

Introduction

One major theme in recent research on the evolution of complex integrated systems focuses on the possibility that conflicting functional demands may constrain the performance and potential evolution of a system (Gans, 1970; Wake, 1982; Liem & Wake, 1985; Liem, 1988, 1989; Harris, 1989; Roth & Wake, 1989). Design features which enhance performance of one function may do so while sacrificing performance in another function. This possibility raises questions about the evolution of multi-function systems. When complex systems undergo major evolutionary transformations do they retain their suite of primitive functions? If so, do major changes in one function accompany significant alterations in other functions performed by the same system?

An example of such a system is provided by chamaeleonid lizards that both capture and process prey with a feeding mechanism highly specialized for tongue projection. Chameleons possess an extraordinary prey capture apparatus, featuring a ballistically projectile tongue, that is unique among squamate reptiles. Novel specializations of the hyolingual apparatus permit chameleons to capture prey by projecting the tongue through distances up to two snout-vent lengths (Gans, 1967; Bell, 1990; Wainwright & Bennett, unpubl. obs). The morphological basis of tongue projection in chameleons involves extensive modifications of the bones and muscles of the hyobranchial apparatus and tongue (Gnanamuthu, 1930, 1937; Schwenk & Bell, 1988; Bell, 1989). These specializations include an elongate basihyal bone that supports the tongue and provides the foundation from which the tongue is launched during prey capture. The sticky tongue pad is connected to the hyoid skeleton by paired hyoglossal muscles that function to retract the tongue following projection. The hyoglossal muscles of chameleons function over more than a 17-fold length change during a typical feeding attempt and this supercontracting capacity is unique among vertebrate striated muscles (Rice, 1973).

Both the morphology and the mechanism of tongue projection in chameleons have been extensively studied (Houston, 1828; Gnanamuthu, 1930; Zoond, 1933; Altevogt & Altevogt, 1954; Bell, 1989, 1990), yet few data exist on prey processing behaviours (Bels & Baltus, 1987). Comparative data are available for several other squamate taxa (Throckmorton, 1976, 1980; Smith, 1984, 1988; Bels & Goosse, 1989; Schwenk & Throckmorton, 1989), including representatives of the Iguanidae and Agamidae, taxa believed to be outgroups to the Chamaeleonidae (Estes, de Queiroz & Gauthier, 1988). Furthermore, a model has been proposed that attempts to summarize the transport cycles of many amniotes (Bramble & Wake, 1985), suggesting that there is a common, conservative pattern of head and hyoid movements found among generalized amniotes.

This study has two primary purposes. First, we provide the first quantitative analysis of prey processing behaviours in a representative species of chameleon, *Chamaeleo jacksonii*. This permits a comparison of jaw and hyoid movements during chewing and prey transport behaviours. Secondly, we ask if the kinematics of prey transport in *C. jacksonii* are specialized relative to previously published data for other iguanian taxa that possess a more generalized prey capture apparatus. Has the evolution of the highly specialized tongue projection mechanism of chameleons influenced other tongue-mediated behaviours?

Materials and methods

Kinematic data were obtained from 3 adult *Chamaeleo jacksonii* (snout-vent lengths; 117, 121, 123 mm) collected in Nairobi, Kenya (under permit #OP.13/001/18c94/19 to AFB). Anatomical observations (summarized in Fig. 1) were made on dissections of 2 additional specimens from the same collection (115 and

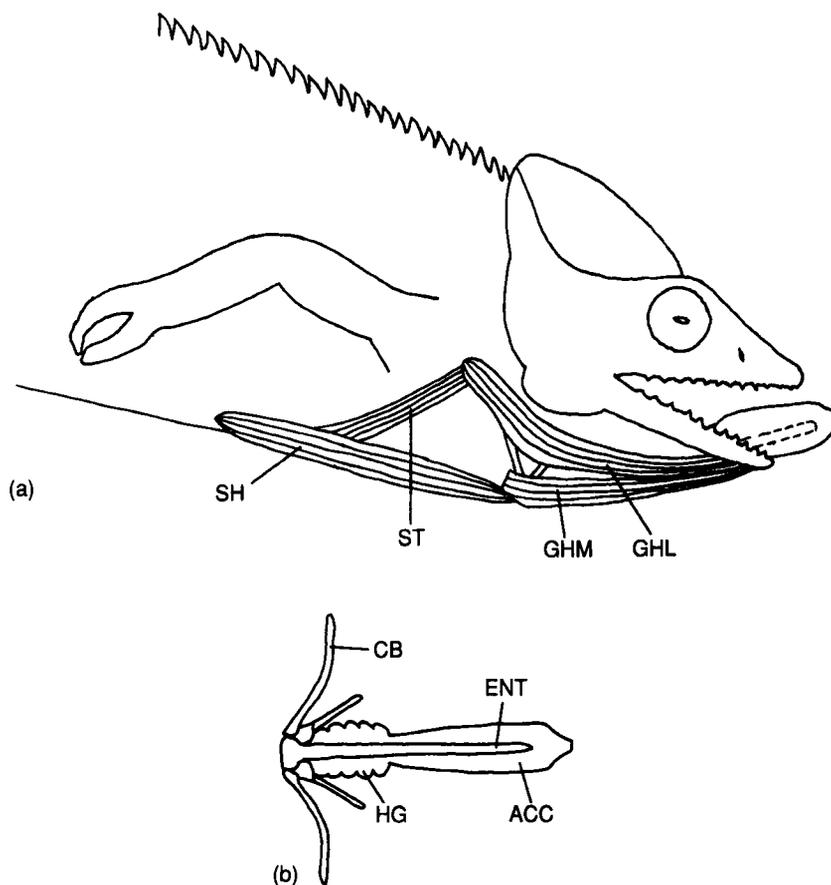


FIG. 1. Anatomical diagram of the hyolingual apparatus in the chameleon, based on observations of *C. jacksonii*, *C. oustaleti* and *C. dilepis*. (a) The position of the tongue and hyoid structures within the throat region is emphasized. Only the major muscles believed to be involved in prey processing are illustrated. (b) Isolated hyoid skeleton and tongue. Tongue pad is not shown to indicate the size of the accelerator muscle. Abbreviations: ACC, accelerator muscle; CB, ceratobranchial; ENT, entoglossal process; GHL, geniohyoideus lateralis muscle; GHM, geniohyoideus medialis muscle; HG, hyoglossus muscle; SH, sternohyoideus muscle; ST, sternothyroideus muscle.

127 mm SVL), as well as 3 individuals of *Chamaeleo oustaleti* (198, 221 and 239 mm SVL) and 2 *Chamaeleo dilepis* (98, 132 mm SVL). Animals were trained to feed by placing them at one end of a wooden rod and offering them adult crickets (*Acheta domesticus*), which were loosely held by a clip fastened to the end of a long wooden dowel. Prey processing cycles were filmed with a high-speed video system (NAC HSV 400) at 200 fields per second. The system was synchronized with 1 or 2 strobes to ensure adequate lighting during recording sessions. All feedings were filmed against a light background with a 1.0 cm grid. Body temperature was measured cloacally after each filming session and varied between 20 and 22 °C. In order to initiate feeding of an individual and obtain a clear lateral view of jaw and hyolingual movements, crickets were held anteriorly and slightly above the head. Crickets were of uniform size (sample of 10 crickets; mean mass = 0.487 g, S.E. = 0.015) to reduce the potential variation in prey processing behaviour that could be caused by varying prey size. Video-recording commenced when the prey item was captured and terminated when prey processing ceased.

For each individual, 2 or 3 cycles of both chewing and transport behaviours were selected for analysis (a total of 15 cycles was analysed). No more than one cycle of each behaviour was selected from a single feeding event. Only sequences that could be unambiguously identified as chewing or transport based on the following 2 criteria were analysed. First, during chewing the prey is not transported through the buccal cavity towards the oesophagus; rather the prey is positioned anteriorly and reduced between the jaws. Secondly, extensive posterior excursions of the hyoid skeleton are only seen during prey transport behaviour. It has been proposed that in some lepidosaurs mechanical reduction can be subdivided into crushing, chewing, side-to-side repositioning, and shaking the prey (e.g. Gorniak, Rosenberg & Gans, 1982; Bramble & Wake, 1985). In the current study we did not analyse any side-to-side repositioning cycles and never observed head shaking with this prey type. Except in some specialized species (Gans, de Vree & Carrier, 1985), the distinctions between chewing and crushing have not been clearly elucidated. The chewing cycles we analysed did involve physical reduction of the prey through cyclic jaw movements, indicating that this behaviour is best described as chewing, and not crushing, which would involve prolonged periods of jaw adduction against the prey (e.g. Gans *et al.*, 1985). We therefore term this behaviour 'chewing' for the remainder of this paper. Additional criteria for film selection were clarity of focus, determination of a clear lateral view for movements of the jaw and hyolingual complex, and body landmarks that could be easily identified.

Sequential fields from each chewing and transport cycle were viewed on the video monitor of a computer image analysis system and kinematic variables were measured with the aid of custom software. Field zero (= time zero) was defined as the field prior to the onset of mouth opening at the start of each cycle. For prey transport cycles, kinematic variables were measured every 25 msec from 250 msec prior to field zero, up to 1800 msec after field zero, for a total of 60 or more fields analysed per sequence. Analysis of chewing cycles began 250 msec prior to field zero but generally ended by 800 msec after field zero. Seven variables representing the positions of the head, jaws, body and hyoid skeleton were measured from each field. Several methods were available to quantify the skull bone movements during prey processing cycles. However, in order to obtain an accurate comparison between these data and the previously published kinematic data in lizards and other tetrapods, variables were selected that best resembled the published data. The 7 kinematic variables are described in the following list and illustrated in Fig. 2.

Angles (measured in degrees):

1. Head angle (HDA): the angle between line AB (a reference line drawn between 2 visible body landmarks) and a line drawn along the upper jaw. It decreases when the head is elevated.
2. Lower jaw angle (LJA): the angle between line AB and a line drawn along the lower jaw. It increases as the mouth is opening, and will decrease when the head is elevated.

Distances (measured in millimetres):

1. Gape distance (GD): the linear distance between the anterior tips of the upper and lower jaw.
2. Hyoid distance (HYD): the distance between the vertex of the jaw angle and the point at the gular region where the posterior tip of the basihyal bone bulges ventrally through the skin.
3. Intermandibular distance (IMD): the perpendicular distance from the ventral margin of the throat to the midpoint of a line that is defined by the anterior tip of the lower jaw and the vertex of the upper and lower jaw.
4. Head position (HP): the horizontal distance between a reference line (CD) on the background grid and the vertex of the jaw angle.
5. Body position (BP): the horizontal distance between line CD and a body landmark (B).

To examine feeding profiles statistically, 11 additional variables were directly calculated from plots of the kinematic variables against time. Five peak-amplitude variables (for GD, HDA, LJA, HYD, IMD) were measured as the difference between the field zero value and the maximum value. Five time-to-peak duration variables (for GD, HDA, LJA, HYD, IMD) were measured from time zero to the time of maximum. One cycle time (for GD) was measured from time zero to the time of return to a closed position.

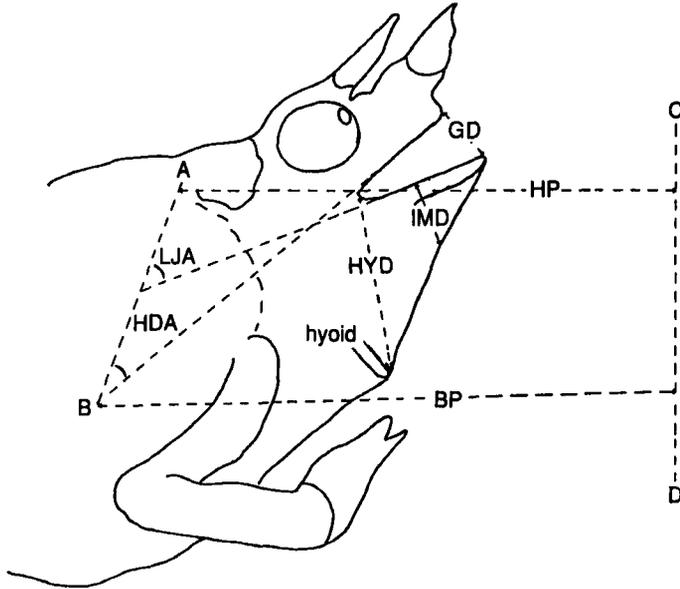


FIG. 2. Kinematic variables measured from video-fields of prey processing in *Chamaeleo jacksonii*: HDA, head angle; LJA, lower jaw angle; GD, gape distance; HYD, hyoid distance; IMD, intermandibular distance; BP, body position; HP, head position. Points A and B are visible body landmarks. Line CD is a reference line from the background grid. See text for further variable descriptions.

Two analyses were performed on this set of 11 variables to explore the differences between chewing and transport behaviours. First, 2-way analyses of variance were performed on each variable. These were mixed model designs (Sokal & Rohlf, 1981) that crossed the fixed behaviour effect (chewing and transport) with the random individual effect (3 individuals). The *F*-ratios constructed to test the behaviour effect consisted of the behaviour term mean square divided by the interaction term mean square. All other tests used the error term as the denominator in the *F*-ratio. Secondly, in order to explore differences between the behaviour in multivariate space, a principal components analysis was performed on the correlation matrix for the entire data set. All calculations were performed on untransformed data using Systat v 4.0 on an IBM microcomputer.

Terminology

We follow previous workers in our use of terminology (Bramble & Wake, 1985; Hiimae & Crompton, 1985; Schwenk & Throckmorton, 1989), to facilitate comparisons to previous studies. Below we define the terminology that we use in our descriptions of prey processing cycles. The slow open phase (SO) begins with the onset of mouth opening and ends with fast gape opening and rapid hyoid retraction. The end of SO is often very difficult, or impossible to identify precisely (see **Discussion**), and may not be possible to define unambiguously. We retain and use the term to facilitate comparisons to previous work, for which the above noted problems also apply (e.g. Smith, 1984; Schwenk & Throckmorton, 1989). Fast open (FO) begins with the end of SO and ends with maximum gape. Closing (C) begins with the first closure of the mouth following peak gape and ends at minimum gape. The power stroke (PS) is defined by no gape movements and slow protraction of the hyoid. Presumably, this phase can only be unambiguously identified based on electromyographic data of the jaw adductor muscles, but we identified its end as the return of the hyoid to its rest position.

Results

The anatomy of the buccal floor and hyolingual apparatus of chameleons has previously been described in detail (Mivart, 1870; Gnanamuthu, 1930, 1937; Gans, 1967; Bell, 1989). Only a brief description of those features central to an understanding of prey processing mechanics is provided here. Functions of muscles are inferred from anatomical positions and limited experimental data (Zoond, 1933; Bels & Goosse, 1989).

The hyolingual apparatus is suspended ventral to the jaws in the gular region (Fig. 1). The intrinsic musculature of the tongue is mounted on the long entoglossal process that runs through the centre of the tongue. The tongue pad is mounted on a large accelerator muscle which is in turn connected to the ceratohyal bones by the supercontracting hyoglossal muscle (Fig. 1). Several muscles which attach the hyolingual apparatus to other structures of the head and body provide the basis for an extensive range of movement within the throat region. The sternohyoideus muscle attaches the base of the hyoid to the sternum and can retract the hyolingual apparatus. The



PLATE I. Nine fields from a video of *C. jacksonii* during chewing behaviour. Elapsed time in seconds and milliseconds is indicated by the video-clock in each field. The first field (time = 2:475) corresponds to field zero, the field immediately prior to mouth opening. Peak gape occurs at 2:875, and jaw closing is complete at 3:150. Note that only slight movements of the hyoid and tongue can be seen (compare to Plate II). This sequence is not the one illustrated in Fig. 3. Scale bar in last field = 15 mm.

sternothyroideus muscle connects the sternum to the distal tip of the ceratobranchial. The geniohyoideus medialis and lateralis muscles connect the hyoid to the symphysis of the lower jaw. These muscles can protract the hyolingual structures. Additional transverse intermandibular muscles in the floor of the throat (not shown in Fig. 1) can elevate the base of the buccal cavity (Gnanamuthu, 1937).

Processing and transportation of the captured cricket from the buccal cavity to the oesophagus involved approximately 15–20 prey processing cycles, which included variable numbers of chewing, transport and swallowing cycles. Normally, transport cycles only occurred after all chewing cycles were completed. Both chewing and transport were associated with repeated cycles of jaw and hyolingual movements but they differed in magnitude and pattern. Plates I and II show video-fields from typical chewing and transport sequences.

Kinematic profiles of seven digitized variables (GD, HDA, LJA, HYD, IMD, BP, HP) from typical chewing and transport cycles are shown in Fig. 3. During chewing cycles (Fig. 3; triangles), a rapid increase in GD was coupled with large increases in LJA (mean peak lower jaw

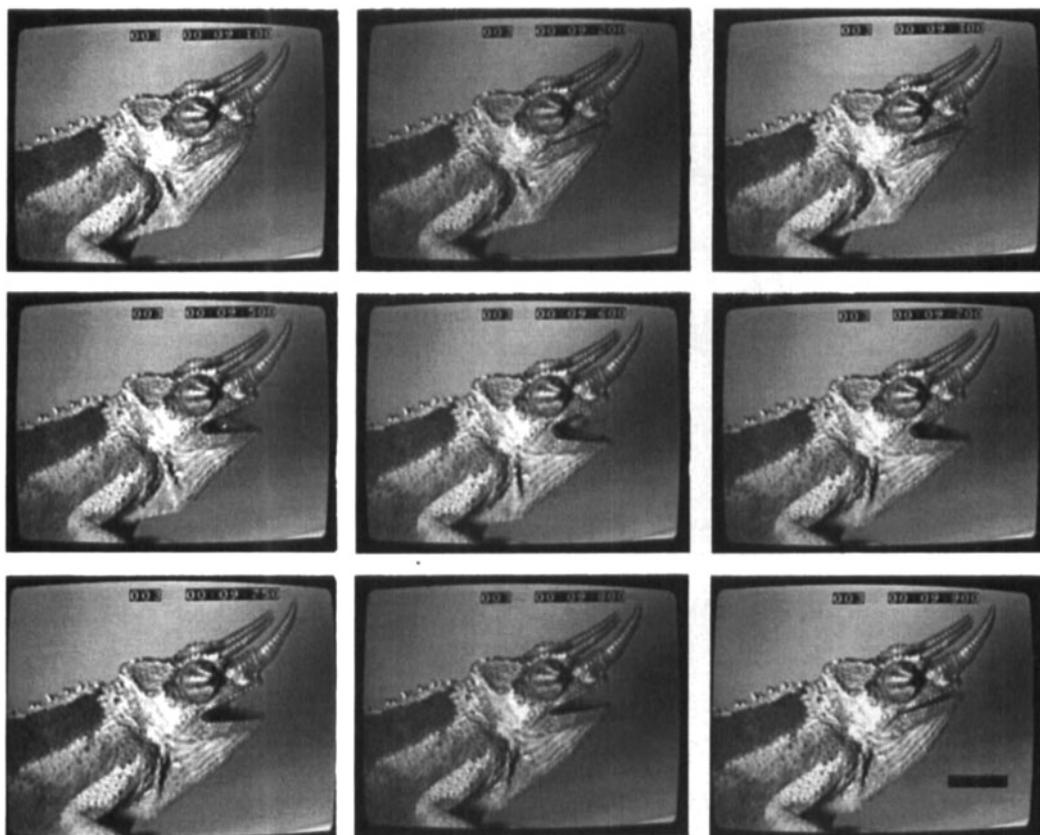


PLATE II. Nine fields from a video-recording of prey transport in *C. jacksonii*. Elapsed time in seconds and milliseconds is indicated by the video-clock in each field. The first field (time = 9:100) corresponds to field zero, the field immediately prior to the onset of mouth opening. Peak gape occurred at 9:700. At 9:900 the gape is almost closed and the hyoid is beginning to recover following extensive retraction between 9:500 and 9:800. This sequence is not the one illustrated in Fig. 3. Scale bar = 15 mm.

angle = 37.6°) and only slight changes in HDA (mean peak head angle = 8.03° ; Table I and Fig. 3a and b). GD peaks with maximum LJA and minimum HDA (Plate I; Fig. 2; Table I). The patterns of gape cycles were quite variable in both behaviours such that an SO phase could not always be unambiguously identified (i.e. Fig. 4). Figure 4 illustrates some of the variation seen among the transport cycles analysed in this study. While some cycles show a discernible SO phase (e.g. Fig. 4a), others show no clear break in the rate of jaw opening (e.g. Fig. 4d). The causes of variation in

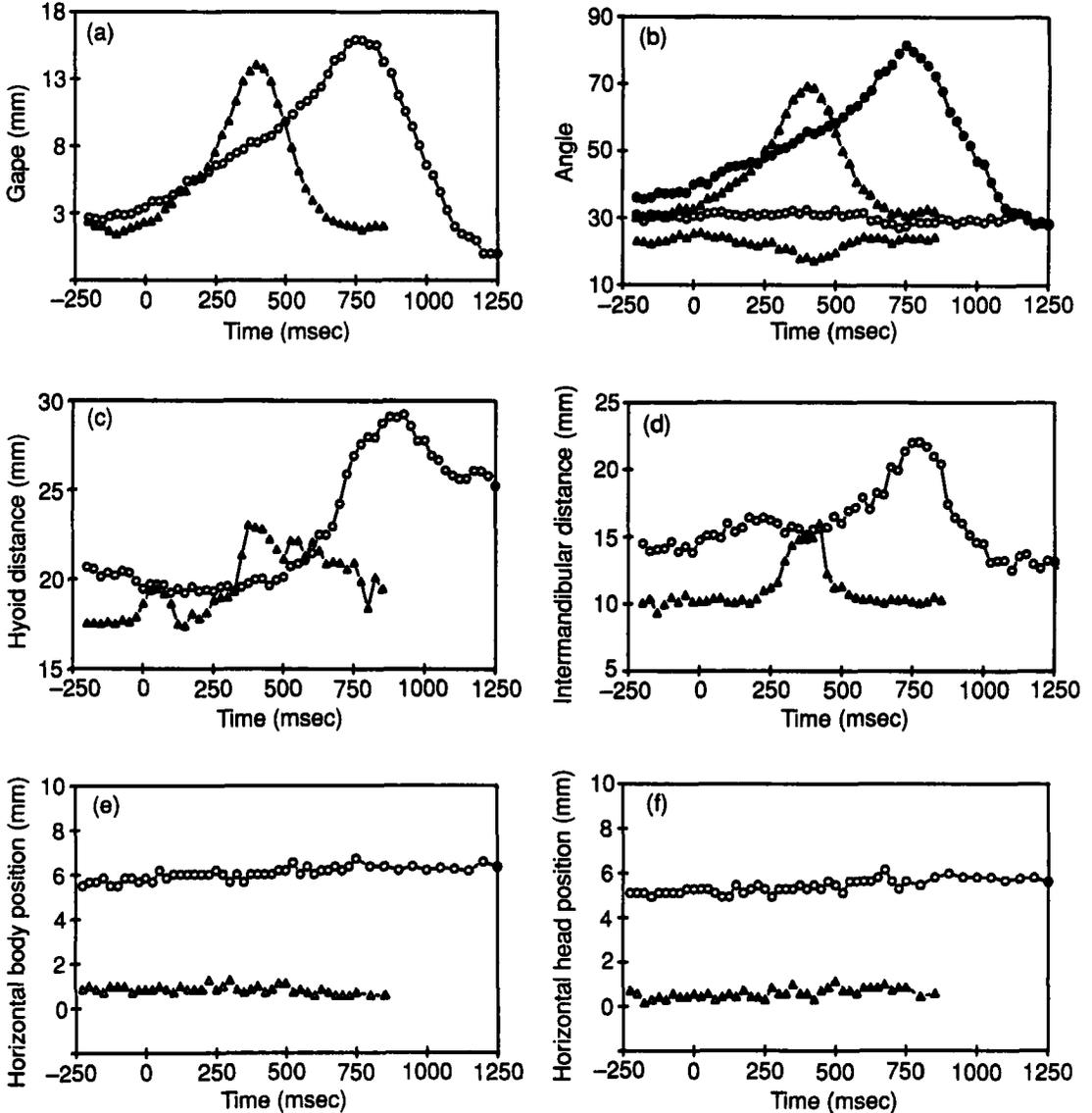


FIG. 3. Sample kinematic profiles of seven variables measured from video-recordings of prey processing from one chewing and one transport sequence from the same *Chamaeleo jacksonii*. In panel (b), head angle is represented by open symbols and lower jaw angle by filled symbols. These sequences are not the same as illustrated in Plates I and II. Symbols: Δ = chewing behaviour, \circ = prey transport.

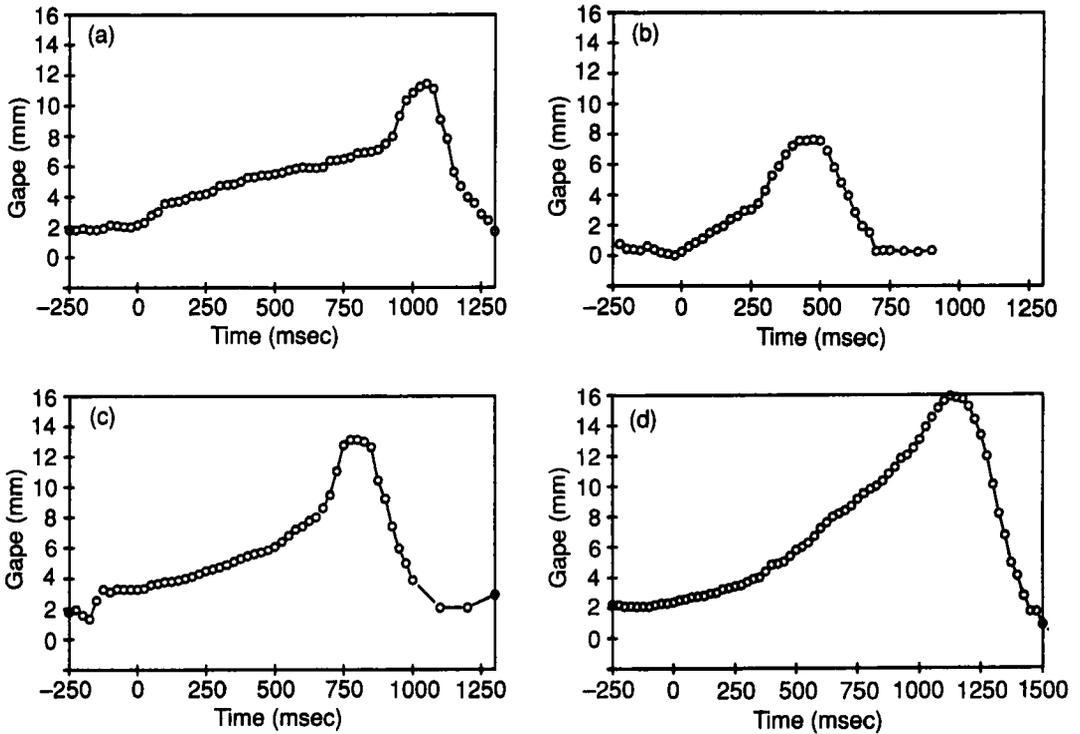


FIG. 4. Plots of gape distance against time for four different prey transport sequences in two individual *Chamaeleo jacksonii*. All four sequences were from the second, third or fourth transport sequence of the feeding. Panel (a) and (b) are from one animal, (c) and (d) from the second individual. Gape profiles are highly variable in this behaviour, particularly prior to peak gape.

TABLE I

Summary statistics for 11 kinematic variables describing chewing and prey transport behaviours in three individual *Chamaeleo jacksonii*

Variable	Chewing (N=8)		Transport (N=7)	
	Mean	S.E.	Mean	S.E.
Peak gape distance	1.41	0.03	0.97	0.09
Time to peak gape	703.21	86.82	1037.17	121.11
Gape cycle time	1070.01	107.21	1490.43	152.05
Peak head angle	8.03	1.32	4.51	0.97
Time to peak head angle	728.11	103.79	1090.06	121.84
Peak lower jaw angle	37.6	1.57	32.42	4.97
Time to peak lower jaw angle	700.28	91.41	1042.21	122.55
Peak hyoid distance	2.56	0.29	9.05	0.18
Time to peak hyoid distance	200.33	15.73	1296.22	173.67
Peak intermandibular distance	1.23	0.05	1.81	0.11
Time to peak intermandibular distance	609.72	75.32	839.33	88.10

Units: Time variables = milliseconds, Distance variables = centimetres, Angle variables = degrees

TABLE II

Results of two-way ANOVAs contrasting kinematic variables from chewing and prey transport behaviours. Behaviour (chewing and transport) was crossed with Individuals (three individuals) in these mixed models. Table entries are the F-ratios from each significance test

Variable	Behaviour (1,2)	Individual (2,9)	Interaction (2,9)
Peak gape distance	22.2*	1.3	3.4
Time to peak gape	176.3**	4.9*	0.4
Gape cycle time	18.0	2.2	1.4
Peak head angle	7.7	6.4*	1.4
Time to peak head angle	72.1*	0.5	0.6
Peak lower jaw angle	7.1	16.6**	10.0*
Time to peak lower jaw angle	229.5**	0.4	0.2
Peak hyoid distance	249.0**	0.1	0.1
Time to peak hyoid distance	418.5**	0.7	0.1
Peak intermandibular distance	0.5	9.0*	7.8*
Time to peak intermandibular distance	35.2*	2.0	0.8

* = $P < 0.05$

** = $P < 0.0045$ (the column-wise Bonferroni correction of $P < 0.05$)

transport kinematics from cycle to cycle are not known. Hyoid movements were minimal during chewing, as reflected by the fact that HYD never changed by more than 4 mm in any one sequence. Peak intermandibular distance occurred about 100 ms prior to peak gape. No head or body movements were observed during either prey processing behaviours (Fig. 3e and f).

Extensive changes in HDA did not occur during transport (e.g. Plate II; Fig. 3b; mean peak head angle = 4.51°), while LJA, HDA and GD peaked at about the same time (Table I). Hyoid excursions were extensive during transport, first decreasing during the period from 0 (field zero) to 200 ms, then increasing slightly from 200 to 500 ms, and finally increasing rapidly to a maximum from 500 to 900 ms (Fig. 3c). In addition, peak HYD always occurred after peak GD. IMD profiles illustrated a frequently changing pattern that usually peaked prior to peak gape (Table I).

Analyses of variance revealed significant differences between behaviours in seven of the 11 kinematic variables (Table II). All timing variables except the gape cycle time were significantly longer during prey transport. Of the five amplitude variables, peak gape was greater in chewing sequences and peak hyoid retraction distance was greater in transport behaviour (Table I and II; but see Fig. 3 for a counter example). Peak head angle and peak lower jaw angle showed a trend of being larger in chewing sequences but were not significantly different in the ANOVA. Four of the 11 variables exhibited significant variation among individuals.

The correlation matrix for the entire data set confirmed the very strong associations (correlations > 0.95) among several timing variables; times to peak gape, peak lower jaw angle, peak head angle and gape cycle time (Table III, below the diagonal). Time to peak hyoid distance also showed a positive association with the other timing variables with correlations ranging from 0.57 to 0.74. Correlations among variables within only the transport sequences reveal a very similar pattern (Table III, above the diagonal). Very strong correlations exist among peak gape and peak lower jaw angle. There was no correlation of peak gape with peak head angle within the transport data, reflecting the minimal contribution of this variable to gape (Fig. 3). Time to peak gape, peak lower jaw angle, peak head angle, and gape cycle time were all very highly correlated.

TABLE III

Correlation matrix for the 11 kinematic variables measured from eight chewing and seven prey transport cycles in *Chamaeleo jacksonii*. Correlations for the entire data set are presented below the diagonal. Correlations above the diagonal are for the seven transport sequences only. For the entire data set, correlations above a magnitude of 0.51 are significant at $P < 0.05$. For the transport data correlations above 0.71 are significant at $P < 0.05$. See text for variable descriptions

Variable	PG	TPG	GCYC	PHA	TPHA	PLJA	TPLJA	PHD	TPHD	PIM	TPIM
Peak gape distance	—	-0.15	-0.06	0.19	-0.15	0.92	-0.11	-0.60	-0.48	0.81	0.03
Time to peak gape	-0.46	—	0.97	0.47	0.99	-0.01	-0.99	-0.17	0.44	0.03	0.60
Gape cycle time	0.37	0.98	—	0.33	0.96	0.08	0.97	-0.19	0.42	0.19	0.51
Peak head angle	0.54	0.04	0.03	—	0.48	0.42	0.45	-0.36	0.75	0.11	0.83
Time to peak head angle	-0.43	0.99	0.96	0.04	—	-0.00	0.99	-0.14	0.44	0.02	0.58
Peak lower jaw angle	0.72	-0.08	-0.06	0.41	-0.05	—	0.02	-0.76	0.75	0.73	0.35
Time to peak lower jaw angle	-0.46	0.99	0.97	-0.02	0.98	-0.08	—	-0.15	0.42	0.07	0.56
Peak hyoid distance	-0.30	0.22	0.28	-0.17	0.22	-0.55	0.22	—	-0.85	-0.30	-0.61
Time to peak hyoid distance	-0.42	0.61	0.58	-0.23	0.57	0.15	0.60	0.10	—	-0.05	0.87
Peak intermandibular distance	-0.34	0.45	0.46	-0.33	0.40	0.15	0.46	0.14	0.74	—	0.79
Time to peak intermandibular distance	0.31	0.39	0.40	0.68	0.41	0.34	0.35	-0.04	0.08	-0.32	—

TABLE IV

Component loadings from a principal component analysis run on the correlation matrix in Table III. Entries are correlations of each variable with the first four principal components. Correlations above 0.5 are highlighted in bold print. The percentage of total variance explained by each principal component is indicated in parentheses

Variable	PC1 (46.3%)	PC2 (24.4%)	PC3 (14.3%)	PC4 (6.8%)
Peak gape distance	-0.57	0.67	-0.16	0.31
Time to peak gape	0.97	0.18	0.09	-0.10
Gape cycle time	0.95	0.20	0.09	0.01
Peak head angle	-0.13	0.83	0.25	0.14
Time to peak head angle	0.95	0.21	0.11	-0.10
Peak lower jaw angle	-0.15	0.72	-0.64	0.10
Time to peak lower jaw angle	0.97	0.15	0.07	-0.09
Peak hyoid distance	0.32	-0.38	0.50	0.70
Time to peak hyoid distance	0.73	-0.06	-0.50	0.12
Peak intermandibular distance	0.59	-0.25	-0.65	0.29
Time to peak intermandibular distance	0.25	0.83	0.34	0.01

The first principal component from the factored correlation matrix reflected the strong association among the timing variables (Table IV) and a plot of the factor scores of the eight chewing and seven transport cycles on the first two principal components reveals complete separation between the behaviours in multivariate kinematic space, particularly along the first principal component (Fig. 5).

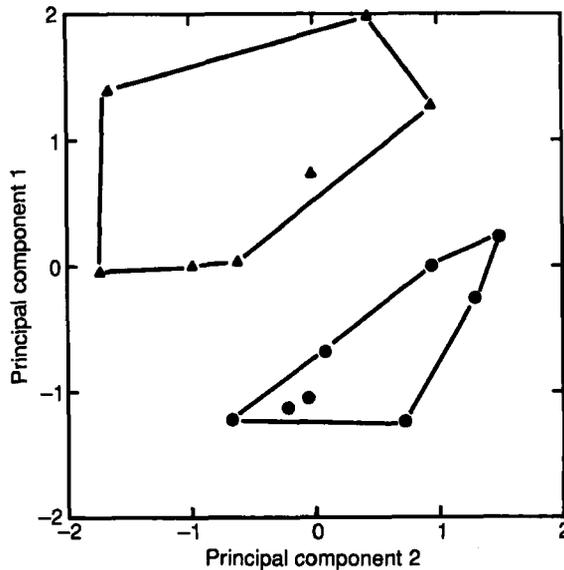


FIG. 5. Plot of the positions of eight chewing and seven transport sequences along the first two principal components of a PCA performed on the correlation matrix of 11 kinematic variables. Chewing (▲) and transport (●) kinematics are completely distinguished along these multivariate descriptions of jaw and hyoid movements.

Discussion

Kinematics of prey processing

We have confirmed the existence of two distinct behaviours in the prey processing repertoire of *Chamaeleo jacksonii*: chewing and transport. Though we have focused on these behaviours in this analysis, it is likely that *C. jacksonii* and other chameleons exhibit additional behaviours (e.g. side-to-side positioning, crushing and shaking of prey) that were not considered in this study. Chewing behaviour, associated with only a slight antero-posterior hyoid movement (mean peak hyoid retraction = 2.56 mm), functions as a means for killing, holding and reduction of prey. Movements of prey during chewing cycles primarily consisted of tongue-mediated manipulations that positioned the cricket body between the adducting jaws. Transport behaviours, in contrast, were associated with extensive retraction of the hyolingual complex (mean peak hyoid retraction = 9.05 mm) and transport the prey posteriorly from the oral cavity to the pharynx. The extent of hyolingual retraction, used *a priori* to separate the behaviours, therefore serves as a basic phenomenon which distinguishes chewing and prey transport.

Our quantitative analysis confirmed the difference between behaviours in the extent of hyoid retraction and identified an additional suite of characteristics that distinguish chewing from transport (Table II): (1) Chewing occurs more quickly than prey transport. This difference is reflected by the suite of timing variables that all have significantly lower means in chewing cycles relative to transport (Table I and II). (2) The average velocity of gape opening was slower during transport than in chewing sequences, and sometimes indicated a clear slow opening phase (Fig. 4). The slower opening velocity was indicated by the combination of a longer time to peak gape and a smaller peak gape distance in transport cycles (Tables I and II). Though the actual shape of the opening phase varied widely among prey transport sequences (Fig. 4), it was an average of 300 msec longer than in chewing behaviour. (3) During chewing cycles the mouth was opened significantly wider than in transport cycles. This was reflected by the greater peak gape distance, peak head angle, and peak lower jaw angle that occurred in transport sequences. Quantitatively, seven of the 11 variables that were measured in this study from gape and hyoid profiles varied significantly between the two behaviours. Patterns of correlation within the whole data set were very similar to the patterns of correlation among only prey transport data (Table III). In some instances, this is due partly to the interdependence of variables. For example, peak gape is highly correlated with peak lower jaw angle because they both represent the same event. However, other variables that are not mechanically linked show similar patterns of correlation within the transport data and in the entire data set. An example is the significant negative correlation between peak hyoid distance and peak lower jaw angle. This similarity in the patterns of association that one sees within and among behaviours indicates that some aspects of prey processing kinematics may be constrained to a particular pattern of covariation. All of the sequences that were analysed could be unambiguously assigned to the correct behaviour based on the multivariate principal components analysis, confirming our *a priori* categorization (Fig. 5).

While the behaviours clearly can be distinguished, it is important to emphasize that our selection of representative sequences of these behaviours was focused on what we perceived to be unambiguous cases. Sequences that were difficult to categorize *a priori* occurred frequently in our videos but were not analysed. Thus, chewing and transport behaviours may represent two extremes of a continuum, rather than entirely distinct activities. This proposal could be tested by analysing all processing cycles from each feeding and exploring the variation seen in kinematic

patterns with cluster analysis. Can processing cycles always be unambiguously assigned to a particular behaviour? Even in our data set there were extensive similarities between chewing and prey transport in *Chamaeleo jacksonii*. First, no horizontal body or head movements occur during either behaviour, demonstrating that no inertial body or head movements assist in prey transport (Fig. 3e and f). Secondly, in both cases, mouth opening is accomplished predominantly by lower jaw depression with minimal head elevation (Fig. 3b). Thirdly, the overall sequence of jaw and hyoid movements, with the important exception of the time to peak hyoid distance, was the same in the two behaviours (Tables I and II; Fig. 3).

Comparative prey transport kinematics

One major finding of this study is that chameleons, despite having a highly specialized prey capture mechanism, exhibit prey transport kinematics similar to those described for other iguanian lizards. In this section, we contrast our findings for *C. jacksonii* with previously published data for movements of the body, skull, jaw and hyoid in representative members of the Iguanidae and Agamidae. It is important to emphasize that the Iguanidae and Agamidae are taxa believed to be outgroups to the Chamaeleonidae (Estes *et al.*, 1988; Schwenk, 1988). Together with the Chamaeleonidae they comprise the Iguania, a monophyletic group within the Squamata (Estes *et al.*, 1988). The condition found in agamids and iguanids thus represents a reasonable estimate of the more generalized condition from which the chameleon feeding apparatus evolved (Schwenk & Bell, 1988; Smith, 1988), and provides a basis for comparison of chameleonid prey transport behaviours. Below, we explore this comparison to test the possibility that there have been substantial modifications of chameleon prey transport in association with specialization of the prey capture mechanism.

Comparative kinematic data for prey transport behaviour have been reported for several iguanian taxa (Throckmorton, 1976, 1980; Smith, 1984, 1988; Bels & Baltus, 1989; Schwenk & Throckmorton, 1989), including a second chameleon species (Bels & Baltus, 1987). Movements of the *gape cycle* during prey transport are the most frequently discussed, and data from several iguanian taxa are summarized in Fig. 6. The *head angle* movements that contribute to gape distance have been described for only three species (Bels & Baltus, 1989; Schwenk & Throckmorton, 1989), and *jaw* movements are reported for one agamid (Throckmorton, 1980). Comparative data for *hyoid* movements during prey transport are only available for two species of Iguanidae (Smith, 1984; Bels & Baltus, 1989). There are no comparative data available for *horizontal body* movements, and data from two species have been reported for *horizontal head* movements (Schwenk & Throckmorton, 1989).

Transport behaviour of *Chamaeleo jacksonii* (Fig. 6a), as in *C. dilepis* (Bels & Baltus, 1987), can be divided into four of the basic phases previously described for other lizards (Fig. 6b and c; Smith, 1984; Schwenk & Throckmorton, 1989) and generalized amniotes (Fig. 6c; Bramble & Wake, 1985). These include slow opening (SO), fast opening (FO), closing (C), and a recovering phase (PS). As noted above, the SO phase was a highly variable stage of the gape cycle, and could not always be unambiguously identified (see Fig. 4). A similar situation has been noted by Schwenk & Throckmorton (1989) in work on iguanids and agamids, and examination of other published prey transport sequences confirm the observation of a variable SO phase in additional iguanian taxa (e.g. Smith, 1984). When present, the SO phase begins with slow hyoid protraction and the gape begins to open (Figs 4 and 6a). The phase ends at the onset of rapid jaw opening (Fig. 6) and the onset of rapid retraction of the hyoid. The FO phase occurs simultaneously with rapid hyoid

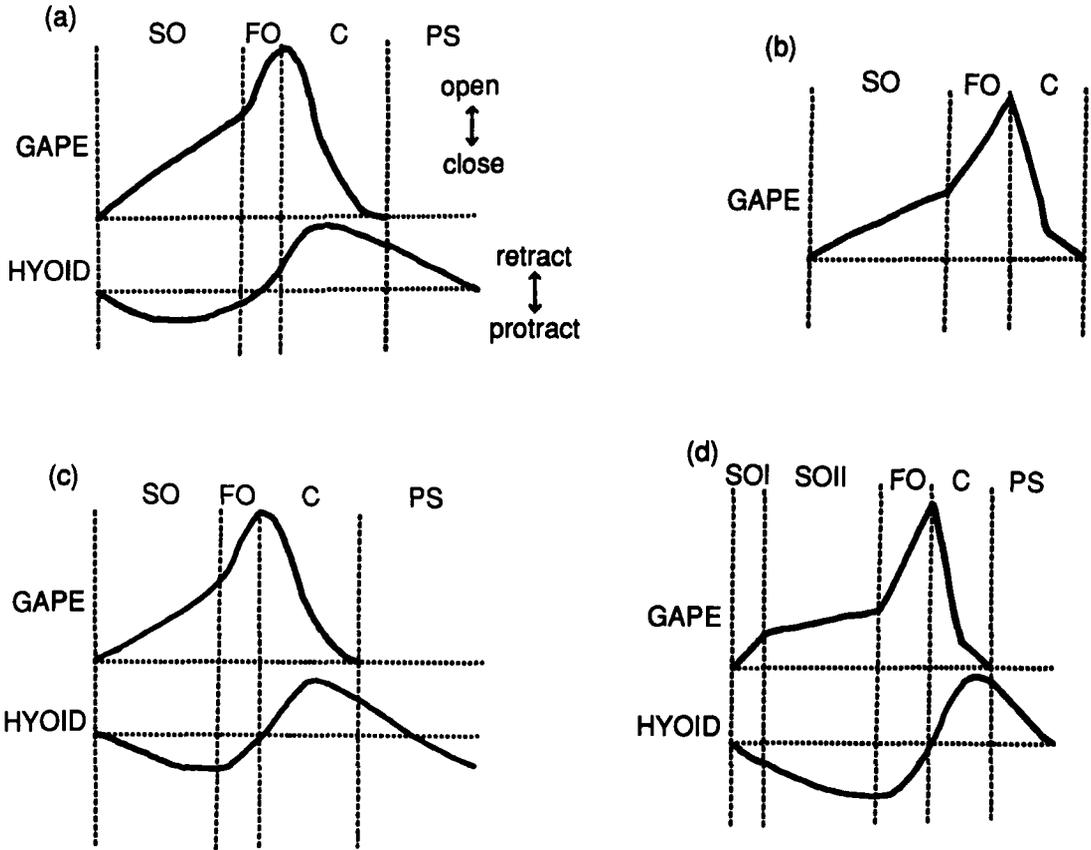


FIG. 6. Prey transport gape and hyoid cycles during prey transport in lizards from several studies. (a) Summary of gape and hyoid movements during prey transport in *C. jacksonii* from the present study; (b) gape profile only from *Uromastix aegyptius* (modified from Schwenk & Throckmorton, 1989); (c) profile of gape and hyoid movements during prey transport in the iguanid lizard *Ctenosaura similis* (modified from Smith, 1984; fig. 6); (d) a generalized model of prey transport in amniotes (modified from Bramble & Wake, 1985). Abbreviations: SO, slow opening phase; SOI and SOII, slow opening I and 2 phases; FO, fast opening phase; C, closing phase; PS, power stroke phase.

retraction and ends with peak gape. The C phase begins with the onset of gape closing and continuing retraction of the hyoid and ends with minimum gape. This phase also encloses the maximum hyoid retraction as well as a brief period of hyoid protraction. FO and C are the two phases of prey transport during which an extensive retraction of the hyoid occurs that forcefully moves the prey, adhering to the tongue, posteriorly from the oral cavity towards the pharynx. Finally, during the PS phase, while the minimum gape remains static, slow protraction of the hyoid under the prey begins and continues up to a position where the next transport cycle starts. The hyoid sometimes will remain at this position for an extended time before the next transport cycle is initiated. Or, once it reaches that position the subsequent cycle starts immediately. The alternatives varied widely among cycles and individuals in our data set.

The pattern of gape and hyoid kinematics during prey transport in *C. jacksonii* is strikingly similar to that found in the iguanids *Ctenosaura similis* and *Anolis equestris* (see Fig. 6c; Smith,

1984; Bels & Baltus, 1989). All of the gape and hyoid features described above for the chameleon transport cycle also apply to these taxa. Gape cycles from two additional iguanids (*Iguana iguana*, *Dipsosaurus dorsalis*) and two agamid species (*Uromastix aegyptius* and *Phrynocephalus helioscopus*) also conform very closely to the pattern observed in *Chamaeleo jacksonii* (see Fig. 6b; Throckmorton, 1976, 1980; Schwenk & Throckmorton, 1989). In each case, the SO phase is irregularly present and is followed by FO, peak gape and jaw closing. Finally, the *C. jacksonii* gape and hyoid kinematics do not differ substantially from the generalized amniote model proposed by Bramble & Wake (1985), except that, as previously mentioned, too much variability in the SO phase of *C. jacksonii* is present to warrant the distinction between SOI and SOII phases. Again, we emphasize that such variation in the SO phase appears to be a general characteristic of iguanian prey transport cycles (e.g. Smith, 1984; Schwenk & Throckmorton, 1989). One feature of the gape cycle in *C. jacksonii* that does appear to differ from the taxa cited above is that initial protraction of the hyoid during the slow opening phase in *C. jacksonii* may not exhibit as large an excursion as is seen in *Ctenosaura* or *Anolis* (compare Fig. 3 and 6a with Fig. 6b). This difference may be a result of the hypertrophied chameleon tongue, which cannot be moved anteriorly from its rest position without passing beyond the plane of the gape (see Plates I and II). Determining whether this apparent difference is real must await a quantitative comparative analysis.

Though few comparative data are available on horizontal movements of the head and body during prey transport (Schwenk & Throckmorton, 1989), several authors have commented on the presence or absence of inertial feeding that would be implied by rapid anterior head or body movements coordinated with gape opening (Throckmorton, 1980; Smith, 1984). We find no evidence of inertial transport in *C. jacksonii*. The head and body do not move horizontally in concert with gape opening and hyoid movements (Fig. 3e and f). Comparative data for *Dipsosaurus dorsalis*, *Phrynocephalus helioscopus* and *Agama agama* indicate that these species do not employ inertial transport when feeding on small prey (see Fig. 5 in Schwenk & Throckmorton, 1989; Kraklau, 1990). Throckmorton (1976) stated that *Uromastix* employs inertial feeding only when feeding on very large prey, though no data are presented. Smith (1984) reported that "*Ctenosaura similis* in part transported large pieces of food by inertial feeding". It therefore seems that inertial transport is variably present among iguanians, and may be used primarily when feeding on prey much larger than the crickets used in the present study. This makes any determination of the primitive or derived status of the absence of inertial feeding in *C. jacksonii* problematic. Nevertheless, the absence of inertial feeding in *C. jacksonii* does not differ markedly from the condition seen in other iguanians. Although Bramble & Wake (1985) include inertial feeding as a component of the generalized tetrapod feeding cycle, this may be unjustified given its erratic distribution among lizards and salamanders (Reilly & Lauder, 1990).

Increases in gape reflect depression of the lower jaw relative to the head but during jaw opening in *C. jacksonii* there is also a slight elevation of the head that averages only 4° in prey transport (Table I). Comparative data in *Anolis* reveal a comparable, or smaller, head elevation during prey transport (Bels & Baltus, 1989). Head elevation is seen in *P. helioscopus* but not in *D. dorsalis* (Schwenk & Throckmorton, 1989). Data from *Agama agama* (Kraklau, 1990) show head elevation during transport of about 4°. Hence, the pattern of head elevation in *C. jacksonii* is very similar to that reported for other iguanians, although it appears that at least some species may use significant head elevation during transport behaviour. This pattern within iguanians, like the irregular presence of inertial feeding, does not conform to the model of Bramble & Wake (1985), suggesting that head elevation may not be a general feature of prey transport in all tetrapods either.

Our data match closely those of Bels & Baltus (1987) for *Chamaeleo dilepis*, suggesting that

behavioural patterns do not vary widely within the family. In general then, we see no evidence of specialization in chamaeleonid prey transport behaviour with reference to other iguanians, in spite of major specializations of the hyolingual complex that are related to its function during prey capture. The evolutionary transformations of the hyolingual apparatus in chameleons have occurred while retaining, intact, the generalized iguanian prey transport mechanism. It should be emphasized that these observations are based on qualitative comparisons between *C. jacksonii* and other iguanians and that future *quantitative* studies may well reveal numerous interspecific differences in the details of prey processing behaviours. For example, one feature of chameleon transport that may differ from other lizards is the time course of the behaviour. Chameleons appear to exhibit very slow movements relative to other taxa (compare 1.49 s cycle time in *C. jacksonii* to 0.17 s for *D. dorsalis* and 0.21 s for *P. helioscopus*; Schwenk & Throckmorton, 1989). Our point here is that the basic features of chameleon prey transport, as exemplified by the sequence of movements in *C. jacksonii*, appear to be unmodified from the presumed primitive condition.

Summary

The hyolingual apparatus of iguanian lizards has several functions, including prey capture and prey processing. In chameleons this structure is highly specialized for ballistic tongue projection. Numerous modifications of the tongue and hyoid skeleton permit chameleons to capture prey on a sticky tongue pad that can be rapidly projected up to a full body length out of the mouth. This highly derived hyolingual system also functions as a central element in prey processing behaviours. We have used this system as a case study to explore the effect that specialization for one function (prey capture) has on a second function (prey transport).

The kinematics of prey transport in *C. jacksonii* exhibit little specialization relative to the primitive condition exemplified by several iguanian taxa. The directions and timing of movement in the gape, hyoid, head, jaws and body during slow opening, fast opening, closing and the power stroke in *C. jacksonii* closely match the same activity phases in less specialized taxa. The evolution of uniquely specialized hyolingual morphology and prey capture function in chameleons has taken place without the loss of the primitive prey transport function. Thus, the necessity to perform multiple functions does not seem to have constrained seriously the evolution of this complex functional system.

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