model. All results were identical, except for the orientation of the joint force in case of biting in the molar region. Fig. 3C in SINCLAIR and ALEXANDER (1987) shows a joint force angle of 65° whereas our model predicts 18° [notice that SINCLAIR and ALEXANDER (1987) present joint reaction force ; *cf.* Fig. 2A]. This new angle, however, makes the results consistent with our findings : a drop of the angle with a backwards shift of the bite point. Most likely, this error slipped in during the preparing of their Fig. 3C.

In an effort to mimic the model input by SINCLAIR and ALEXANDER (1987) using our data, a simulation was run in which the intramandibularis (*i.e.*, force 7 in figure 1) was excluded, and the pterygoideus was represented by one single vector (force of bundle 4 in Fig. 1 is added to bundle 5). The bite points 1 and 4 (see Fig. 3) give the best approximation of the points of application used by SINCLAIR and ALEXANDER (1987). The bite forces and according joint forces thus found largely exceed those found by SINCLAIR and ALEXANDER (1987). Bite forces are about 3.5 times larger. For the joint forces a factor equal to 1.6 (bite point 1) or 2 (bite point 4) must be applied. This is surprising as these authors used a scaling factor of 0.33 MPa to convert physiological cross-section to force. Apparently, the specimens they used to determine the physiological cross-section had a more slender jaw musculature, notwithstanding the comparable overall length and mass. This is confirmed by making the sum of all muscle masses presented by SINCLAIR and ALEXANDER (1987) : this equals only half the jaw muscle mass of the specimen used for the present study (Table 1). Also the ratio of bite to joint forces differs considerably between both studies (0.13 versus 0.23 for bite point 4 and 0.32 versus 0.66 for bite point 1 (Fig. 3) ; first value of each couple from SINCLAIR and ALEXANDER, 1987). The same holds for the angles of the joint forces : 25° versus 49° (see above) and 18° versus 33° for bite point 4 and 1 respectively (the first of each couple from SINCLAIR and ALEXANDER, 1987).

These divergences must relate to the large differences in the relative masses of the individual muscles in both studies (compare Table 1 with Table 1 in SINCLAIR and ALEXANDER, 1987), and the differences (although small) in the orientation and point of application of the muscle force vectors. If muscle forces taken from SINCLAIR and ALEXANDER (1987) are combined with the orientation and application of the vectors in this study, joint forces are quite identical (125 N versus 127 N and 114 N versus 112 N for bite point 1 and 4 respectively), and the orientations of these forces approximate each other closely (25° versus 38° and 18° versus 21° for bite point 1 and 4 respectively). Bite forces, however, are still about 1.8 times higher than those found by SINCLAIR and ALEXANDER (1987), notwithstanding the identical muscle force input.

These findings, together with the results of the comparison between the simulations with adjusted recruitment level and fully active muscles or an averaged crushing bite (see first paragraph of the discussion), suggest that joint forces are most sensitive to changes in the magnitude of the muscle forces, but rather insensitive to changes in their orientation. However, bite forces are also largely determined by (even small) changes in the orientation of the muscle forces. The biological implica-

tions are multiple : using different compartments of complex muscles allows an extensive modulation of bite force and slight morphometric differences may determine shifts in feeding ecology of closely related species, consequently a rigorous determination of the orientation of the muscle force vectors appears to be of crucial importance.

BUSBEY (1989) also estimated the reaction forces at the jaw joint during biting with a nearly closed gape in a 87 cm long *Alligator mississippiensis*. This phase is identical to the crushing phase in *Caiman crocodilus*. For crushing, BUSBEY (1989) found a joint force of 317 N at 47° (data transformed to the present reference system ; Fig. 2A). For holding a force of 225 N at 94° is found. These data are largely different from the *Caiman* results. The description of the followed procedure does not allow to judge whether food reaction forces were taken into account or not. If they are omitted from the equilibrium calculations (as we are inclined to believe), the above mentioned results are erroneous and cannot be used for comparison.

KOOLSTRA *et al.* (1988) showed that in humans, the direction of the largest possible bite force does not coincide with the direction perpendicular to the occlusal plane. This is of course determined by the static equilibrium conditions. For a given muscular force input, forces exerted on the food *must* be minimal in a direction perpendicular to the axis interconnecting the biting point and the jaw rotation centre (Figs 2, 3). However, in *Caiman*, joint forces increase with a shift in the orientation of the food reaction force from pointing backwards to forward. In other words : the more a bite force points forwards relative to the lower jaw, the smaller the joint forces will be (Figs 2, 3). SMITH and SAVAGE (1959) argued that in mammals different directions of pull may reduce forces in the jaw articulation. IORDANSKY (1964) showed that this may also be valid for crocodilians. This author stated that the M. adductor mandibulae posterior and the M. pterygoideus posterior prevent luxation of the mandibular joint. Our results show that not only the different direction of pull of all muscles, but also a modification of the force level of each individual muscle, determines (although to a larger extend than initially expected ; see Fig. 3) the magnitude and angle of the joint forces.

Nevertheless, joint forces are still relatively high during holding and crushing of prey items. However, irrespective the orientation of the food reaction forces and the pattern of the jaw muscle forces, the orientation of the joint forces always fits within the heavily ossified triangle at the level of the jaw suspension (see Figs 2B, 2C). The anterodorsally pointing leg of this triangle is formed by the massive quadrate which inclines medially. The quadratojugal and jugal form the other leg : the lower temporal bar, a strong bony strut pointing rostrally in a sagittal plane. This means that joint forces in *Caiman* always result in compressive loading of both bony legs of the triangle (vector resolution). The more the food reaction forces point forwards, the higher the lower temporal bar will be loaded. This is not only because higher joint forces are involved (see above, Figs 2, 3), but also because forward pointing food reaction forces coincide with decreasing joint force angles which tend to come in line with the lower temporal bar. As crushing and holding show symmetrical muscle activity (see Material and Methods), joint forces are most

likely confined to a sagittal plane, premised that also biting occurs symmetrical. The sagittal position of the lower temporal bar thus ensures pure axial loading. In case of the quadrate, the joint forces participate in a bending moment too. This might explain why, in spite of the much smaller axial loading, the quadrate appears to be stronger built than the lower temporal bar.

As the orientation in which the caiman can expect and thus also must absorb joint forces is highly determined by its jaw muscle morphology, reinforcements of the skull can be focused to the essential structures and therefore also kept minimal. This fits into the hypothesis of BRAMBLE and WAKE (1985) that terrestrial species specializing in cranio-inertial feeding are expected to show modification for the cranio-cervical mass in order to minimize inertial forces on the body (see also CLEUREN and DE VREE, 1992).

SINCLAIR and ALEXANDER (1987) premised a relation between the direction of the joint forces and the structure and position of the quadrate. The present results adjust this view in that the role of the temporal bar in stabilizing the joint is as important as this of the quadrate. For *Chrysemys* (turtle), the joint forces slope dorsally and backwards, also more or less in line with the slope of the quadrate. Based on results of SMITH (1982) on *Varanus,* SINCLAIR and ALEXANDER (1987) predicted joint forces in line with the quadrate. The according food reaction force pointed backwards relative to the lower jaw. However, in the present paper it is argued that the slope of the joint forces might not coincide with the orientation of the quadrate. Then the quadrate tends to swing anteriorly or posteriorly depending upon the specific orientation of the joint forces. In crocodilians and chelonians, this is prevented by an immobile quadrate which is wedged between the other cranial bones. However, in many lizard species the quadrate is freed for movement by the loss of the lower temporal bar by reduction of the jugal and the disappearance of the quadratojugal. If the quadrato-squamosal joint allows rotations, the quadrate is streptostylic. It is remarkable that in many lizard species a ligament (the quadrato-maxillary ligament) is found precisely at the position where crocodilians have the lower temporal bar (refs, own observations). This morphological fact strongly suggests that in such lizards joint forces predominantly point backwards, sloping behind the quadrate. As the ligament is loaded in tension, it can fulfil a role in stabilizing the quadrate, as does the lower temporal bar in crocodilians.

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