

# Kinematics of Aquatic and Terrestrial Prey Capture in *Terrapene carolina*, With Implications for the Evolution of Feeding in Cryptodire Turtles

ADAM P. SUMMERS,\* KAYVAN F. DAROUIAN, ALAN M. RICHMOND,  
AND ELIZABETH L. BRAINERD

*Department of Biology and Graduate Program in Organismic and  
Evolutionary Biology, University of Massachusetts, Amherst,  
Massachusetts 01003*

**ABSTRACT** Studies of aquatic prey capture in vertebrates have demonstrated remarkable convergence in kinematics between diverse vertebrate taxa. When feeding in water, most vertebrates employ large-amplitude hyoid depression to expand the oral cavity and suck in water along with the prey. In contrast, vertebrates feeding on land exhibit little or no hyoid depression. In this study we compared the kinematics of terrestrial and aquatic prey capture within one species of turtle, *Terrapene carolina*, in order to determine whether an individual species can modulate the magnitude of hyoid depression between air and water. High-speed video (250 frames per second) showed that hyoid depression was over three times greater in aquatic than in terrestrial feedings, indicating that *T. carolina* is able to modulate hyoid depression magnitude depending on the medium in which feeding occurs. In addition, we observed medium-dependent modulation of hyoid depression in another turtle, *Heosemys grandis*, and large-amplitude hyoid depression during aquatic feeding in *Kinosternon leucostomum*, *Platysternon megacephalum*, and juvenile *Chelydra serpentina*. In all of these turtles, hyoid depression produced oral cavity expansion during aquatic feeding, but the earthworm prey were never sucked toward the predators. Prey were captured by neck extension (ram feeding), and we conclude that the function of hyoid depression during aquatic feeding in cryptodire turtles is to prevent the forward motion of the predator from pushing the prey away (compensatory suction). Aquatic feeding is probably the primitive condition for all extant turtles, and thus terrestrial feeding in *T. carolina* and other turtles is a secondarily derived characteristic. We conclude from this historical pattern that it is not appropriate to use extant turtles in attempts to reconstruct the terrestrial feeding mechanisms of primitive amniotes. *J. Exp. Zool.* 281:280-287, 1998. © 1998 Wiley-Liss, Inc.

Biomechanical studies of feeding in numerous aquatic vertebrates have demonstrated the nearly universal use of suction feeding to acquire prey in the aquatic realm. In suction feeding, depression of the hyoid apparatus expands the oral cavity and water is pulled into the mouth. Sharks, ray-finned fishes, lungfishes, larval and adult salamanders, aquatic turtles, and odontocete whales have all been shown to employ large-amplitude hyoid depression and oral cavity expansion when feeding in water (e.g., Lauder, '80; Bemis and Lauder, '86; Lauder and Reilly, '88; Werth, '89; Lauder and Prendergast, '92; Reilly and Lauder, '92; Motta et al., '97; but see Schwenk and Wake, '88 for an example of aquatic lingual feeding). This remarkable convergence is thought to result from constraints imposed by the high density and viscosity of water (Lauder, '85; Liem, '90).

If an animal generates no suction when feeding

on small prey in water, the prey may be pushed away as the predator approaches. In some cases suction is sufficient only to counter the forward motion of the predator and thus allow it to engulf or grasp the prey in its jaws. This prey capture mechanism has been termed *compensatory suction* (Van Damme and Aerts, '97) or *ram feeding* (Norton and Brainerd, '93). In other cases suction is sufficient to pull the prey towards the mouth and has been termed *inertial suction* (Van Damme and Aerts, '97) or *suction feeding* (Norton and Brainerd, '93). The existence of these different terms high-

Grant sponsor: NSF; Grant number: IBN-9419892.

\*Correspondence to: Adam P. Summers, Department of Biology, Morrill South, University of Massachusetts, Amherst, MA 01003-5810. E-mail: summers@bio.umass.edu

Received 16 September 1997; Accepted 24 February 1998

lights the general perception that a dichotomy exists between the two types of suction feeding.

Turtles (Testudines) are a monophyletic group of armored reptiles with terrestrial and aquatic members. There are two suborders—the totally aquatic Pleurodira, and the aquatic and terrestrial Cryptodira. The extant pleurodires are a southern hemisphere clade distinguished by a neck that is withdrawn laterally into the shell. The cryptodires are a primarily northern hemisphere radiation with necks that are drawn into the shell in the sagittal plane (Ernst et al., '89; Shaffer et al., '97). Terrestrial and semiterrestrial habits have evolved several times within the cryptodires.

Kinematic analyses indicate that aquatic turtles depress the hyoid apparatus and expand the oral cavity during feeding in water (Mahmoud, '68; Bramble, '73, '78; Weisgram, '85; Bels and Renous, '92; Lauder and Prendergast, '92). The most complete kinematic analysis to date was performed on *Chelydra serpentina* feeding on earthworms and fish (Lauder and Prendergast, '92). *C. serpentina* begins posteroventral hyoid movement at the beginning of the fast opening phase of the gape cycle, and peak hyoid depression occurs after peak gape. Although these movements certainly expand the oral cavity and draw in water, Lauder and Prendergast ('92) reported that the prey remains stationary during prey capture. This finding indicates that in *C. serpentina* suction is purely compensatory. Thus, although *C. serpentina* is not sucking the prey into the mouth, its oral cavity expansion does serve a critical role during aquatic feeding. Lauder and Prendergast ('92) also concluded that *C. serpentina* is able to modulate feeding kinematics based on prey type. For example, strikes on goldfish employed faster hyoid depression and involved higher neck extension velocities than strikes on earthworms.

A recent study of terrestrial feeding in *Terrapene carolina* found that, although there is some posteroventral hyoid movement during feeding, the magnitude of this movement is much smaller than has been observed in aquatic turtles (Bels et al., '97). *T. carolina* is a useful species in which to study feeding because it will feed on land and in water. Young box turtles are particularly aquatic, although even as adults they will forage in shallow puddles and along the edges of ponds (Carr, '52; Ernst et al., '89). They are opportunistic feeders and will seemingly eat any available prey item, including frogs, snails, worms, crayfish, and vegetable matter (Barbour, '50; Ernst et al., '89).

In the present study we compare the kinematics of prey capture by *T. carolina* in air and in water. We predict that *T. carolina* will increase the magnitude of hyoid depression when feeding aquatically in order to compensate for the higher density and viscosity of water. Thus we predict that *T. carolina* will be able to modulate its feeding kinematics in response to prey capture in different environments. In addition, we also present a qualitative description of the prey capture kinematics of four other cryptodire turtle species feeding in water and on land.

## MATERIALS AND METHODS

### *The animals*

Prey capture data were collected from three eastern box turtles, *Terrapene c. carolina*. Three terrestrial and three aquatic feedings were analyzed for each of the three individuals. The turtles ranged in size from 105 to 130 mm carapace length and 402 to 475 g body mass. Earthworms were used for the feedings because they were readily available in the lab and *T. carolina* is known to eat them in nature (Ernst et al., '89).

In addition, we recorded a number of sequences of prey capture in four other cryptodire turtle species. Aquatic feedings were recorded from *Kinosternon leucostomum* (6 feedings, 1 individual), *Platysternon megacephalum* (6 feedings, 1 individual), *Heosemys grandis* (21 feedings, 2 individuals), and juvenile *Chelydra serpentina* (25 feedings, 4 individuals). We also recorded 11 terrestrial feedings from two individual *H. grandis*. These additional species were fed earthworms and small pieces of beef heart. While in our care all turtles were maintained according to the guidelines of the animal care and use committee of the University of Massachusetts.

### *High-speed video*

The turtles were filmed with a Kodak EktaPro EM high-speed video system at a rate of 250 frames per second. During filming, each turtle was placed in a 38-l aquarium equipped with a background grid and a 250-W halogen lamp. The worms were cut into small (~1 cm) segments and placed on the aquarium floor with forceps. The worms were oriented perpendicular to the antero-posterior axis of the turtle because this helped to minimize lateral rotation of the turtle's head during the strike, which could obstruct the camera's view of the hyoid depression and gape.

For the aquatic feedings, the aquarium was

filled with 2.5 to 5.0 cm of water, depending on the size of the turtle. *T. carolina* is buoyant in water, and thus if the water was too deep the turtles floated and had difficulty capturing the worm at the bottom of the aquarium.

Many feedings were filmed, but only a small proportion of feedings was found to be suitable for quantitative kinematic analysis. Only sequences with an unobstructed lateral view of the hyoid depression and gape were analyzed. Many sequences were unsuitable because of head rotation during feeding. The video sequences were digitized with Adobe Premiere, and variables were measured with NIH Image on a Macintosh computer. More frames were available than were necessary to describe the movements, and thus the videos were analyzed at half of the filming speed, that is, 125 frames per second.

Four variables were measured from each feeding sequence: time to peak gape, magnitude of peak gape, time to peak hyoid depression, and magnitude of peak hyoid depression. These variables are consistent with previous studies of turtle feeding by Lauder and Prendergast ('92) and Bels et al. ('97). Gape distance was measured as the distance between the anteriormost points on the upper and lower jaws. The hyoid bone retracts ventrally and posteriorly during prey capture. The ventral movement, which we call hyoid depression, is clearly evident through the skin of the throat. Hyoid depression was measured as the difference between position of the hyoid apparatus at the beginning of the gape cycle, relative to the top of the head, and its position in subsequent frames (Fig. 1).

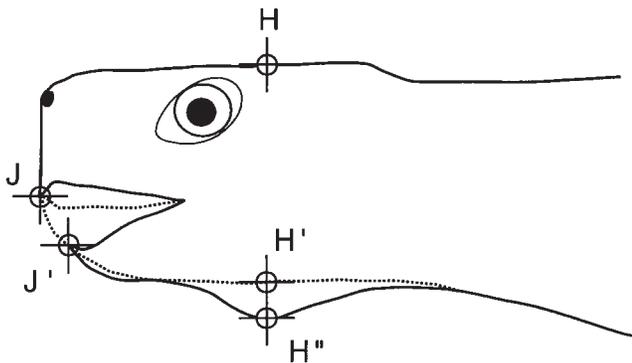


Fig. 1. Drawing of the head of *Terrapene carolina* from two superimposed video frames from aquatic prey capture showing the points that were digitized. The dotted lines are from a frame at time = 0 when the mouth first starts to open. The solid lines are from a frame at time = 100% when gape is at a maximum. Distance from J to J' is gape, and hyoid depression is computed as the distance from H to H'' minus the distance from H to H'.

### Statistical analysis

Kinematic data were collected for three terrestrial and three aquatic feedings for each of three turtles. Data were tested for normality and homogeneity of variance. All of the data were normal and homoscedastic, so no transformations were needed. A two-way, mixed-model ANOVA quantified the effect of the individual turtle, the environment, and their interaction on each of the kinematic variables. Significant differences were assessed at  $P < 0.05$ .

Summary plots of terrestrial and aquatic prey capture were generated by pooling the data from all of the feedings. To remove the variation due to different gape cycle times, the time base of each feeding event was standardized to a percentage of time to peak gape. The frame before the beginning of jaw opening was set to 0%, and the frame with peak gape was set to 100%. The data were then resampled into 25 points between 0 and 100%. Kinematics for both jaw movements and hyoid movements were standardized to the peak gape to allow comparison between the plots. Data points collected beyond peak gape are represented on the same relative time scale. Linear interpolation was used in resampling the data. The Microsoft Excel spreadsheet that performs these calculations is available from the authors.

### RESULTS

During a typical feeding event, either on land or in water, *Terrapene carolina* approached the prey item with its neck retracted. The prey was then captured by an extension of the neck with simultaneous opening of the mouth (Fig. 2). In both terrestrial and aquatic feedings, peak hyoid depression occurred after peak gape (Fig. 3). The magnitude of peak hyoid depression, however, was over three times greater in water than in air (see Figs. 2 and 3; Table 1). A two-way, mixed-model ANOVA indicated that the difference in magnitude of hyoid depression between aquatic and terrestrial feeding was statistically significant (Table 2).

There was no significant difference in the time to peak gape between terrestrial and aquatic feeding, nor in the other kinematic variables that we measured (see Table 2). The gape cycle time was not quantified because the prey item obscured the tips of the jaws, making it impossible to determine when capture ended and processing began. There was significant variation among individuals in the timing of the kinematics, though not in

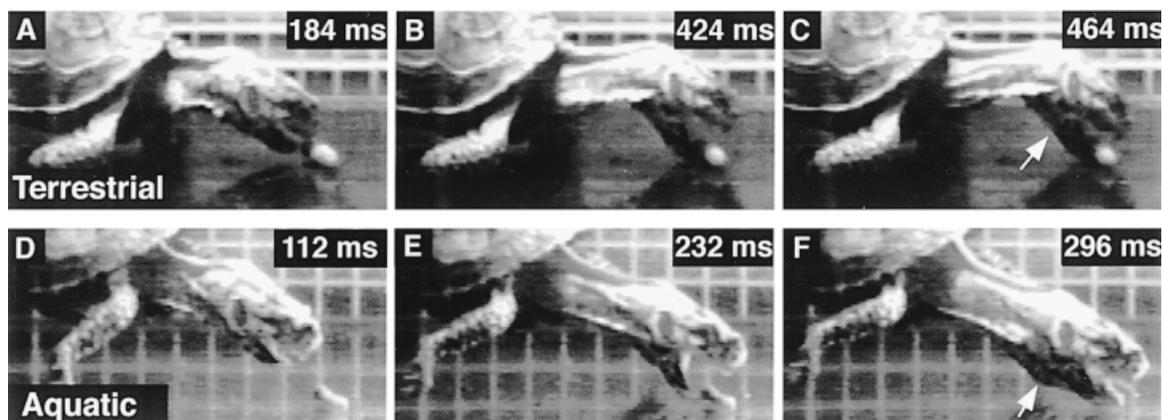


Fig. 2. Video frames from a terrestrial feeding event (A, B, C) and an aquatic feeding event (D, E, F) by an Eastern box turtle (*Terrapene carolina*). Time (msec) is measured from the beginning of jaw opening. Background grid is 1-cm squares. Frames C and F show the maximum posteroventral

excursion of the hyoid apparatus for aquatic versus terrestrial feeding (indicated by white arrows). Note the greater hyoid depression during aquatic feeding than during terrestrial feeding.

the magnitude. The variability in the magnitude and relative timing of kinematic events was low when data from all three turtles were standardized to a common time scale (Fig. 4). Though cycle time was not quantified, it is possible to estimate that the time from peak gape to closure is longer in terrestrial feedings from the slope of the jaw tip curve after peak gape in Figure 4.

During aquatic feedings the prey item did not move at all until it was within the margins of the jaws. The distance to the prey item was closed entirely by neck extension while the gape increased. After capture, the tongue was elevated and trapped the prey against the roof of the mouth and water was expelled by compression of the oral cavity.

High-speed video of a small number of aquatic feedings from *Kinosternon leucostomum*, *Platysternon megacephalum*, *Heosemys grandis*, and juvenile *Chelydra serpentina* showed high-amplitude hyoid depression during prey capture. Despite this expansion of the oral cavity, we observed no movement of the prey toward the predator in any of these species. Furthermore, video of 11 terrestrial feeding events by *H. grandis* confirmed the relatively small hyoid excursion seen during terrestrial feeding by *T. carolina*. The kinematics of these sequences were not quantifiable because of head rotation during the attack or the angle of the attack.

## DISCUSSION

As predicted, we found that *Terrapene carolina* is able to modulate its prey capture kinematics between aquatic and terrestrial environments. We

found over three times greater hyoid depression in animals feeding in water than in animals feeding on land. During aquatic feedings, hyoid depression serves to expand the oral cavity and suck water into the mouth while the head is pushed toward the prey by neck extension. The prey, however, was not sucked toward the predator, and thus the function of oral cavity expansion is to prevent the prey from being pushed away by the movement of the predator's head toward the prey. Similarly, we found that another semiterrestrial turtle, *Heosemys grandis*, also modulates its prey capture kinematics between aquatic and terrestrial environments.

Previous studies of feeding in turtles have found large-amplitude hyoid depression and oral cavity expansion during aquatic feeding in a cryptodire *Chelydra serpentina* (Lauder and Prendergast, '92) and in two pleurodires, *Pelusios castaneus* (Lemell et al., '97) and *Chelodina longicollis* (Van Damme and Aerts, '97). In this study we confirmed large-amplitude hyoid depression in juvenile *C. serpentina* and observed it in four other cryptodire species (see Results). Despite oral cavity expansion during feeding, in no case were the prey items moved toward the predator. Thus we conclude that all of the cryptodire turtles studied to date use only compensatory suction, and not inertial suction, when feeding on small prey items in water (compensatory and inertial suction *sensu* Van Damme and Aerts, '97).

Cryptodires can also be classed as ram feeders (*sensu* Norton and Brainerd, '93), but this highlights a problem with the Ram-Suction In-

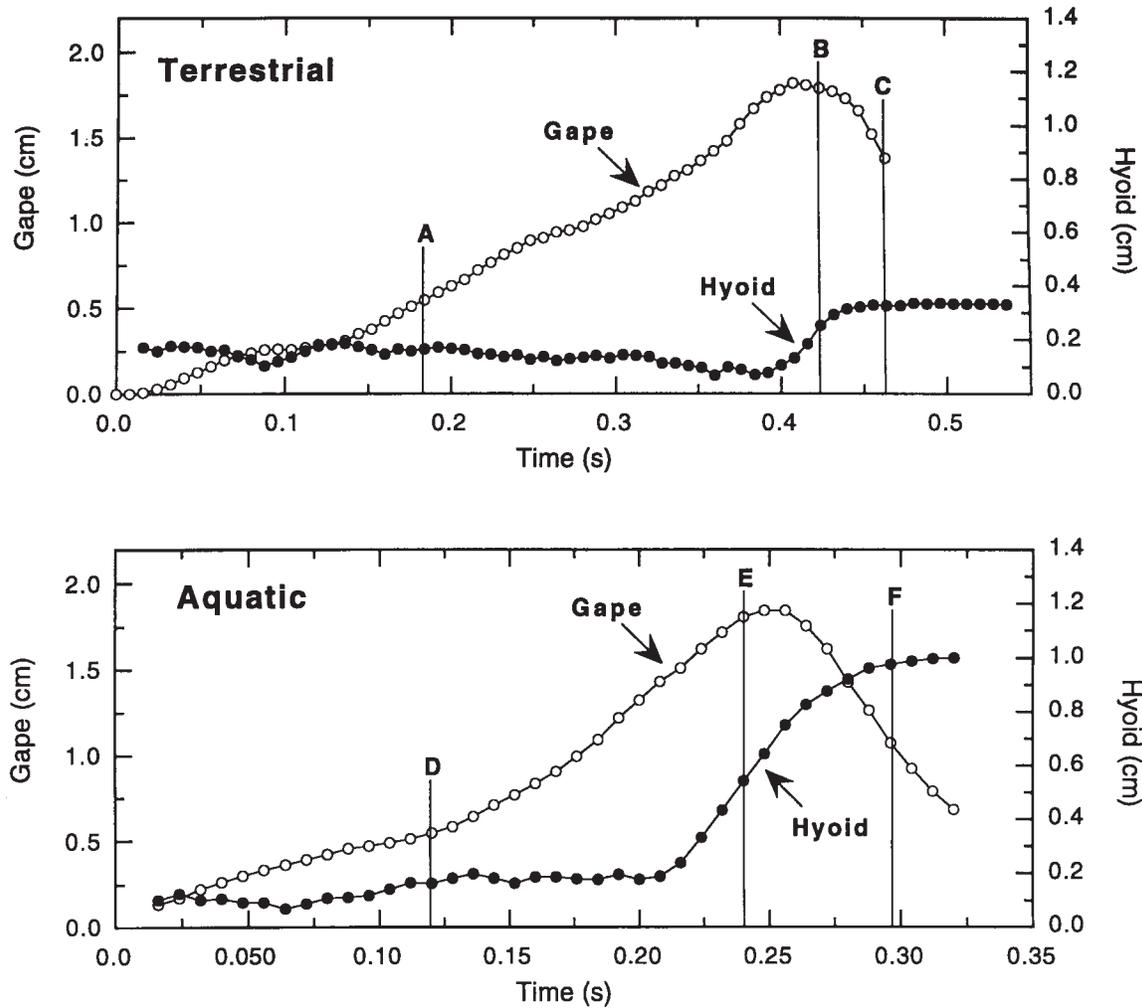


Fig. 3. Plots of jaw and hyoid kinematics for the terrestrial and aquatic feeding events shown in Fig. 1. The letter codes correspond to the particular frames represented in Fig. 1. Note that peak hyoid depression occurs after peak gape in

both aquatic and terrestrial feeding, but that the amplitude of hyoid depression is much greater in aquatic than in terrestrial feedings. Zero time is the beginning of mouth opening. Plots were smoothed by a 5-point running average method.

dex (RSI) of Norton and Brainerd ('93). The RSI is a useful way to quantify the relative contributions of predator movement and prey suction. However, it does not distinguish between (a) compensatory suction, in which the predator is generating some flow into the mouth, and (b) the purest form of ram feeding, in which the predator has the mouth wide open and expanded long before reaching the prey. Only animals with a gill opening, and thus unidirectional water flow during feeding, can perform this pure form of ram feeding. Pure ram feeding is found in some large-mouthed fishes, such as the chain pickerel, *Esox niger*. During a strike the mouth and opercular cavities are fully expanded when the pickerel is still more than half its own body length

from the prey, and it then swims a low-resistance cylinder (the oral cavity) over the prey (ELB, unpublished data). The term *compensatory suction* helps distinguish between these two types of ram feeding, and we recommend its use in studies of aquatic feeding.

Our finding that cryptodire turtles use only compensatory suction cannot be generalized to all turtles. Both of the pleurodires studied to date, *Chelodina* and *Pelusios*, use inertial suction when feeding on small pieces of meat (Lemell et al., '97; Van Damme and Aerts, '97). Both of these turtles have long necks and large hyoids, features that are found in many pleurodire turtles and probably contribute to their ability to generate inertial suction. Several cryptodires have long necks

TABLE 1. Mean  $\pm$  standard error for kinematic variables from nine aquatic and nine terrestrial feeding events by Eastern box turtles (*Terrapene carolina*)

	Terrestrial	Aquatic
Time to peak gape (sec)	0.44 $\pm$ 0.046	0.40 $\pm$ 0.063
Maximum gape (cm)	1.55 $\pm$ 0.070	1.66 $\pm$ 0.069
Time to peak hyoid depression (sec)	0.47 $\pm$ 0.042	0.45 $\pm$ 0.065
Maximum hyoid depression (cm)	0.24 $\pm$ 0.021	0.88 $\pm$ 0.072

and large hyoids, including one that we looked at in this study, *Chelydra serpentina*. Though *Chelydra* did not exhibit inertial suction, we would expect that any cryptodires found to use inertial suction to capture prey will have these two characters (e.g., softshell turtles).

Our results for the kinematics of terrestrial feeding in *T. carolina* agree with a study recently published by Bels et al. ('97), in which the turtles were fed mealworms. Our turtles were approximately the same size as those used by Bels et al., and thus the timing and magnitude of the kinematic variables are expected to be similar. Bels et al. ('97) measured maximum gape of approximately 15 mm (converted from mean gape angle), and we found mean peak gape to be 15.5 mm. They reported a delay between peak gape and peak hyoid depression of 0.01 to 0.03 sec, and we found a mean delay of 0.03 sec. Our results were most dissimilar for the time to peak gape. We found a mean time to peak gape of 0.44 sec, whereas they reported a mean time to peak gape of 0.53 sec. Because these turtles generally begin feeding with a slow opening phase, it is difficult to determine when the mouth actually first be-

gins to open, and the difference between our results could be due to different perceptions of this kinematic event.

Both our study and that of Bels et al. ('97) found that small prey such as mealworms and earthworm pieces are captured primarily by jaw prehension in *T. carolina*, and that rotation of the head is important in collecting these small prey. It was difficult to see the tongue in our video recordings, but it appears that the tongue remained in the mouth, not protracted toward the prey at the time of prey contact. This tongue position is evident in film images of prey capture reproduced in Bels et al. ('97). It is important to recognize, however, that turtles have been shown to modulate their feeding kinematics in response to different food items (Lauder and Prendergast, '92), and it seems likely that the turtles would avoid using tongue prehension on worms, especially earthworms, to which the tongue will not readily stick. It is possible that *T. carolina* would use tongue prehension on larger prey. Tongue prehension can still be an important part of prey capture even if the tongue is not protruded beyond the margins of the jaws. However, in our recordings of *T. carolina*, we did not see the tongue contacting the prey before it was captured in the jaws, and thus we conclude that the tongue is not involved in capturing earthworms in *T. carolina*.

Shaffer and Lauder ('88) compared terrestrial and aquatic feeding in adult phase tiger salamanders, *Ambystoma tigrinum*. As we found for *T. carolina*, Shaffer and Lauder's study showed that *A. tigrinum* uses higher amplitude hyoid depression when feeding in water than on land. Shaffer and Lauder predicted that the time to

TABLE 2. Two-way ANOVA of kinematic variables from aquatic and terrestrial feeding events by three Eastern box turtles (*Terrapene carolina*)<sup>1</sup>

Variable	Effect <sup>2</sup>	df	F	P
Time to peak gape	A vs T	1	0.509	0.48
	I**	2	31.18	<0.0001
	(A vs T) $\times$ (I)	2	0.459	0.64
Maximum gape	A vs T	1	1.493	0.24
	I	2	1.593	0.24
	(A vs T) $\times$ (I)	2	1.513	0.26
Time to peak hyoid depression	A vs T	1	0.0988	0.76
	I**	2	29.99	<0.0001
	(A vs T) $\times$ (I)	2	0.020	0.98
Maximum hyoid depression <sup>3</sup>	A vs T**	1	115.00	<0.0001
	I*	2	4.6050	0.0328
	(A vs T) $\times$ (I)	2	2.4308	0.1299

<sup>1</sup>The effect of individual turtle (I) and feeding regime (A vs T), as well as the interaction of these two effects is compared.

<sup>2</sup>\* and \*\* indicate significance at the  $P < 0.05$  and  $P < 0.01$  levels, respectively.

<sup>3</sup>Note that the only variable that shows a significant effect between aquatic and terrestrial feeding is the magnitude of maximum hyoid depression.

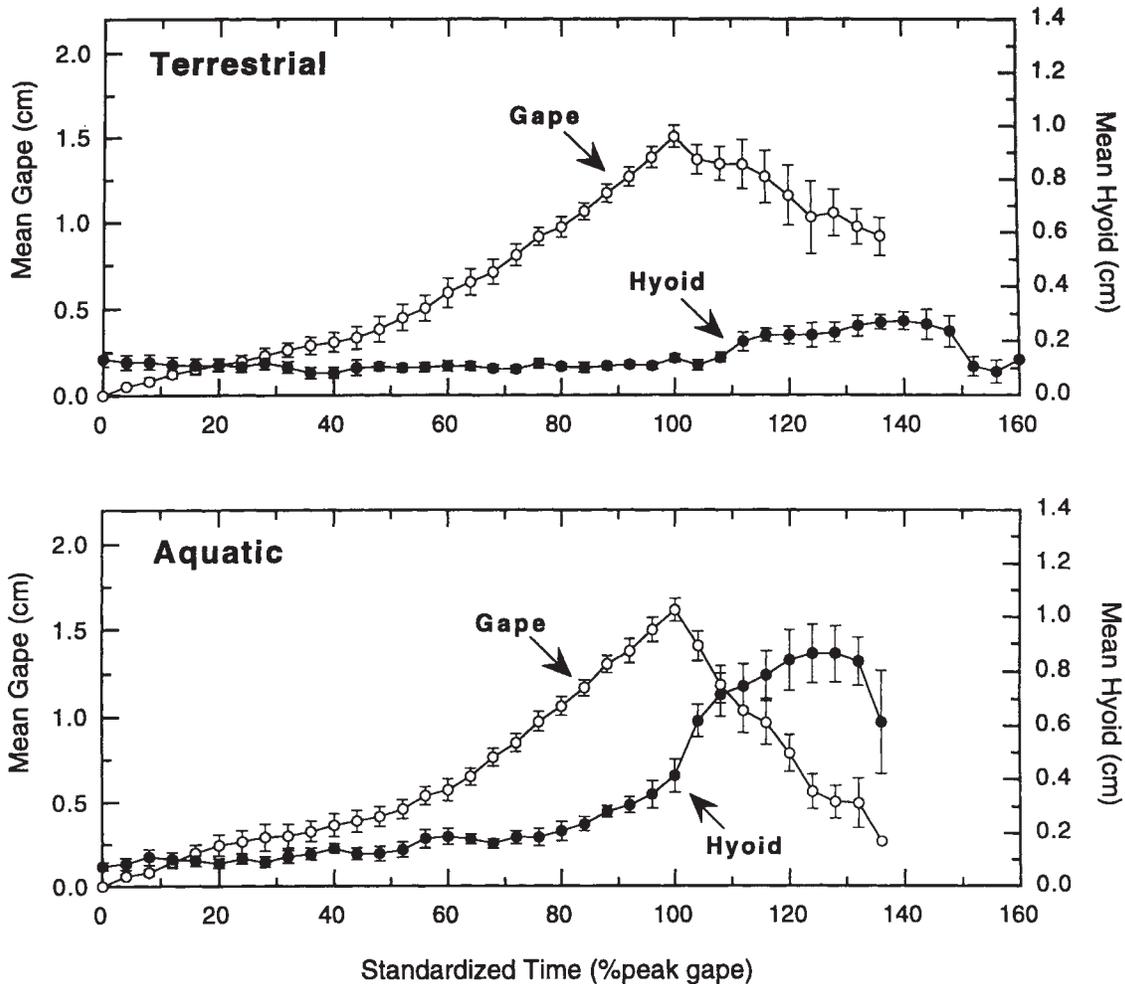


Fig. 4. Summary plot of all aquatic and terrestrial feedings from three Eastern box turtles (*Terrapene carolina*). Kinematic

plots from each feeding were standardized by setting the time of peak gape to 100%. The error bars are standard error.

peak gape would be longer in water than in air because the greater resistance of the water would slow down the feeding. They found, however, that this time was shorter in aquatic feedings, and concluded that the addition of tongue prehension in terrestrial feedings lengthened the gape cycle. In contrast to their results, we did not find a significant difference in time to peak gape between air and water. Perhaps *T. carolina* showed no lengthening of the gape cycle in terrestrial feeding because they were not using tongue prehension to capture earthworm prey.

In summary, both semiterrestrial turtles and salamanders have now been shown to modulate prey capture kinematics between aquatic and terrestrial feeding. These findings reinforce the importance of the differences in viscosity and density between water and air to animals capturing small prey in these media. Hyoid depression and oral

cavity expansion are critical components of feeding in water, even if the prey is not actually drawn into the mouth. Cryptodire turtles primarily use neck extension for prey capture, but oral cavity expansion is essential to generate compensatory suction in water.

As a final point we note that terrestriality has evolved several times within the Testudines, making turtles a particularly interesting clade in which to examine aquatic-terrestrial transitions. For example, our study species, *T. carolina*, is a member of a primitively aquatic clade (Burke et al., '96), indicating that terrestrial feeding is secondarily derived in *T. carolina*. Thus the reduction in hyoid depression seen during terrestrial feeding in *T. carolina* is likely to be a derived condition.

The preceding example also points out a difficulty of using turtles to study the evolution of terrestrial feeding in amniotes. The pattern of a

primitively aquatic lifestyle and a secondarily derived terrestrial lifestyle may be general for all living turtles. The currently accepted hypothesis is that the ancestor to recent turtles was terrestrial (Gaffney et al., '87), but that an aquatic lifestyle evolved early in the history of the clade and is probably primitive for all extant turtles (Gaffney et al., '87, '91; Carroll, '88). Thus terrestrial feeding in turtles is a derived behavior, and the use of turtles in historical reconstructions of terrestrial feeding in amniotes is problematic (*contra* Bels et al., '97).

#### ACKNOWLEDGMENTS

We thank K. Schwenk, J. O'Reilly, T. Hiebert, and N. Kley for reading and commenting on the manuscript. We also thank A. Whitlock and M. Winhold for lending us *T. carolina* for the study, and we especially thank the staff of the Live Herpetological Collection of the University of Massachusetts Museum of Natural History for supplying diverse turtle species for comparison. This work was done in a laboratory supported by NSF grant IBN-9419892 to E.L.B.

#### LITERATURE CITED

- Barbour, R. (1950) The reptiles of Big Black Mountain, Harlan County, Kentucky. *Copeia*, 1950:100–107.
- Bels, V.L., and S. Renous (1992) Kinematics of feeding in two marine turtles (*Chelonia mydas* and *Dermochelys coriacea*). In Proceedings of the Sixth Ordinary General Meeting, S.E.H. Z. Korsos and I. Kiss, eds. Hungarian Natural History Museum Press, Budapest, pp. 73–78.
- Bels, V.L., J. Davenport, and V. Delheusy (1997) Kinematic analysis of the feeding behavior in the box turtle *Terrapene carolina* (L.) (Reptilia: Emydidae). *J. Exp. Zool.*, 277:198–212.
- Bemis, W.E., and G.V. Lauder (1986) Morphology and function of the feeding apparatus of the lungfish, *Lepidosiren paradoxa* (Dipnoi). *J. Morphol.*, 187:81–108.
- Bramble, D.M. (1973) Media dependent feeding in turtles. *Am. Zool.*, 13:13–42.
- Bramble, D.M. (1978) Functional analysis of underwater feeding in the snapping turtle. *Am. Zool.*, 18:623.
- Burke, R.L., T.E. Leuteritz, and A.J. Wolf (1996) Phylogenetic relationships of emydine turtles. *Herpetologica*, 52:572–584.
- Carr, A. (1952) Handbook of Turtles. Cornell University, Ithaca, p. 542.
- Carroll, R.L. (1988) Vertebrate Paleontology and Evolution. W.H. Freeman and Co., New York.
- Ernst, C.H., J.E. Lovich, and R.W. Barbour (1989) Turtles of the United States and Canada. Smithsonian, Washington, D.C.
- Gaffney, E.S., J.H. Hutchinson, F.A. Jenkins, and L.J. Meeker (1987) Modern turtle origins: The oldest known cryptodire. *Science*, 237:289–291.
- Gaffney, E.S., P.A. Meylan, and A.R. Wyss (1991) A computer assisted analysis of the relationships of the higher categories of turtles. *Cladistics*, 7:313–335.
- Lauder, G.V. (1980) Evolution of the feeding mechanism in primitive actinopterygian fishes: A functional anatomical analysis of *Polypterus*, *Lepisosteus* and *Amia*. *J. Morphol.*, 163:283–317.
- Lauder, G.V. (1985) Aquatic feeding in lower vertebrates. In: Functional Vertebrate Morphology. M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake, eds. Harvard University Press, Cambridge, pp. 210–229.
- Lauder, G.V., and T. Prendergast (1992) Kinematics of aquatic prey capture in the snapping turtle *Chelydra serpentina*. *J. Exp. Biol.*, 164:55–78.
- Lauder, G.V., and S.M. Reilly (1988) Functional design of the feeding mechanism in salamanders: Causal bases of ontogenetic changes in function. *J. Exp. Biol.*, 134:219–233.
- Lemell, P., C.J. Beisser, and J. Weisgram (1997) Feeding patterns of *Pelusios castaneus* (Chelonia: Pleurodira) with comments on the morphology of its tongue. *J. Morphol.*, 232:285.
- Liem, K.F. (1990) Aquatic versus terrestrial feeding modes: Possible impacts on the trophic ecology of vertebrates. *Am. Zool.*, 30:209–221.
- Mahmoud, I.Y. (1968) Feeding behavior in kinosternid turtles. *Herpetologica*, 24:300–305.
- Motta, P.J., T.C. Tricas, R.E. Hueter, and A.P. Summers (1997) Feeding mechanism and functional morphology of the jaws of the lemon shark, *Negaprion brevirostris* (Chondrichthyes, Carcharhinidae). *J. Exp. Biol.*, 200:2765–2780.
- Norton, S.F., and E.L. Brainerd (1993) Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.*, 176:11–29.
- Reilly, S.M., and G.V. Lauder (1992) Morphology, behavior, and evolution—comparative kinematics of aquatic feeding in salamanders. *Brain Behav. Evol.*, 40:182–196.
- Schwenk, K., and D.B. Wake (1988) Medium-independent feeding in a plethodontid salamander: Tongue projection and prey capture underwater. *Am. Zool.*, 28:115A.
- Shaffer, H.B., and G.V. Lauder (1988) The ontogeny of functional design: Metamorphosis of feeding behaviours in the tiger salamander (*Ambystoma tigrinum*). *J. Zool. (London)*, 216:437–454.
- Shaffer, H.B., P. Meylan, and M.I. McKnight (1997) Tests of turtle phylogeny: Molecular, morphological, and paleontological approaches. *System. Biol.*, 46:235–268.
- Van Damme, J., and P. Aerts (1997) Kinematics and functional morphology of aquatic feeding in Australian side necked turtles (Pleurodira: *Chelodina*). *J. Morphol.*, 233:113–125.
- Weisgram, J. (1985) Feeding mechanics of *Claudius angustatus* COPE 1865. *Fortschr. Zool.*, 30:257–260.
- Werth, A.J. (1989) Suction feeding in odontocetes: Water flow and head shape. *Am. Zool.*, 29:92A.