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DRINKING IN SNAKES: KINEMATIC CYCLING AND WATER TRANSPORT

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Summary

Snakes are purported to drink by sucking water into their mouths and then compressing the oral cavity to force water into the oesophagus. Video recordings of drinking behaviour in 23 snakes representing 14 species from three families, combined with simultaneous recordings of water volumes consumed, show that all the snakes vary widely in the amount of water taken in when drinking. This variation is not correlated with kinematic events. Kinematic recordings and indirect measurements of water flow suggest that moving water into the mouth can be decoupled from the processes that move water into the oesophagus and that, infrequently, water may continue flowing into the mouth during both opening (suction) and closing (presumed compression) of the mouth. Drinking in snakes is not a simple, stereotyped behaviour.

Different snake species differ in both drinking kinematics and water inflow patterns. Vertical excursions of the mandible are smallest in booids and larger, but highly variable, in different viperids and colubrids. Cyclic movements of the tongue seen in booids are not evident in viperids or colubrids. All the snakes usually take in water at rates far below their potential maximum rate.

Although drinking is apparently achieved by suction, a single model cannot explain all water movement patterns in snakes. At a practical level, functional morphological studies of drinking in snakes (and possibly many other animals) must demonstrate that fluid flow actually correlates with kinematic events. Without such an empirical demonstration, interpretation of other measurements (pressure, movement, etc.) is unlikely to produce meaningful models.

Key words: drinking, snake, kinematics, intraspecific variation, interspecific variation.

Introduction

Most terrestrial vertebrates are able to replace water lost to the environment by drinking water. In amniotes, drinking is a function of the structures of the mouth, the oral cavity and the pharynx. Most of the structures of the mouth, however, vary dramatically among amniotes as presumed adaptive responses to feeding, not drinking, because water, unlike food, is physically uniform (at least between 1 and 99 °C). Modifications of the feeding apparatus are associated in some clades (birds have been best studied: Zweers, 1992) with extraordinarily complex and divergent mechanisms for drinking. In birds, these mechanisms seem to be associated with structural and functional limitations imposed by the essentially nondeformable keratinized beak. The association of drinking mechanisms with adaptive changes in feeding mechanics prompted Homberger (1983) to suggest that the different drinking mechanisms in birds may all be nonadaptive. In other words, the different drinking mechanisms are pleiotropic effects of feeding adaptations. This suggests that, despite the frequent need to regain lost water, drinking is secondary to feeding. Furthermore, if drinking is achieved by structures actively selected for a separate function (feeding), drinking performance (in terms of the efficiency of water transport, such as volume per kinematic cycle) may be randomly variable with little relationship to kinematic events.

Snakes display considerable trophic diversity (Greene, 1997; Cundall and Greene, 2000) but, unlike birds, they are all carnivorous. All snakes have slender, bifid tongues that emerge from a tongue sheath at the anterior edge of the lower jaw. As a result, the tongue of snakes does not carry or move water (Kardong and Haverly, 1993) and, in many snakes, the tongue does not visibly move during drinking (Gove, 1979; Berkhoudt et al., 1995). As far as is known, all snakes are suction drinkers, and the only critical structural variations that might be predicted to influence drinking performance are the relative dimensions and shapes of the mandibles and their suspensorial elements and the arrangements of intermandibular muscles and connective tissues.

Kardong and Haverly (1993) described drinking in the boid snake *Boa constrictor* as a process of sucking water into the mouth and then forcing it into the oesophagus. They noted that, during four separate drinking bouts, a single 2.1 m *Boa constrictor* drank between 0.09 and 0.265 ml per kinematic cycle, averaging 0.181 ml per cycle. Assuming that the snake used the suction–compression model proposed, the variations in volumes taken in per cycle indicate that the pumping

mechanism can be modulated and that, given the sizes of their mouths, snakes drink remarkably little per cycle. Berkhoudt et al. (1995) have since elaborated on drinking kinematic differences between *Boa constrictor* and the colubrid *Boiga irregularis*, and Bels and Kardong (1995) provided evidence that an oesophageal sphincter functions during drinking in *Elaphe obsoleta*. Neither of the last two studies measured the volume of water transported.

Drinking in snakes differs from that of many lizards (Smith, 1984; Bels et al., 1993), birds (Homberger, 1980; Zweers, 1992) and mammals (Hiiemae and Abbas, 1981; Hiiemae and Crompton, 1985), which use the tongue to collect or move water. In lingual-drinking amniotes, cyclic movements of the tongue carry water into the oral cavity where it is stripped, drained or impelled off the tongue surface by one of a number of methods (Zweers, 1992). Many lingual drinkers use multiple tongue cycles to accumulate a water volume in the pharynx that is then drained in a single swallowing cycle. Swallowing may involve a variety of muscle-powered water-moving mechanisms including tip-down drinking (Homberger, 1980; Zweers, 1992) or tip-up drinking in which elevating the head allows water collected in the pharynx to drain into the oesophagus (Zweers, 1992). Some suction-drinking squamates (Auffenberg, 1981; Smith, 1986), turtles (Bels et al., 1995), birds (Homberger, 1980; Zweers, 1982) and mammals (Hiiemae and Crompton, 1985) may also use tip-up drinking behaviour to drain the pharynx. Others, such as suckling mammals (German and Crompton, 1996; Cameron et al., 1999) and those snakes previously studied (Kardong and Haverly, 1993; Berkhoudt et al., 1995), use compressive forces to drive fluid into the oesophagus. The two-phase nature of buccal pump suction drinking in snakes provides opportunities for various modulatory processes whose existence is explored here through recordings showing both kinematics and water movement.

The object of this study was to determine how much water is transported per cycle and to relate water transport to the kinematics of drinking in snakes. All previous studies of drinking in snakes have examined the process primarily in instrumented animals. Kardong and Haverly (1993) measured the volume imbibed during four immersions in one uninstrumented snake and showed wide variation in volume imbibed per cycle. I focused solely on the relationship between kinematic events and the volume transported in uninstrumented animals. The hypothesis tested was that kinematic cycles of jaw movement are related to the volume of water transported.

Materials and methods

Water transport

Video recordings of drinking were made between March 1995 and March 1998 from 23 snakes representing 14 species in nine genera from four families. These included one *Boa constrictor* and one *Epicrates cenchria* (Boidae), three *Python regius* (Pythonidae), two *Agkistrodon piscivorus*, one *Crotalus horridus*, one *C. mitchellii* and one *C. viridis* (Viperidae), one

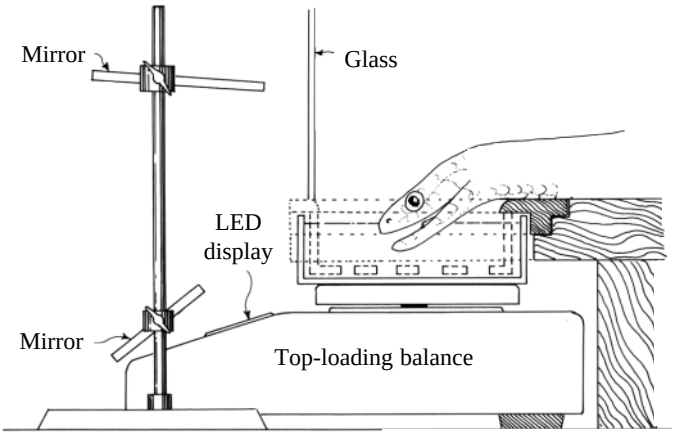

Fig. 1. Diagrammatic view of the apparatus used to record the kinematics and water transport during drinking. The video camera was placed to the left. LED, light-emitting diode.

Fig. 2. The appearance of a video recording of a drinking snake (*Boa constrictor*) with the balance readout. The acrylic screen inside the reservoir prevented the snake from pressing on the bottom of the reservoir.

Elaphe guttata, two *E. obsoleta*, one *Lampropeltis getula*, three *Nerodia sipedon*, two *N. fasciata*, two *N. rhombifer* and two *Farancia abacura* (Colubridae). Video recordings were made using a Sony 8 mm 12X CCD FX620 Handycam recorder or a Panasonic AG-456UP S-VHS video camera. Videotapes were analysed using a Sony 8 mm EV-A50 video recorder or a Panasonic AG-1980P video recorder and a variety of monitors.

All snakes were recorded drinking water at room temperature (23–28 °C) from a small acrylic container (inside dimensions 9.8 cm×9.6 cm×3.3 cm) resting on a top-loading Ohaus electronic balance (model TS400) whose light-emitting diode (LED) display was shown in a mirror below the acrylic water container (Figs 1, 2). The acrylic container lay below the edge of a small square cut-out in the floor of a wooden filming box arranged such that the snakes could not rest on the edge of the container.

Most snakes were deprived of water for 3–5 days prior to recording. Some species, notably *Crotalus mitchellii*, *C. viridis* and *Lampropeltis getula*, were maintained without water in their cages for months and offered opportunities to drink at intervals of 3–7 day but sometimes did not drink for periods as long as 3 or 4 months. During this time, however, they were fed at weekly or biweekly intervals.

Each snake was placed in the filming box and allowed to drink to satiation, each placement being considered a replicate. Drinking involved immersion of part or all of the head, and snakes drank either for one long, continuous immersion period or for a number of shorter immersions (Myer and Kowell, 1971; Kardong and Haverly, 1993). Satiation was assumed when the snake left the water container and began crawling out of the wooden filming box.

Water movement analysis

For each replicate, the number of immersion–emersion periods, the number of jaw movement cycles (open–close cycles) and the volume of water removed per immersion were recorded. All volumes were adjusted to a body mass of 1 kg (actual volume×1000/body mass, with volume in ml and body mass in g). The average volume of water removed per cycle was calculated for each immersion and compared across immersions and replicates for each snake. To determine whether volumes transported changed over time within immersion periods, volumes transported during 10-cycle intervals were measured at various points during an immersion. These measurements were made for 160 immersions approximating or exceeding 100 cycles for the 19 snakes having at least five immersions exceeding 100 cycles. Analyses of volumes per replicate, immersion and cycle were performed using pair-wise Mann–Whitney *U*-tests because the data were not normally distributed and variances were very high and unequal.

Kinematic analysis

Movements of the snakes during drinking were variable but in most cases small. Information was gleaned from recordings showing as many different views of each animal as possible. Some of the most instructive recordings were of lateral and posterior views of the lower jaw and anterior trunk. To analyse the relationship between kinematics and water flow, selected segments (230 cycles representing 11 snakes) of videotape were analysed frame-by-frame, and tongue (booids) or mandibular movements (colubroids) between frames were recorded using behavioural notation together with the balance reading for every frame. This analysis did not allow quantitative comparisons of movements, but gave time courses of movement profiles for each of the 11 snakes.

Kinematic differences among individuals and species were analysed by measuring the vertical movements of the mandibles during the first and last thirds of five immersions for all 23 snakes. Mandibular movement was measured as a function of head height at the level of the external naris because movements in some taxa were so small that using more typical measures of snake size (head length, head width, etc.) would have given extremely small values with proportionately high errors. Variances among individuals were heteroscedastic. After an initial Kruskal–Wallis test had shown that mandibular movements differed significantly among individuals, pairwise Mann–Whitney tests of values for families, genera and species were used to determine whether kinematic differences related to phylogeny.

Kinematic changes over time were examined using a paired-samples *t*-test of mandibular excursion values and the duration of 10-cycle intervals for 5–10 cycle intervals from each of the first and second halves of 13 immersions exceeding 500 cycles in duration. These 13 immersions came from only five of the 23 snakes, but all families were represented. Values for each of the families were examined separately to estimate the uniformity of response to long drinking bouts among the different snakes.

Calibration of the balance

One of the problems in measuring the rate at which snakes remove water from a container is that a relatively large surface area is required to encourage the animal to drink, but the amount removed by the snake per cycle is small. It was this consideration that led to measuring volume indirectly through mass loss. Most balances, however, do not give instant measurements of mass change. Furthermore, to measure mass loss in a relatively large volume of water (250–350 ml), it was necessary to use a top-loading balance with a maximum capacity approximating 400 g and measuring to at least the nearest 0.01 g, inasmuch as snakes might be taking this much or less per cycle. The reason for using a balance rather than a strain gauge (the latter would have given more accurate measurements of the time course of water transport) was because overall volume changes were suspected to be more important than short-term water movements. However, it was hoped that the balance would give some measure of the volume transported during each kinematic cycle.

Calibrations of the balance lag time both in tracking mass change and in reaching equilibration were performed by videotaping movement of water into and out of the container using a 2.5 ml syringe (Fig. 3). On the basis of 81 measurements of the number of frames separating a syringe reading from a corresponding balance reading in Fig. 3, the mean lag time is 0.67±0.11 s (20±3.25 frames; means ± S.D.). The range, however, is 0.46–1.03 s (14–31 frames). Although all graphs of mass change and behaviour are plotted assuming a 20-frame delay in mass change, two aspects of the calibration results are critical. First, although the mean was used as the length of the delay, the response appeared to be random and, hence, unpredictable within the range of values obtained. The range provides the window of time within which events must have occurred. Second, as the rate of change increased, the balance simply increased the difference between successive readings but the rate of LED reading presentation remained unchanged at a new reading every 0.17–0.2 s (five or six video frames at the standard replay framing rate of 30 frames s^{-1}). Reversals of mass change that occurred at frequencies shorter than the equilibration time of the balance resulted in cutting

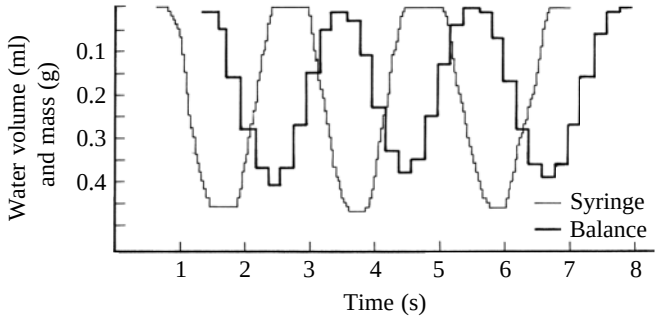

Fig. 3. Plot of volume change in a syringe pump *versus* mass change in the water reservoir as given by the top-loading balance. Both sets of values were derived from videotape recordings made at 30 frames s^{-1}.

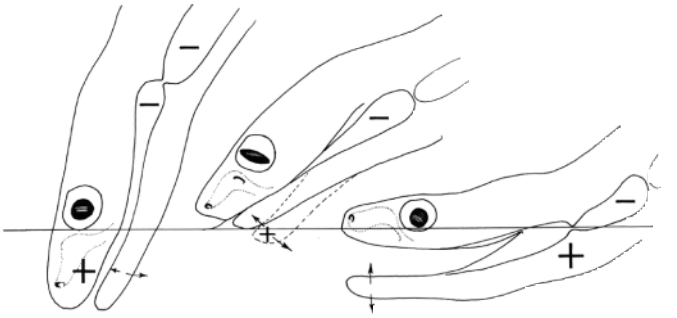

Fig. 4. Possible positions of the head of a snake during drinking. The parts of the head below the surface of the water add a mass equivalent to the volume of water displaced to the mass registered by the balance. In the central diagram, surface tension and capillarity may combine to cause a loss of mass as soon as the snout or lower jaw of the snake touches the water surface. Any water raised above the surface of the water in the reservoir is registered as a loss of mass, as suggested by the areas denoted by – in the buccal and oesophageal regions.

Table 1. *Body mass, number of drinking immersion and replicates recorded and values for jaw movement cycles per immersion and per replicate for 23 snakes*

Family/Species	*M* (g)	No. of immersions	Total no. of replicates	No. of immersions per replicate	Range	No. of cycles per immersion	Range	No. of cycles per replicate	Range
Boidae									
Boa constrictor	230[a]	57	14	4.07	1–8	89±101	1–449	363±247	15–1027
Epicrates cenchria	790	15	6	2.14	2–4	325±320	28–1163	812±445	77–1296
Pythonidae									
Python regius 1	1050	8	4	2.00	1–4	101±136	4–427	202±152	93–427
Python regius 2	840[b]	5	4	1.25	1–2	62±42	9–110	76±34	39–110
Python regius 3	375[c]	30	11	2.80	1–4	158±167	7–532	444±182	219–733
Viperidae									
Agkistrodon piscivorus 1	990[d]	58	16	3.56	1–8	65±66	2–292	238±106	69–394
Agkistrodon piscivorus 2	550	10	6	1.67	1–2	104±92	27–326	173±144	42–431
Crotalus horridus	525	35	10	3.50	1–7	214±407	1–1967	748±773	55–2226
Crotalus mitchellii	340	29	12	2.42	1–5	69±85	3–365	168±117	15–379
Crotalus viridis	540	31	10	3.10	1–5	41±29	4–96	127±36	81–184
Colubridae									
Elaphe guttata	400	15	10	1.38	1–3	134±118	6–357	201±133	58–463
Elaphe obsoleta 1	1120	39	19	2.05	1–5	116±97	6–358	248±85	147–381
Elaphe obsoleta 2	500	14	13	1.08	1–2	140±86	5–355	150±79	41–355
Lampropeltis getula	360	19	12	1.58	1–4	169±98	44–393	268±166	71–674
Nerodia sipedon 1	230	12	5	2.40	1–6	36±18	16–72	85±71	36–209
Nerodia sipedon 2	90	8	3	2.67	1–4	38±39	7–130	100±57	42–182
Nerodia sipedon 3	350	22	11	2.00	1–5	102±57	6–220	204±119	107–468
Nerodia fasciata 1	200	10	2	5.00	1–9	81±78	5–204	404±363	147–661
Nerodia fasciata 2	130	5	3	1.67	1–2	85±56	31–153	142±33	105–167
Nerodia rhombifer 1	450	16	10	1.60	1–3	92±87	2–313	147±94	33–313
Nerodia rhombifer 2	500	15	11	1.36	1–2	287±216	5–859	392±218	43–859
Farancia abacura 1	885	18	12	1.50	1–3	303±312	4–1293	454±322	94–1293
Farancia abacura 2	710	24	11	2.18	1–7	151±182	2–577	329±192	30–577

M, approximate mass of snake, except as noted: [a]mass 135 g at first observation and 230 g at last (all summer 1997); [b]mass 610 g at first observation and 840 g at last (summer 1995 to spring 1997); [c]mass 300 g at first observation and 375 g at last (all summer 1997); [d]mass 570 g at first observation and 990 g at last (autumn 1995 to spring 1997).

Values are means ± S.D. and the range is given for each set of values.

off the full range of mass change (the peak of the curve was lopped off). However, the balance accurately reflected the frequency of cycling at rates used by some of the slower snakes (1.4–2.0 s per cycle). Faster cycling rates, such as those sometimes used by *Boa constrictor*, *Epicrates cenchria* and *Python regius* (0.4–0.7 s per cycle), produce a steady change in balance readings every 0.17–0.2 s.

One other factor that influences the measurement of the volume of water transported per cycle is movement of the head or neck relative to the water surface (Fig. 4). Submergence of the entire head was seen periodically in most snakes but was especially common in *Boa constrictor*, *Lampropeltis getula*, *Nerodia* spp. and *Farancia abacura*. Because it was impossible to differentiate balance-reading changes produced by head movements from those due to water transport, volumes transported per 10 cycles were measured only in sequences with no detectable motion of the whole head relative to the water surface.

Results

When snakes were placed in the filming chamber and given the opportunity to drink, with few exceptions they either drank within a few minutes of being placed in the chamber or they did not drink within the 30 min during which they were given the opportunity to drink. Whereas the minimum number of immersions per replicate was one for all but one snake (*Epicrates cenchria*), the maximum number varied by individual (Table 1).

Drinking is a highly variable behaviour in snakes despite the fact that it appears to be kinematically conservative. Extraordinary variability (standard deviations approaching or exceeding the mean) is seen in all quantified aspects of drinking behaviour, including the numbers of kinematic cycles per replicate and per immersion (Table 1) and all measurements of water volumes imbibed (Table 2). The variability in volumes and cycles characterising each snake is matched by an apparent absence of patterns among congeneric species, and it was this feature of the data that predicated the listing of all animals individually in Tables 1 and 2.

Volume and cycle relationships

There is a significant correlation (r=0.38; P<0.01; N=150) between volume consumed and the number of cycles per

Table 2. *Adjusted water volumes transported per replicate, immersion and cycle*

Family/Species	Volume per replicate (ml)	Range (ml)	Volume per immersion (ml)	Range (ml)	Volume per kinematic cycle (ml)	Range (ml)
Boidae						
Boa constrictor	41±31	2–121	10±12	–0.5–49	0.11±0.09	–0.48–0.25
Epicrates cenchria	24±14	1–43	9±11	0–39	0.03±0.01	0–0.04
Pythonidae						
Python regius 1	19±11	10–34	10±11	–0.1–34	0.09±0.06	–0.02–0.20
Python regius 2	29±10	15–37	23±14	3–37	0.40±0.15	0.24–0.65
Python regius 3	43±8	27–55	16±15	0–48	0.17±0.33	0–1.87
Viperidae						
Agkistrodon piscivorus 1	30±16	4–62	8±11	0.1–62	0.11±0.04	0.03–0.26
Agkistrodon piscivorus 2	52±32	11–85	31±24	4–67	0.31±0.12	0.15–0.51
Crotalus horridus	45±20	28–87	13±15	–0.2–46	0.32±0.36	–0.10–1.77
Crotalus mitchellii	30±20	2–69	13±14	0.1–48	0.16±0.09	0.03–0.38
Crotalus viridis	24±9	9–38	8±7	0.4–20	0.10±0.06	0.10–0.32
Colubridae						
Elaphe guttata	29±12	13–48	20±14	0.8–43	0.18±0.07	0.09–0.40
Elaphe obsoleta 1	24±8	7–36	12±10	0.1–32	0.10±0.04	0.02–0.17
Elaphe obsoleta 2	35±12	15–52	33±15	0.7–52	0.25±0.06	0.14–0.36
Lampropeltis getula	40±18	14–74	25±12	8.7–54	0.17±0.07	0.08–0.32
Nerodia sipedon 1	48±36	27–111	20±11	3.3–36	0.56±0.23	0.28–0.99
Nerodia sipedon 2	61±35	27–97	23±20	5.0–67	0.65±0.12	0.48–0.79
Nerodia sipedon 3	53±25	27–107	27±17	1.0–67	0.25±0.06	0.13–0.37
Nerodia fasciata 1	145±35	120–170	29±38	3.2–120	0.57±0.38	0.06–1.06
Nerodia fasciata 2	60±17	42–77	36±23	15.6–61	0.43±0.05	0.39–0.51
Nerodia rhombifer 1	63±38	20–132	39±39	0.1–132	0.39±0.22	0.02–0.69
Nerodia rhombifer 2	26±11	11–47	19±15	0.4–53	0.09±0.07	0.01–0.27
Farancia abacura 1	76±33	20–113	51±37	–0.4–113	0.18±0.09	–0.11–0.29
Farancia abacura 2	75±43	11–169	34±38	0.2–121	0.34±0.38	0.10–2.06

Means ± S.D. and ranges are given. Values of N for replicates and immersions are given in Table 1.
Water volumes are adjusted to a body mass of 1 kg.

Table 3. *Correlations between volume of water transported, number of cycles and number of immersions in 15 snakes*

	Volume/cycle		Volume/immersion		Cycle/immersion	
Snake	*r*	*P*	*r*	*P*	*r*	*P*
Boa constrictor	0.35	0.32	–0.27	0.45	0.18	0.63
Python regius 3	0.31	0.39	0.70*	0.03	0.29	0.42
Agkistrodon piscivorus 1	0.78**	<0.01	0.08	0.83	0.58	0.08
Crotalus horridus	0.54	0.11	0.45	0.20	0.38	0.29
Crotalus mitchellii	0.62	0.05	0.07	0.84	0.01	0.98
Crotalus viridis	0.76*	0.01	0.41	0.24	0.62	0.06
Elaphe guttata	0.96**	<0.01	0.22	0.54	0.10	0.78
Elaphe obsoleta 1	0.54	0.11	0.30	0.40	0.55	0.10
Elaphe obsoleta 2	0.86**	<0.01	–0.08	0.84	–0.08	0.83
Lampropeltis getula	0.86**	<0.01	0.78**	<0.01	0.89**	<0.01
Nerodia sipedon 3	0.95**	<0.01	0.89**	<0.01	0.94**	<0.01
Nerodia rhombifer 1	0.97**	<0.01	0.25	0.49	0.42	0.22
Nerodia rhombifer 2	0.65*	0.04	0.22	0.55	0.07	0.85
Farancia abacura 1	0.78**	<0.01	0.37	0.29	0.01	0.98
Farancia abacura 2	0.81**	<0.01	0.75*	0.01	0.37	0.29

*P<0.05; **P<0.01.

replicate and between the number of cycles per replicate and the number of immersions per replicate (r=0.28; P<0.01; N=150) for the first 10 replicates of the 15 snakes for which 10 or more replicates were recorded. In other words, it generally takes more cycles to drink more water, and snakes tend to increase cycle number per replicate by increasing the number of immersions rather than by increasing the duration of immersions. However, these values hide considerable variation among snakes (Table 3), and this variation shows no obvious trends that might be linked to phylogeny. Of the 15 snakes, one-third, including at least one species from each family, show no significant correlation between volume and number of cycles, but two snakes (the colubrine *L. getula* and one natricine *N. sipedon*) show significant correlations between all three pairs of variables. In contrast, there is little relationship between the volume consumed per replicate and the number of immersions per replicate (r=0.08; P=0.32; N=150). Using data on immersions for all 23 snakes, the correlation between volume and number of cycles increases (r=0.55; P<0.01; N=495), suggesting that the amount of water snakes drink is generally related to kinematic behaviour.

The volume of water imbibed per cycle, determined from total volume consumed per immersion, differs widely between immersion periods for the same snake (Table 2), supporting data reported by Kardong and Haverly (1993). Because these volumes represent average values for a whole immersion period that may have lasted from as few as one to nearly 2000 cycles (Table 1), the variation could arise either from kinematic modulation between immersion periods (drinking different volumes per cycle during different immersions, but keeping volume per cycle nearly constant within an immersion) or from modulation of volumes taken in between cycles within immersion periods. Video recordings of changes in mass indicate that both mechanisms may be used.

Gradual changes in volumes transported per cycle over the course of an immersion are typical of the drinking behaviour of most snakes. The middle two plots in Fig. 5 and both plots in Fig. 6 show how the pattern of water transport changed within a single immersion period. In both cases, jaw movement patterns varied slightly between the upper and lower plots in the relative duration of opening and closing. Inasmuch as every snake recorded exhibited this kind of behaviour in one or more immersion periods, it appears to be a common feature of drinking. Modulation of transport between cycles also occurred in most snakes but, because its appearance was irregular, it was difficult to analyse. A comparison of successive cycles in Figs 5 and 6 gives some indication of the nature of variation between cycles, but these do not show the more extreme variations.

Transport over 10-cycle intervals provided measurements of variations in reservoir mass loss between cycles and revealed some extraordinary patterns. Typically, snakes continue drinking movements, but the balance shows reduction or cessation of water removal for one to as many as 10–15 cycles, sometimes many more. One pattern is gradual reduction of volume taken in as the immersion proceeds, but often it is not quite that simple, and snakes frequently begin imbibing for short periods later in the immersion (Fig. 7). Water may also be added to the reservoir during one or more cycles (e.g. Fig. 8), a phenomenon seen in 12 of the 23 snakes recorded. In both specimens of *F. abacura*, volumes added often amounted to appreciable percentages of the total volume imbibed in the preceding period (Fig. 9A) and were accompanied by a number of marked behavioural events not seen in the other species. First, prior to the outflow of water, the anterior trunk swelled noticeably but very gradually, suggesting that some of the water imbibed was retained in the oesophagus. Second, the outflow was accompanied by a brief cessation of mandibular drinking movements and spasmodic contractions of the anterior trunk wall. Often, this type of

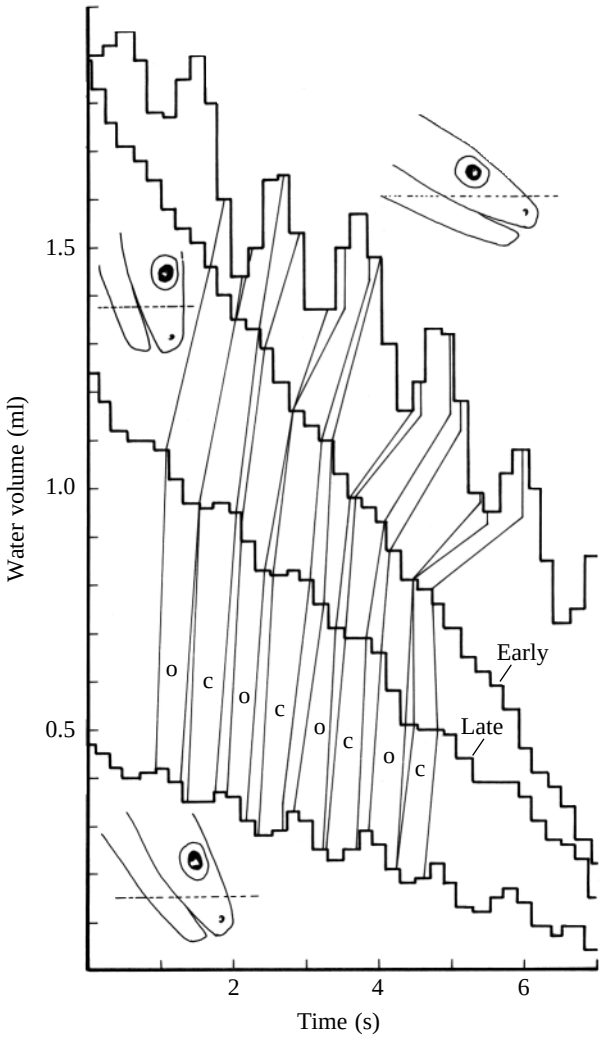

Fig. 5. Four recordings of water loss from the reservoir (water transport) during drinking by *Elaphe obsoleta* 1 for three immersion periods on three different days in 1995. The two middle lines plot the amount lost early and late in the same immersion period. Vertical fine lines demarcate the open (o) and closed (c) phases of kinematic cycles. Volume change values are shifted 20 frames to the left (0.67 s) relative to kinematic cycles to correct for the delay in the LED display of the balance. Superimposed drawings show the position of the head.

behaviour followed a prolonged period of very slow water intake; after the outflow, intake usually increased and the volume lost by the snake was quickly regained. Most longer immersions for the two specimens of *Farancia abacura* involved more than one outflow period, but few had the volume of outflow shown in Fig. 9B.

Kinematic events

Although much of the behaviour of the snakes corresponds to descriptions provided by Kardong and Haverly (1993) for booids and by Berkhoudt et al. (1995) for colubroids, a number of features vary or differ in timing. Furthermore, division of the cycle into suction and compression phases confers

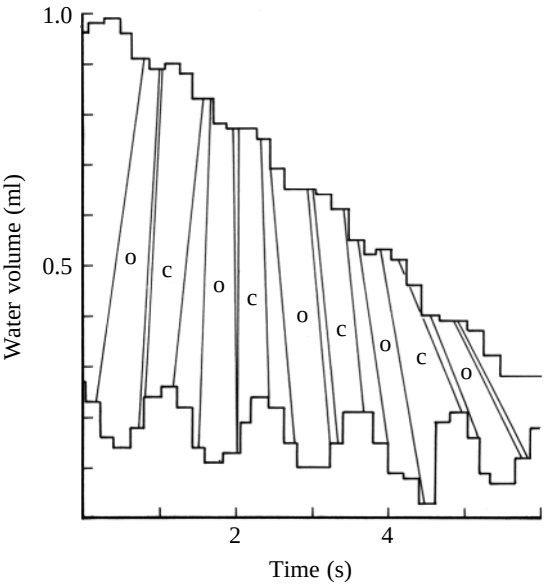

Fig. 6. Water transport by *Nerodia fasciata* 2 early (upper recording) and late (lower recording) in the same immersion period. Vertical fine lines demarcate the open (o) and closed (c) phases of kinematic cycles.

functional characteristics that fit only loosely with water flow data given here. Cycle kinematics appear to be complex. The most obvious aspects in booids are widening and narrowing of the rear of the head that may also be seen in some immersions as closing and opening, respectively, of the anterior mouth combined with periods of tongue protrusion. In colubroids, the tongue appears to remain immobile in most individuals but the jaws move more, and hence the most convenient names for cycle phases refer to jaw opening and closing, the descriptive terminology used by Berkhoudt et al. (1995) and similar to that widely used for feeding in snakes (Cundall, 1987).

In booids, opening is preceded by depression of the anterior floor of the neck. Bone movements appear to be as described by Kardong and Haverly (1993) except that there is often no detectable flaring of the anterior maxillae as the pterygoids move medially. The rear of the head simply gets narrower. In colubroids, the first event in opening is rapid depression of the mental scale and slower depression of the genial scales. In those cases in which the mouth was actually closed, the ventral flip of the mental scale opens the lingual canal. Following this, the quadrates and maxillae move medially and the mental scale is raised as the anterior ends of the mandibles drop slightly and the genial region begins rising as the skin immediately behind the genial region is depressed. In booids, the hyoid and tongue are retracted at this point. In views that show the anterior part of the ventral trunk, the ventral skin usually appears to rise during the period that the genial region is depressed. As the genials rise, the anterior trunk begins depression, but usually after the onset of tongue and hyoid retraction. The early part of opening, in some cycles more than half of the opening phase, appears as a relaxation of the head, which is essentially a drooping of the jaws that is difficult to track in frame-by-frame

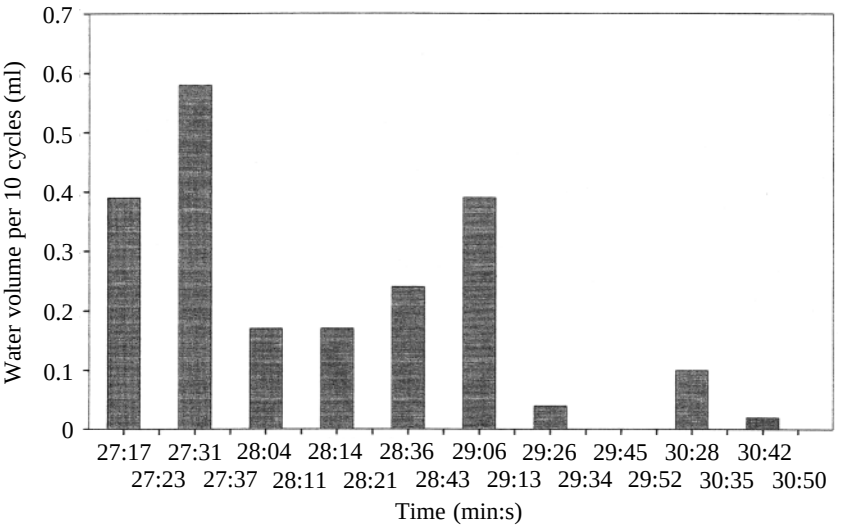

Fig. 7. Volumes of water transported per 10 cycles for nine successive periods of a single immersion by *Python regius* 3.

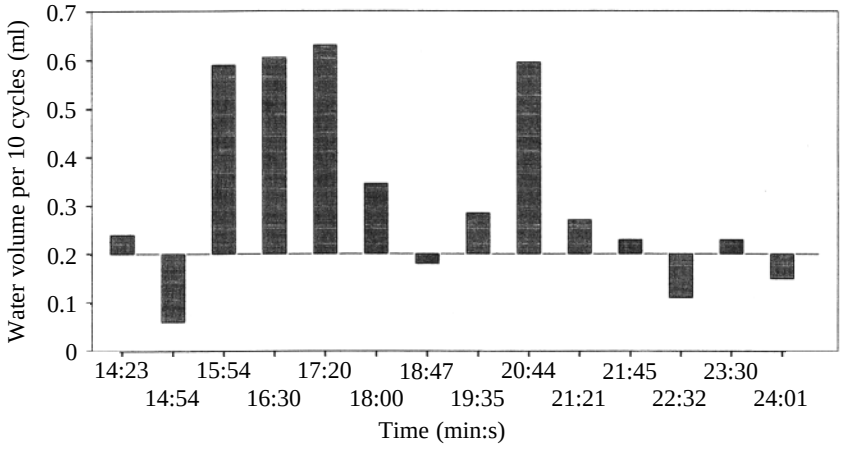

Fig. 8. Volumes transported per 10 cycles for 14 successive periods covering two immersions for *Nerodia rhombifer* 2. The first immersion ended at 19 min 35 s and the second began at 20 min 44 s.

analysis. Included in this drooping are a slight depression and medial movement of the mandibles and maxillae and, in some species, slight depression of the snout. The early part of this phase is usually part of the gap that occurs between the end of closing and the beginning of opening in Figs 5 and 6. Following this period, which is often associated with the most rapid inflow of water, the mandibles drop.

Opening the mouth increases the size of the oral cavity, but from the perspective of driving water flow, the slowness of the movement is unlikely to generate significant suction because the edges of the oral cavity become increasingly widely separated. Closing begins when the mandibles reverse direction. As this occurs, the floor of the mouth caudal to the genial region is depressed. In booids, the hyoid appears to move anteriorly just after closing is initiated, and the tongue emerges from the lingual canal during the latter half of the closing phase. As the lower jaws approach the upper jaws, the genial region remains elevated. After the jaws have met, the maxillae are often elevated and carried slightly laterally, and the snout is elevated as closing is continued. The floor of the mouth immediately caudal to the genials elevates and the tongue protrudes in booids. The ventral skin of the anterior trunk may be depressed at this time and then opening begins.

Although these patterns loosely correlate with ‘aspiration’ and ‘compression’, the mouth is actually open for much of the cycle. In some snakes, the mouth is never closed and hence the oral cavity is not sealed to generate compression, although water is still lost from the reservoir. In most snakes, and during most immersions, if the mouth is closed it appears to be sealed for relatively short periods (30–60 ms). Both the duration of closing and the short period of actual closure correlate with loss of water from the oral cavity during closure and with the small volumes of water actually moved per cycle. However, when relatively large volumes are imbibed, apparently continuously but usually with cyclic fluctuations in rate (see the ‘late’ trace in Fig. 5 and the upper trace in Fig. 6), movements of the floor of the oral cavity and anterior throat may drive water movement. Unfortunately, movements of the skin of the throat were not analysed because they are usually too small to measure accurately in the video recordings. In addition, it remains unclear how movements of the lining of the oral cavity, pharynx and oesophagus relate to movement of

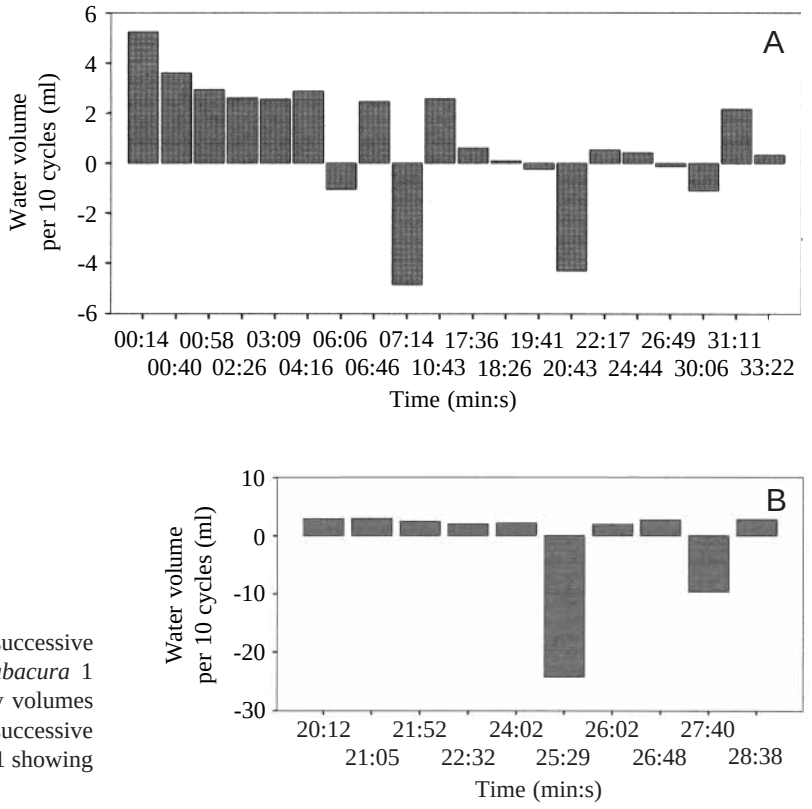

Fig. 9. (A) Volumes transported per 10 cycles in 20 successive periods in one immersion of 1293 cycles in *Farancia abacura* 1 showing numerous reversals in transport and extraordinary volumes per cycle. (B) Volumes transported per 10 cycles in 10 successive periods during one immersion of 388 cycles in *F. abacura* 1 showing two large reversals.

the skin. Bels and Kardong (1995) measured the radiographic profile of the gut wall, but their figures suggest little correlation between movements of the gut wall and the skin.

With respect to water flow at the edge of the oral cavity, recordings of reservoir mass loss show that 'compression' can be associated with flow in either direction or, as suggested by sealing models (Kardong and Haverly, 1993; Berkhoudt et al., 1995), with no flow at all. As explained in the Materials and methods section, rapid cycling may conceal short periods of stasis. Slower cycling, however, should show stasis or reversals if they occur. In most of the viperid and colubrid species, some immersions showed short periods of drinking in which there were no periods of stasis (e.g. the 'early' trace in Fig. 5) and mouth closing and closure lasted at least 0.5 s, approximately twice the time necessary for the balance response (see Fig. 2). During these periods, the mass of the reservoir decreased continuously, i.e. during both opening and closing of the mouth.

Kinematic changes over time

Mandibular movements and cycle duration from the first and second halves of 13 immersions lasting more than 500 cycles show a trend for cycle duration to increase over time (10-cycle duration during first half of immersion 9.96 s, during second half of immersion 10.74 s, t=–4.29, d.f.=81; P<0.01). Mandibular excursion increases but not significantly (first half mean 19.7 % of snout height, second half mean 20.2 %, t=–0.58, d.f.=81, P=0.56). When booids, viperids and colubrids are examined separately, essentially the same pattern holds except that the single viper (*Crotalus horridus*) does not show a significantly longer cycle duration during the second half of the immersions. Given that the average increase in cycle duration is less than 0.1 s per cycle and that mandibular excursion tends to increase rather than decrease over time, snakes show no evidence of fatigue even during very long immersions.

Kinematic differences among snakes

Boa constrictor, *Epicrates cenchria* and *Python regius* all use the kinematic pattern described by Kardong and Haverly (1993) as characteristic of *Boa constrictor*. The mandibular, quadrate and supratemporal movements that can be detected in video recordings all agree with the analysis of Kardong and Haverly (1993), and the tongue appears in the lingual groove during closure in most but not all cycles. In some cycles during some immersion periods, the edges of the labial scale rows did not seal during closure, a feature most prominent in *Python regius* but also seen in the single *Boa constrictor* examined. This was not correlated with changes in volume transported per cycle.

Most of the colubroids examined showed mandibular and quadrate movements similar in pattern to those described for *Boiga irregularis* by Berkhoudt et al. (1995). The major differences among snakes and between my data and those of Berkhoudt et al. (1995) relate to the extent of mandibular excursion, the behaviour of the upper jaw and snout and the use of lip sealing.

Mean mandibular excursions as a function of snout height

Table 4. *Mandibular displacements during drinking in 23 snakes arranged in order by mean value and by Kruskal–Wallis rank*

Snake	Mean	Range	Snake	Mean Kruskal–Wallis rank
1. *Boa constrictor*	0.03±0.01	0.01–0.04	1	13.7
2. *Epicrates cenchria*	0.04±0.02	0.01–0.08	2	17.7
3. *Python regius* 1	0.06±0.03	0.03–0.11	3	31.7
4. *Python regius* 3	0.07±0.02	0.03–0.08	4	33.1
5. *Python regius* 2	0.08±0.05	0.03–0.20	5	39.6
6. *Lampropeltis getula*	0.12±0.04	0.08–0.20	6	62.6
7. *Elaphe obsoleta* 2	0.18±0.05	0.09–0.25	7	93.5
8. *Crotalus mitchellii*	0.19±0.05	0.13–0.25	8	94.8
9. *Elaphe guttata*	0.20±0.07	0.09–0.32	9	103.0
10. *Elaphe obsoleta* 1	0.20±0.03	0.16–0.25	10	104.2
11. *Farancia abacura* 1	0.22±0.11	0.11–0.44	11	111.2
12. *Nerodia sipedon* 3	0.23±0.07	0.15–0.32	12	118.8
13. *Agkistrodon piscivorus* 1	0.25±0.05	0.20–0.33	13	136.5
14. *Agkistrodon piscivorus* 2	0.27±0.07	0.17–0.40	14	140.8
15. *Nerodia sipedon* 2	0.29±0.11	0.20–0.56	15	151.4
16. *Crotalus viridis*	0.29±0.05	0.21–0.38	18	155.0
17. *Nerodia rhombifer* 2	0.31±0.07	0.21–0.42	16	160.1
18. *Nerodia fasciata* 1	0.31±0.13	0.18–0.61	21	160.9
19. *Nerodia sipedon* 1	0.32±0.07	0.23–0.43	17	162.0
20. *Nerodia fasciata* 2	0.34±0.09	0.24–0.58	19	171.3
21. *Farancia abacura* 2	0.35±0.16	0.15–0.60	20	178.6
22. *Nerodia rhombifer* 1	0.49±0.05	0.42–0.57	23	202.4
23. *Crotalus horridus*	0.51±0.19	0.19–0.78	22	214.5

Mean values are given ± S.D.
Mandibular excursion is measured as a proportion of snout height.

Table 5. *Mann–Whitney* U *pairwise comparisons of volumes per cycle and adjusted volumes per cycle for immersions by families*

Family	*N*	Mean	S.D.	*P* of pairwise comparisons: Boid	Python	Viper
Volume per cycle						
Boidae	72	0.024	0.019			
Pythonidae	43	0.100	0.142	<0.01		
Viperidae	163	0.115	0.103	<0.01	<0.01	
Colubridae	217	0.119	0.114	<0.01	<0.01	0.36
Adjusted volume per cycle						
Boidae	72	0.091	0.088			
Pythonidae	43	0.180	0.290	0.08		
Viperidae	163	0.191	0.196	<0.01	0.07	
Colubridae	217	0.265	0.237	<0.01	<0.01	<0.01

Adjusted volume is the water volume normalized to a body mass of 1 kg.

varied from 3% in *Boa constrictor* to 51% in *Crotalus horridus* (Table 4). Kruskal–Wallis analysis of variance (ANOVA) showed significant differences among snakes (χ^2=176.6, d.f.=22, P<0.01), and Kruskal–Wallis ranks correspond closely to ranks based on means (Table 4). Pairwise Mann–Whitney tests show that booids use significantly smaller mandibular excursions than do the other snakes (Mann–Whitney U=21.5 between *P. regius* 2, which gave the highest value for booids, and *L. getula*, which gave the lowest value for colubroids; P=0.03). Within colubroids, however, individuals of the same species differ almost as much as do different species of a genus. It is particularly striking that the three individuals representing three species of *Crotalus* nearly span the range of values for colubroids.

In booids, small movements of the mandibles are matched by equally small movements of other parts of their heads. In colubroids, however, mandibular adduction during mouth closure is often accompanied by raising of the snout and by abduction and elevation of the maxillae. The whole head flattens at the end of closure, and the quadrates and rear ends of the mandibles flare laterally. As mouth opening begins, the snout and mandibles drop, and the maxillae and quadrates move medially, making the head more rounded in anterior view.

Although most colubroids show no evidence of the rhythmic tongue movements that characterise booid drinking, such movements are occasionally seen in both *Farancia abacura* and some *Nerodia* species. The pattern is readily visible, the tongue emerging quickly during closing and lying in the lingual groove at closure. It is retracted slowly during early opening as it is in booids. An alternative tongue cycle, in which the tongue emerges during opening and is retracted during closing, is typical of tongue-flicking cycles presumably used for vomolfaction, and most snakes used these occasionally but very infrequently when drinking.

In species of *Nerodia*, *Farancia* and *Crotalus*, the anterior mouth sometimes remained partly open at the end of closing cycles. Lip sealing did not occur, and the mucosal membranes associated with the tooth rows did not meet anteriorly, although water flow into the snake often continued.

Water flow differences among snakes

Kinematic differences could translate to differences in the volumes moved per cycle by different snakes. Pairwise comparisons of conspecific individuals for adjusted volumes per cycle showed that most pairs differ significantly. Exceptions are the two *Elaphe obsoleta* and the two *Nerodia fasciata*. Comparing congeneric species (*Crotalus*, *Elaphe* and *Nerodia* species), all *Crotalus* species pairs do not differ significantly. The two *Elaphe* species differed significantly and *N. rhombifer* was significantly different from both *N. fasciata* and *N. sipedon*. Differences among individuals could reflect the absence of any phylogenetic signal in volumes moved per cycle despite the differences in kinematic pattern between booids and colubroids. However, the kinematic differences are reflected in the volumes of water transported (Table 5). Boids transport significantly less per cycle than colubroids but not

significantly less than pythonids, and pythonids and viperids are also indistinguishable, although both move significantly less water per cycle than colubrids.

Discussion

Kinematics and water transport

The data reveal no simple relationship between kinematics and water transport. All snakes show the same kinds of variations, regardless of phylogenetic relationship, and despite adhering closely to the general kinematic models described by Kardong and Haverly (1993) and Berkhoudt et al. (1995). Suction appears to be the general mechanism for getting water into the mouth. After the water has entered the mouth, it can either be moved into the oesophagus or returned to the environment. If water enters the oesophagus, it can either be swallowed or returned to the mouth and external environment. These options are exercised irregularly with no obvious change in kinematic pattern.

Kardong and Haverly (1993) presented one model of alternating sequential suction and compression cycles. Their model should produce cyclic transport profiles, possibly with short periods of transport stasis at the transition from suction to compression. Kardong and Haverly (1993) and Berkhoudt et al. (1995) stressed that the edge of the oral cavity must be sealed during compression, either by the tongue (*Boa constrictor*) or the mental scale (*Boiga irregularis*), to leave the oesophagus as the only route for water flow. The cavity edge was assumed to be the labial scales and possibly the mucosa at the lateral tooth rows. Both studies assumed suction and compression to be driven by movements of the mandibles and intermandibular soft tissues that changed the volume of the oral cavity. Bels and Kardong (1995) provided additional radiographic support for this model based on less than 1 min of drinking in one specimen of *Elaphe obsoleta*. However, their Fig. 2 shows several oropharyngeal cycles preceding, and not matched by, oesophageal sphincter cycles, suggesting possible periodic decoupling of oral and oesophageal cycling.

All boids and pythonids so far examined use tongue movements similar to those described by Kardong and Haverly (1993), and most colubroids lifted the mental scale prior to closure so that the lingual groove was sealed for at least 15–60 ms before the mental scale flipped ventrally to initiate opening. Although the kinematic pattern does not fit exactly the timing described for *Boiga irregularis* by Berkhoudt et al. (1995), the net result is the same. If the mouth closed (it sometimes is not), the lifted mental scale fitted it into the lingual groove of the opposing rostral scale, presumably sealing the lingual canal. However, the occasional absence of complete closure but continued transport of water, the tiny volumes of water transported and the frequent outflow of water after suction (Figs 5, 6) suggest that one or more other models must be working some of the time. To account for all the data presented here, snakes must use a number of pumping mechanisms that differ in critical features.

The most common deviation from the model of Kardong and Haverly (1993) is a drinking pattern in which much of the water taken in during opening is released during closing. This model simply requires that the mouth is not sealed for most of the time it is closed. Raising the floor of the mouth during closing would force water out of the mouth as long as the edges of the mouth were unsealed and the oesophagus generated no suction. Subtle modulation of movements of the floor of the mouth and oesophagus could account for the varying volumes of water transferred from the oral cavity to the oesophagus (Figs 5, 6).

To account for water flow that appears continuous (Fig. 5), water must be imbibed during both opening and most of closing. An oral–oesophageal peristaltic model in which a region of expansion travels from the front of the oral cavity to its rear in a continuous wave could account for this flow pattern. This model is possible despite the relative rigidity of the mandibles because the intermandibular tissues are flexible and the mandibular suspension is mobile in snakes. The curvature of the mandibles and their rotation around their long axes in addition to simple adduction–abduction movements provide the potential for complex changes in oral cavity shape (Kardong and Haverly, 1993; Berkhoudt et al., 1995). In this model, there need be no actual sealing of the edges of the mouth. A posteriorly travelling region of constriction lying anterior to the region of expansion would retard backflow of water. This model is essentially the same as that illustrated by Kardong and Haverly (1993) in their Fig. 7 but with (i) either no anterior sealing or a much shorter period of sealing, and (ii) with a shorter period of closure at the oesophageal sphincter.

This model fits some aspects of the kinematics, particularly the slow but more or less continuous motions of the caudal ends of the mandibles and the floor of the mouth. It also accords loosely with the pressure profile of the ‘posterior throat’ given by Kardong and Haverly (1993). In many recordings, the anterior tips of the mandibles move for only part of the cycle (0.5–0.8 of total cycle duration, as can be inferred from the boundaries between opening and closing in Figs 5, 6), but lateral and medial movements at the quadrate appear continuous and fill the cycle. These latter movements both drive and delimit the kinematic cycle and occur even when the anterior ends of the mandibles appear to be stationary, as in booids. The existence of a rolling pressure wave (or negative pressure region) is consistent with data provided by Kardong and Haverly (1993), Bels and Kardong (1995) and Berkhoudt et al. (1995), but is only loosely concordant with tongue and hyoid motions. However, a similar model was proposed for drinking in *Varanus exanthematicus* on the basis of cineradiographic evidence of waves of water progressing through the oral cavity and into the pharynx (Smith, 1986). These data for *Varanus exanthematicus* showed no correlation between water flow and hyoid movements. *Ctenosaura similis*, *Tupinambis nigropunctatus* and *Lacerta viridis*, in contrast, collect water by lapping (Smith, 1984; Bels et al., 1993). In *Lacerta viridis*, tongue and throat movements correlate with increases in the volume of water stored in the buccal chambers (Bels et al., 1993). In *Varanus*

exanthematicus and *Lacerta viridis*, and presumably in other scleroglossan lizards, water collected in the gular region is moved into and through the oesophagus by raising the head and lifting the hyoid, a mechanism similar to tip-up drinking in birds (Zweers, 1992).

A corollary of both models is that movement of water into the oesophagus requires the active participation of the oesophagus. Either the oesophagus has a sphincter to prevent backflow of water (Bels and Kardong, 1995) or it generates suction during periods when inward water flow occurs during both opening and closing. The independence of oesophageal and oral kinematic cycles is most graphically demonstrated in those immersions characterised by periodic massive outflows of water (Fig. 9).

Variations in drinking behaviour

Both Kardong and Haverly (1993) and Berkhoudt et al. (1995) treated drinking as a relatively uniform behaviour. Berkhoudt et al. (1995) analysed three cycles from the beginning, middle and end of an unspecified number of immersions and found that the frequency of kinematic cycling increased over time but that the amplitude of mandibular movement decreased, the opposite of the results obtained here for very long immersions. Inasmuch as their recorded variation in immersion duration was 40–80 cycles, the patterns they found appear to reflect small sample sizes and, perhaps, artefacts of their methods (recording drinking the same day that snakes had been subjected to anaesthesia and surgery for electrode implantation). None of the snakes examined here showed such limited immersion duration and none showed consistent patterns of kinematic change over short periods. Furthermore, the range of volumes per cycle given for one *Boa constrictor* by Kardong and Haverly (1993), and considered large when this project was begun, grossly underestimated the potential variation.

Variation in drinking patterns may be an intrinsic element of the behaviour of the snake, but it is also likely to be influenced by the duration of water deprivation. Different snake species suffer different rates of evaporative water loss (Mautz, 1982), and there may be a complex relationship between water relations and a host of environmental factors and food intake (Minnich, 1982). Myer and Kolwell (1971) showed that snakes typically drink an amount proportional to the loss in body mass during water deprivation and that their latency to begin drinking decreased as the length of deprivation increased. Whereas some, perhaps most, of the variation in total volumes consumed and cycle numbers within snakes undoubtedly reflects differing deprivation periods and conditions, volume per cycle variations show no patterns attributable to deprivation except in *Farancia abacura*. Massive outflows occurred primarily during long immersions following body mass losses of 10–12 %, never during short immersions or during drinking following body mass losses of 5 % or less. Although water expulsion in the turtle *Malaclemys terrapin* has been attributed to disturbance during drinking (Bels et al., 1995), its cause in snakes remains unclear.

Differences in normal use of water in the field may underlie some of the variations among the snakes examined. *Agkistrodon piscivorus*, all *Nerodia* species and *Farancia abacura* are semi-aquatic taxa that forage in or near water (Conant and Collins, 1998). Other species, such as *Boa constrictor* and *Crotalus mitchellii*, may endure long periods in captivity without water, show low rates of mass loss during water deprivation, and presumably regain water from their food (D. Cundall, personal observation). Drinking patterns in squamates generally may be diverse. The Australian agamid lizard *Moloch horridus* channels water condensing on its skin to its mouth (Gans et al., 1982), and a desert viper (*Bitis peringueyi*) is known to drink condensation droplets off its skin (Robinson and Hughes, 1978). However, even if the snakes recorded here exhibited diverse patterns of drinking behaviour in the field, that diversity would not explain the low correlation between kinematics and water intake in all the snakes.

Drinking performance in other vertebrates remains largely unexplored. Cameron et al. (1999) recently showed that time spent suckling does not predict volumes of milk intake in suckling foals, but no measurements were made to test relationships between suckling kinematics and milk volume gained. Most drinking studies do not measure fluid intake, and the few that have (e.g. Kooloos and Zweers, 1989; Kardong and Haverly, 1993) have simply measured total fluid lost from a reservoir during a drinking bout or immersion.

Comparative performance of drinking and feeding

Although *Boa constrictor* may drink without submerging its head (Kardong and Haverly, 1993), and all snakes could potentially ventilate their lungs if the external nares were not submerged by inserting the glottis into the nasopharyngeal duct (Kardong and Haverly, 1993), most of the snakes recorded occasionally drank with the entire head submerged. Kinematic cycling occurred in most snakes regardless of the position of their mouth and external nares. In other words, they continued to drink regardless of whether they could ventilate the lungs. The fact that some snakes drank without ventilating for periods in excess of 30 min, and one for 56 min, indicates that drinking is metabolically cheap.

Electromyographic recordings of drinking given by Berkhoudt et al. (1995) showed that most of the muscles from which recordings were made had some level of activity. Exceptions that remained silent were the adductor externus profundus and cervicomandibularis. Berkhoudt et al. (1995) did not compare electromyograms of drinking with those for feeding in the same animal but unpublished electromyograms recorded by me in the late 1970s and early 1980s for *Agkistrodon piscivarus*, *Elaphe obsoleta* and *Heterodon platirhinos* showed that muscle activity during drinking was only a fraction of the amplitude and duration typical of feeding.

Feeding, in contrast to drinking, is invariably associated with prominent periods of ventilation, particularly during transport of prey of relatively large diameter or large mass (D. Cundall, personal observation). In addition, apart from manipulatory movements at the beginning of transport that

may appear to have no obvious product, most kinematic events during feeding have a measurable product in that they move the head of the snake some distance over the prey.

Role of the oesophagus

Snakes are similar to some other terrestrial vertebrates, such as tip-down drinking birds (Homberger, 1980; Zweers, 1992) and most mammals (Hiiemae and Crompton, 1985), in that their oesophagus may be kept continually elevated relative to their mouth during drinking. Unlike birds and mammals, however, snakes use very slow oral cycles to get water into the mouth and cannot drive water into the oesophagus by ballistic lingual pumping, as in some endotherms (Zweers, 1992). The available pharyngeal collection chambers in snakes appear to be structurally limited in size, preventing oral collection of water as in some lizards (Smith, 1984, 1986; Bels et al., 1993), birds (Zweers, 1992) and mammals (Hiiemae and Crompton, 1985; German and Crompton, 1996). As a result, swallowing water in snakes could involve oral compression, oesophageal suction and compression, and oesophageal valves that prevent backflow of water from the oesophagus to the mouth.

Kardong and Haverly (1993) found both compressive cycling and radiographic evidence of an oesophageal valve (the oesophageal sphincter, shown in their Fig. 7), but were unable to find a structure in a preserved boa that correlated with the position of the radiographic sphincter. Bels and Kardong (1995) provided further radiographic evidence of an oesophageal sphincter in the colubrid *Elaphe obsoleta*, but could find no anatomical evidence of a sphincter in this species either. I have been similarly unable to find any structure that approximates a sphincter in hemisected heads of *Python molurus* (Lehigh University 1093), *Agkistrodon piscivorus* (LU 2320, 2321) or *Nerodia fasciata* (LU 2322), nor is there evidence of intrinsic musculature that might form such a sphincter. Instead, there is a loose transverse fold in the oesophageal wall at this position that may interdigitate longitudinal mucosal folds on the dorsal wall with similar mucosal folds on the ventral wall. The transverse fold may serve a sphincter-like function that diminishes in effectiveness as water volume or mass increases behind or above it when the head and oesophagus are tilted down. In most snakes, the anterior throat region can be seen to swell during drinking, and this swelling always disappears in those instances when snakes added appreciable amounts of water to the reservoir. Interestingly, the radiographs of Bels and Kardong (1995) do not support the idea that the oesophagus actually fills with water. Instead, their images, drawn from only the first seven cycles of a single immersion, suggest that the oesophagus is in the form of a wide inverted U and that, during oesophageal filling, water occupies the width of the oesophagus without causing appreciable separation of the dorsal and ventral surfaces. If this is the case, capillarity may play a role in water transport.

Phylogenetic patterns

Apart from the brief comparisons of Berkhoudt et al. (1995), there have been no detailed comparisons of drinking behaviour among different snake taxa. The results for the booids examined here agree with the description by Kardong and Haverly (1993) in using small mandibular excursions and tongue protrusions at the end of closing. Tongue cycles in booids are matched to prominent hyoid movements that include a rapid antero-posterior twitch as the tongue is protruded. This hyoid movement was not seen in colubroids, and its relationship to drinking in booids remains obscure.

The significant differences in mandibular movement patterns that exist between booids and colubroids do not correlate with significant differences in the way the two groups handle water. In both groups, variation within individuals is very high and correlations between kinematic events and water movement are very low. Hence, although the observable kinematic patterns in the two clades are different, some essential features of drinking are similar. This presumably arises from the basic similarity in body form, the small metabolic costs of drinking and the fact that both clades use relatively slow cycle rates linked to suction-driven mechanisms. Possibly, drinking is driven by soft tissue movements that occur independently of skeletal movements.

Varanus exanthematicus appears to use cycle rates equivalent to, but move volumes of water greater than, those of snakes of the same body mass (Smith, 1986). Smith (1986) also noted that *Varanus exanthematicus* usually uses small tongue movements during drinking, but it is not clear whether these movements are similar to those used by booids. The absence of lapping and the apparent use of suction by *Varanus exanthematicus* could support hypotheses of a close relationship between snakes and varanoid lizards (e.g. Lee, 1998). However, *Varanus exanthematicus* moves water from the phaynx to the oesophagus by tipping the head up (Smith, 1986), unlike the methods of oesophageal filling used by snakes. Drinking pattern similarities shared by *Varanus exanthematicus* and snakes could as easily derive from behavioural convergences associated with tongue modifications for vomolfaction (Schwenk, 1995).

Booids and lapping scleroglossan lizards all use rhythmic tongue movements during drinking (Smith, 1984; Kardong and Haverly, 1993; Bels et al., 1993). Although this appears to be a behavioural similarity, lapping lizards protract the tongue as jaw opening begins, whereas booids protract the tongue as jaw closing ends. Thus, there is a fundamental rearrangement of tongue motor patterns in booid drinking unrelated to either tongue-flicking during vomolfaction or to scleroglossan lapping. Until aspects of varanid drinking are clarified and a greater diversity of snakes are examined, it must be assumed that there are no snakes that show a lizard-like drinking pattern.

The suggestion of Homberger (1983) that drinking mechanisms are cobbled together using an apparatus shaped by adaptive responses to feeding, an argument she applied originally only to birds, seems to be partially supported by kinematic patterns in snakes. Virtually every feature of the head of a snake has been interpreted as an adaptive response to feeding requirements, and it seems unlikely that the same

set of structures serves as an optimal device for drinking. However, few structural systems achieve optimality for any one function because few biological systems have the luxury of doing only one thing (e.g. Gans, 1983). What is puzzling about drinking in snakes is that the performance of the system rarely approaches its potential, regardless of the limitation of potential through adaptive design for other functions such as feeding. Hence, from the perspective of musculoskeletal structure and function, the head of a snake appears to consist of two partially overlapping but identifiably different functional units (Schwenk, 2000), one of which (the feeding unit) rarely operates at its potential because of the distribution of shapes and sizes of available prey, while the other (the drinking unit) rarely operates at its potential for reasons currently not understood.

Many snakes are small to moderate-sized predators that are themselves subject to predation (Greene, 1997). Drinking must often involve exposure. Because a reduction in the duration of exposure should decrease the probability of being eaten, one might then predict that increased drinking efficiency would have been selectively favoured in snakes. Of various possible explanations for the lack of efficiency, the most appealing are that captivity changes drinking behaviour or that drinking plasticity simply matches water fluidity. In other words, water can be gained in any shape and quantity, and its fluid nature releases the system from size and shape constraints. Furthermore, as noted by M. S. Y. Lee (personal communication), once water is found, it is likely to be available for as long as it takes a snake to recover volumes lost, regardless of the efficiency of the drinking mechanism. As a result, drinking, despite its essential nature, cannot be assessed using optimisation models (Seger and Stubblefield, 1996). The structure–function matching models that functional morphologists invoke with some hazard (e.g. Lauder, 1996) may apply even less to drinking than to other functions.

Kinematic differences between booids and colubroids cannot be easily correlated with morphology, feeding mechanics or current hypotheses of phylogeny. Two possibilities are (i) that the similarities in feeding mechanics represent convergences and that the differences in drinking reflect an underlying deep divergence between booids and other snakes or (ii) that booids and colubroids independently evolved a very different drinking kinematic pattern. Currently, there are too few data on drinking in other snake taxa to provide a meaningful map of the distribution of behavioural states within the clade.

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References

Auffenberg, W. (1981). *The Behavioral Ecology of the Komodo Monitor*. Gainesville, FL: Univerity of Florida Press.

Bels, V. and Kardong, K. V. (1995). Water drinking in snakes: evidence for an esophageal sphincter. *J. Exp. Zool*. **27**, 235–239.

Bels, V. L., Davenport, J. and Renous, S. (1995). Drinking and water expulsion in the diamondback turtle *Malaclemys terrapin*. *J. Zool., Lond*. **236**, 483–497.

Bels, V. L., Goosse, V. and Kardong, K. V. (1993). Kinematic analysis of drinking by the lacertid lizard, *Lacerta viridis* (Squamates, Scleroglossa). *J. Zool., Lond*. **229**, 659–682.

Berkhoudt, H., Kardong, K. V. and Zweers, G. A. (1995). Mechanics of drinking in the brown tree snake, *Boiga irregularis*. *Zoology* **98**, 92–103.

Cameron, E. Z., Stafford, K. J., Linklater, W. L. and Veltman, C. J. (1999). Suckling behavior does not measure milk intake in horses. *Anim. Behav*. **57**, 673–678.

Conant, R. and Collins, J. T. (1998). *A Field Guide to Reptiles and Amphibians: Eastern and Central North America*. Third edition. Revised. Boston: Houghton-Mifflin.

Cundall, D. (1987). Functional morphology. In *Snakes: Ecology and Evolutionary Biology* (ed. R. A. Seigel, J. T. Collins and S. S. Noval), pp. 106–140. New York: Macmillan.

Cundall, D. and Greene, H. W. (2000). Feeding in snakes. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 293–333. San Diego: Academic Press.

Gans, C. (1983). On the fallacy of perfection. In *Perspectives on Modern Auditory Research: Papers in Honor of E. G. Wever* (ed. R. R. Fay and G. Gourevitch), pp. 101–114. Groton, CT: Amphora Press.

Gans, C., Merlin, R. and Blumer, W. F. C. (1982). The water-collecting mechanism of *Moloch horridus* re-examined. *Amphib.-Rept*. **3**, 57–64.

German, R. Z. and Crompton, A. W. (1996). Ontogeny of suckling mechanisms in opossums (*Didelphis virginiana*). *Brain Behav. Evol*. **48**, 157–164.

Gove, D. (1979). A comparative study of snake and lizard tongue-flicking, with an evolutionary hypothesis. *Z. Tierpsychol*. **51**, 58–76.

Greene, H. W. (1997). *Snakes: The Evolution of Mystery in Nature*. Berkeley: University of California Press.

Hiiemae, K. M. and Abbas, P. (1981). Viscosity as a regulator of lapping in cats. *J. Dent. Res*. **60**, 474.

Hiiemae, K. M. and Crompton, A. W. (1985). Mastication, transport and swallowing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 262–290. Cambridge, MA: Belknap Press.

Homberger, D. (1980). Funktionell-morphologische Untersuchungen zur Radiation der Ernahrungs- und Trinkmethoden der Papageien (Psittaci). *Bonn. Zool. Monogr*. **13**, 1–92.

Homberger, D. (1983). Nonadaptive evolution of avian drinking methods. *Am. Zool*. **23**, 894.

Kardong, K. V. and Haverly, J. E. (1993). Drinking in the common boa, *Boa constrictor*. *Copeia* **1993**, 808–818.

Kooloos, J. G. M. and Zweers, G. A. (1989). Mechanics of drinking in the mallard (*Anas platyrhynchos*, Anatidae). *J. Morph*. **199**, 327–347.

Lauder, G. V. (1996). The argument from design. In *Adaptation* (ed. M. R. Rose and G. V. Lauder), pp. 55–91. San Diego: Academic Press.

Lee, M. S. Y. (1998). Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biol. J. Linn. Soc*. **65**, 369–453.

Mautz, W. J. (1982). Patterns of evaporative water loss. In *Biology of the Reptilia*, vol. 12 (ed. C. Gans and F. H. Pough), pp. 443–481. New York: Academic Press.

Minnich, J. E. (1982). The use of water. In *Biology of the Reptilia*, vol. 12 (ed. C. Gans and F. H. Pough), pp. 325–395. New York: Academic Press.

Myer, J. S. and Kowell, A. P. (1971). Loss and subsequent recovery of body weight in water-deprived snakes (*Elaphe obsoleta obsoleta*). *J. Comp. Physiol. Psychol*. **75**, 5–9.

Robinson, M. D. and Hughes, D. A. (1978). Observations on the natural history of Peringuey's adder, *Bitis peringueyi* (Boulenger) (Reptilia: Viperidae). *Ann. Transvaal Mus*. **31**, 189–193.

Schwenk, K. (1995). Of tongues and noses: chemoreception in snakes and lizards. *Trends Ecol. Evol.* **10**, 7–12.

Schwenk, K. (2000). Functional units and their evolution. In *The Character Concept in Evolutionary Biology* (ed. G. P. Wagner). San Diego: Academic Press (in press).

Seger, J. and Stubblefield, J. W. (1996). Optimization and adaptation. In *Adaptation* (ed. M. R. Rose and G. V. Lauder), pp. 93–123. San Diego: Academic Press.

Smith, K. K. (1984). The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*). *J. Zool., Lond*. **202**, 115–143.

Smith, K. K. (1986). Morphology and function of the tongue and hyoid apparatus in *Varanus* (Varanidae, Lacertilia). *J. Morph*. **187**, 261–287.

Zweers, G. A. (1982). Drinking in the pigeon (*Columba livia*). *Behaviour* **80**, 274–317.

Zweers, G. A. (1992). Behavioral mechanisms of avian drinking. *Neth. J. Zool*. **42**, 60–84.