

Feeding Begets Drinking: Insights from Intermittent Feeding in Snakes

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Summary Statement: I quantified freshwater drinking in relation to feeding in four species of snakes and report that postprandial relative to preprandial drinking is greater in all species, indicating that meal digestion increases the physiological requirement for water.

ABSTRACT

An important question related to survival of dehydrating animals is whether feeding provides a net gain of water — contributing postprandial free water and metabolic water — or, alternatively, whether digestion and assimilation of ingested food incur a net loss of water because of requirements for digestion and the excretion of resulting metabolic wastes. Here I address the question whether voluntary drinking increases or decreases following the ingestion of food. Increased postprandial drinking implies that food consumption increases rather than decreases the requirement for free water, whereas decreased postprandial drinking suggests there is a net profit of water from food. Snakes are ideally suited for such inquiry because they feed intermittently, and the temporal separation of meals allows relatively clear examination of the associated patterns of pre- and postprandial drinking. Voluntary drinking associated with meal consumption was quantified during consecutive feeding trials in four species representing two families of snakes. Postprandial relative to preprandial drinking increased in all four species, indicating that eating increases the physiological requirement for water. These data add to a growing literature pointing to some generality that eating can have negative rather than positive consequences for fluid homeostasis in some dehydrating animals.

INTRODUCTION

Water is essential to life and is procured by drinking in many terrestrial animals. However, various species living in arid environments have been shown to rely heavily on dietary and metabolically produced water, and in some species these totally satisfy water requirements (Nagy and Gruchacz, 1994; Znari and Nagy, 1997). Many desert and marine reptiles have been thought to live independently of drinking from free water sources (Randall et al., 2002). However, binge drinking in response to dehydration has been documented in some species (Bonnet and Brischoux, 2008; Davis and DeNardo, 2007), and in others free-standing water for drinking is necessary for achieving a net profit of energy from feeding (Peterson, 1996). Moreover, water supplementation leads to greater food acquisition in Gila monster lizards that are subjected to seasonal drought in arid environments (Davis and DeNardo, 2009).

Reliance on dietary water (present in food) can influence foraging behaviours, and some species shift to dietary items having greater water content when free water in the environment becomes increasingly limited (e.g., Nagy and Gruchacz, 1994). Such behaviour is most characteristic of herbivorous animals, however, and carnivorous reptiles may not have such options available to them. While the prey of many reptiles generally contains 60 to 75% water content, it is not clear whether consumption of prey can satisfy water requirements when sources of free drinking water are scarce or absent.

One important question related to water balance and the survival of animals is whether ingestion of food suffices for, or supplements, the water needs of an animal, contributing both free water and metabolic water as a result of digestion and metabolism. Alternatively, might the digestion and metabolism of ingested food increase the need for water because it is required for digestion and the excretion of resulting metabolic wastes, especially the nitrogenous products from protein metabolism? Additional evaporative losses of water might

occur during the behavioural activities associated with foraging and capture of prey and possibly postprandial elevation of body temperature (e.g., Tattersall et al., 2004).

Here I address the question whether voluntary water consumption increases or decreases following the ingestion and processing of meals. Increased ingestion of water associated with feeding implies that food consumption increases rather than decreases requirements for free water, whereas decreased ingestion of water suggests there is a net profit of water from food. Snakes are ideally suited for such inquiry because they are intermittent feeders. Hence, the temporal separation of feeding events allows relatively clear examination of associated patterns of drinking and consumption of water.

MATERIALS AND METHODS

Background for rationale and design of experiments

During the course of keeping numerous snakes in captivity for scientific research, I have observed that voluntary drinking of water appears to increase following the consumption of meals. This was a subjective impression, however, so I quantified drinking associated with meal consumption in four species of snakes: yellow rat snakes (*Pantherophis alleghaniensis*), California king snakes (*Lampropeltis californiae*), banded water snakes (*Nerodia fasciata*), and Florida cottonmouths (*Agkistrodon conanti*). The former three species are members of the family Colubridae, whereas the cottonmouth is a member of Viperidae. The availability of animals was opportunistic and related to other projects. However, I quantified drinking in several species in order to examine some generality of responses that are here quantified following my subjective impressions. The care and experimental use of animals were with the approval of and within institutional guidelines of the NASA Ames Research Center and the University of Florida. Data will be provided by the author upon request.

Feeding and drinking experiments

Snakes were kept individually in plexiglass cages with floors that were covered with newspaper, and no other object was inside the cage during periods between drinking bouts. Periodically (see below) I provided individual snakes access to water. All snakes were maintained in rooms with controlled temperatures $\sim 25^{\circ}\text{C}$. Mean temperature was $24.6 \pm .08^{\circ}\text{C}$ for king snakes, $25.3 \pm .09^{\circ}\text{C}$ for cottonmouths, $24.6 \pm .06^{\circ}\text{C}$ for water snakes, and $24.2 \pm .04^{\circ}\text{C}$ for the single water snake that was tested separately (see below). Room temperature varied between 23 and 28°C for rat snakes (a record is not available for averaging; see Conklin et al., 1996). Mean relative humidity was $29.8 \pm .68$ RH for king snakes, 36.9 ± 1.49 RH for cottonmouths, $41.5 \pm .35$ RH for all water snakes, and $30.18 \pm .53$ RH for the single water snake that was tested separately (see below). For all groups of snakes, there was no significant correlation between the amounts of water drunk and either temperature, RH, or calculated ambient water vapor pressure.

Data for 11 *Pantherophis alleghaniensis* were collected during a research project at NASA Ames Research Laboratory, Mountain View, California. Each snake was offered fresh water for drinking every three days during an experimental period of eight weeks. Water was provided in a water bowl placed inside the cage with the snake. Each snake had its head gently lifted over the water bowl so that its flicking tongue contacted the water. Many times snakes drank immediately, but in other cases the water was left inside the cage for two hours while the snake was not disturbed. In order to estimate the amount of water consumed each snake was weighed to nearest 0.01 g before and after drinking. If drinking was not observed directly, a snake was weighed after being in the cage with water that was accessible for two hours. Care was taken during weighing to avoid agitating a snake or lowering its head to prevent the possible loss of ingested water from the mouth or anterior

digestive tract. The overall strategy was to weigh snakes after allowing sufficient time for ingested water to reach the stomach, while not yet stimulating urination or defecation. At specific intervals (see Fig. 2) each snake was fed 2–3 mice representing 12–26 % of its body mass.

Data for *Lampropeltis californiae* ($n = 10$), *Nerodia fasciata* ($n = 5$), and *Agkistrodon conanti* ($n = 8$) were collected during research projects conducted at the University of Florida. As with *Pantherophis*, each snake was kept in its own container and offered water at 3-day or weekly intervals during experimental periods of 9–11 weeks (Figs. 3–5). Snakes were fed periodically at variable intervals several weeks apart. At each feeding, two adult *Lampropeltis* were each fed 2–3 mice representing about 20 % of body mass; an additional eight baby snakes of this species were each fed a single “pink” neonatal mouse representing similar relative mass. *Nerodia* were fed goldfish representing 2.5–33.2 (mean \pm SE = 11.7 ± 2.6) % body mass. The *Agkistrodon* were each fed either 1–2 mice representing 12–18 % body mass, or fish representing 20–40 % body mass.

Because of uncertainties in drinking patterns related to defecations and urinations in *Nerodia fasciata* (see below), further detailed investigation was carried out using a single snake. This individual *N. fasciata* was weighed and offered water daily for 167 days during which it was fed goldfish (2–25, representing 0.5 to 7% body mass) at intervals of 21 to 48 days (Fig. 6). Drinking was not measured during a period of 17 days when the author was away from the laboratory.

RESULTS

General results

All snakes drank water at nearly every opportunity when it was provided (except for the single *Nerodia* that was offered water daily). Snakes drank more water after feeding

compared to before feeding (with exceptions discussed below). Across all species and a total of 104 drinking events before and after feeding, there were only three instances involving *Pantherophis*, nine involving baby *Lampropeltis*, four involving *Nerodia*, and one involving *Agkistrodon* in which the amount of water consumed before feeding exceeded that following the consumption of a meal. Thus, postprandial drinking exceeded preprandial drinking in 84% of the total individual drinking bouts. As in previous studies (Lillywhite et al., 2008, 2012, 2014a), snakes were judged to have drunk water if increases in mass were ≥ 1 g following access to water.

Species results

With respect to *Pantherophis alleghaniensis*, the amount of water consumed during three days before and three days after feeding was averaged for the three feeding trials, and the means were used to compare the change in drinking for each individual snake. Thus, each mean provided a single measure for drinking before and after feeding for each individual. A paired *t*-test indicated that water consumed following feeding exceeded significantly the amount consumed before the meal, using comparable periods when snakes were without access to water ($P = 0.0003$). The pattern of drinking in relation to meal consumption is shown in Fig. 2. Note that the mean water consumption increased considerably following each of three meals during the course of the experiment.

Data were collected for two adult *Lampropeltis californiae*, and because of the small sample size the pattern of drinking and meal consumption is shown using the total amount of water that was drunk by both snakes during the points of measurement (Fig. 3a). The total amount of water consumed by the two snakes increases more than two-fold following feeding compared with before. After these data were collected, I procured eight baby *L. californiae* and ran additional trials with these. Similarly to adults, the mean water consumption

increased following each of five feeding events (Fig. 3b). Using the larger data set for the baby snakes, I compared the change in mean water consumption before and after feeding (as in *Pantherophis*). A paired *t*-test indicated that water consumed following feeding exceeded significantly the amount consumed before the meal, using comparable periods when snakes were without access to water ($P = 0.0017$).

As with *Pantherophis*, data for eight individuals of *Agkistrodon piscivorus* are plotted as the mean amount of water that was consumed by all of the snakes (Fig. 4). The amount of water that was drunk following feeding more than triples for each of the feeding trials. A paired *t*-test indicated that water consumed following feeding exceeded significantly the amount consumed before the meal, using comparable periods when snakes were without access to water ($P=0.0008$). During the trials with cottonmouths, four of the snakes did not eat in certain of the tests so data for post-meal drinking was not included for these individuals and particular trials. For all individuals, however, the amount of water that was drunk following eating exceeded the water that was drunk before eating.

Data for four *Nerodia fasciata* are shown in Fig. 5. With exception of the first feeding at day 10, drinking increased following feeding and decreased thereafter until the next feeding bout. The change of this pattern at day 10 is partly attributable to one snake not drinking during day 6 and subsequently drinking a larger volume than usual during day 9 that preceded the first feeding trial. With respect to the second feeding trial (day 22), two snakes urinated or defecated, and a third snake regurgitated several fish, thereby confounding the measurements of drinking in these snakes on day 24 following feeding. Drinking showed a very high increase on day 27, however, as shown in Fig. 5. Subsequently, drinking declined until the next feeding when the postprandial drinking again increased.

Because of the smaller sample size for *Nerodia*, these data were not subjected to statistical analysis. The amount of water that was drunk following eating exceeded the water that was drunk before eating except for three out of a total of 12 feeding events.

Drinking in *N. fasciata* was examined in further detail using a fifth individual snake for which drinking was quantified on a daily basis. Drinking occurred on 60% of the days that it was measured. The amount of water drunk was highly variable, representing generally a few to 7 or 8% of body mass (Fig. 6). The total water consumption was quantified for each 10-day period before and after feeding. Drinking increased after feeding to amounts ranging from 3.3% to 114.7% (mean % = 39.0 ± 0.3 SE) during four of five feeding trials, and it decreased by 28.0% in one feeding trial (day 150, Fig. 6). Over time, body mass declined in a relatively linear fashion except for abrupt increases after feeding (Fig. 6).

Evaporative and metabolic losses of mass in *Nerodia*

Data depicted in Fig. 6 enable estimates of evaporative and metabolic losses of mass to be discriminated. A simple linear regression of these data for mass changes reflects losses of mass attributable to substrate metabolism, assuming that losses of water in evaporation and excretion are made up by daily voluntary drinking. That is, with daily access to water the animal maintains a steady state with respect to water balance. However, the animal ingested fish over the experimental period, and the cumulative mass attributable to feeding must be taken into account. Assuming that 90% of the mass of ingested fish are incorporated into body tissue (Lillywhite, 2014), 90% of the cumulative mass of ingested fish can be subtracted from the ending mass of the snake to increase the magnitude of the slope of the regression, which then represents the losses of mass attributable to metabolism. That is, the snake is in water balance, and losses of mass are no longer confounded by consumption of food.

The daily loss of mass measured before the daily access to fresh water summed over the trial provides an estimate of the mean (\pm SE) daily water loss = 6.04 ± 0.43 g/day.

Comparison of this loss with the daily loss of mass attributable to metabolism (= 0.93 g/day, slope of regression) suggests that the metabolic component of mass loss is about 13% of the total.

A second method for estimating the evaporative loss of mass is to “correct” the regression by subtracting the cumulative volume of water that was drunk over the trial from the final mass at the end of the trial and computing a “corrected” slope (as above for the food that was eaten). This slope indicates a loss of mass attributable to water = $7.04 - 0.93 = 6.11$ g/day. This number compares favorably with the mean daily water loss estimate by direct measurement (6.04 g/day) described above. Both corrections of slopes neglect any correction for losses of mass attributable to excretion (which did not change the calculated slopes in separate regression analysis).

DISCUSSION

Dehydration, feeding and drinking

Terrestrial snakes are generally resistant to dehydration (Lillywhite, 2006), but in various habitats must cope with periods of prolonged drought from time to time. This is variably true for all four species that are included in this study. *Lampropeltis californiae* evolved in habitats with a Mediterranean climate where periods of drought can exceed more than half of the year or even longer in California. *Pantherophis alleghaniensis* occur in more mesic habitats in Florida (where specimens were collected), but they are highly arboreal and are also subject to periodic drought. The *Agkistrodon conanti* included in this study are from a coastal island in the Gulf of Mexico (Seahorse Key) where there is no permanent source of fresh water and periodic droughts can exceed six months or longer (unpublished

observations). Periodic drought can also affect *Nerodia fasciata*, although this amphibious species generally has access to water in characteristically mesic, freshwater habitats.

In this study I have quantified the voluntary drinking of water in captive snakes, and I have examined the pattern of drinking as it related to intermittent feeding. Changes in consumption of water related to feeding were discernible because of the periodic feeding that is characteristic of snakes, so consumption of food was separated in time as discrete events. Considering all the combined individual feeding trials that were conducted successfully and represented in the figures ($n = 104$), postprandial drinking of water increased in 84% of trials in individual snakes. Estimates of total body water in the two prey that were fed to snakes vary in the literature but are generally between 70–74% of body mass (Thorson 1961; Sheng and Huggins, 1979). Considering the variation in water consumption among individual snakes, small differences in the water content of total prey consumed are insignificant. Further evaluation relating postprandial water consumption and the water content of specific prey is beyond the scope of this study.

In the case of data for *Nerodia fasciata*, the pattern is somewhat less clear than in the other species, related at least partly to consumption of fish and smaller voluntary meals in comparison with the other species. The total water consumed did not increase following the first of three drinking bouts following feeding, although the postprandial increases were evident during the second and third feeding (Fig. 5). Overall with respect to this species, drinking increased following feeding in 75% of the feeding events featured in Fig. 5 and in 80% of the feeding events for the single individual featured in Fig. 6.

The clarity of drinking pattern is further illuminated for *N. fasciata* by inspection of Fig. 6, noting that increased consumption of water following feeding occurred over a period of some days rather than as single large drinks. This tends to increase or maintain mass for periods of about 12 to 16 days when food is being digested and assimilated (upper part of Fig.

6). This is likely also true for the other species, but the design of the drinking trials did not capture this detail.

Dividing all the respective measurements of daily loss of mass (before drinking) by the corresponding mass of the snake indicates that daily losses of water averaged 1.53 ± 0.5 % body mass per day. In comparison, daily loss of mass to evaporation in the amphibious sea krait *Laticauda semifasciata* was 0.98% body mass reported in a study by Lillywhite et al. (2008). Thus, not surprisingly, the mesic freshwater amphibious *N. fasciata* appears less resistant to evaporative water losses than is the marine amphibious *L. semifasciata*. These snakes are in different families, but this comparison nonetheless complements adaptive interpretations of the physiology (Lillywhite, 2006; Lillywhite et al., 2009).

Is there a net gain of water from feeding?

Three sources of water are generally available to animals: “dietary” water in food, “metabolic water” as a byproduct of metabolism, and “free” water that is present in the environment (e.g., rainfall, freshwater streams or ponds). Some species of terrestrial animals living in arid environments can rely on dietary and metabolic water and do not require free water in their environment for maintaining water balance, at least for short or moderate periods (Schmidt-Nielsen and Schmidt-Nielsen, 1951; Schmidt-Nielsen and Haines, 1964; MacMillen and Lee, 1967; Takie et al., 2012). Generally, these animals either are herbivores or they consume prey with relatively high content of water. The amount of water in food is greater, and protein less, in the diets of herbivores compared with carnivores. Several studies of carnivorous vertebrates suggest that free water in the environment is either required or critically important for water balance, even though other sources might also be significant (Peterson, 1966; Henen et al., 1998; Davis and DeNardo, 2009; Davis and DeNardo, 2010; Wright et al., 2013).

Given the variable dependence of vertebrates on drinking from sources of free water, the question arises whether consumption of food is beneficial or deleterious to water balance. Theoretical considerations as well as empirical data from desert and marine reptiles suggest that consumption of prey without drinking does not contribute a net gain of water (Lillywhite et al., 2008; Wright et al., 2013; Lillywhite et al., 2014a; Lillywhite et al., 2014b). Moreover, because of requirements for water with respect to digestion, excretion, and defecation, it is possible that consumption and metabolism of food increases rather than decreases the requirement for water, which could actually exacerbate dehydration during conditions of drought.

With respect to this issue, two further observations are significant. The first is the fact that marine snakes that are captured during seasonal drought are thirsty and dehydrated, even though regurgitation of fish indicated that some of these snakes had been feeding (Lillywhite et al., 2014a, b). Secondly, marine snakes (*Acrochordus granulatus*, *Nerodia clarkii*) and cottonmouths (*Agkistrodon piscivorus*) that are kept in captivity tend to cease feeding once they become partially but not critically dehydrated, again suggesting that the consumption and processing of food incurs net losses rather than net gains of water (Lillywhite et al., 2014a; unpub. obs.; see also French, 1956).

The key question in deciding the importance of dietary water is whether the gains of water from dietary and metabolic sources exceed the losses of water that are required for digestion of food and elimination of associated metabolic wastes. The observation that voluntary drinking of water increases following consumption of food (Figs. 2–5) indicates that eating increases rather than decreases the requirement for water. These data complement other evidences for water losses attributable to eating and would explain why some animals cease feeding when dehydration advances to a significant (but not critical) stage. Eating tends to be inhibited during extended periods of cellular dehydration through the action of a

set of inhibitory circuits, and dehydrating rats experience anorexia that is proportional to the degree of dehydration (Watts, 1999; Watts and Boyle, 2010; Boyle et al., 2012). Thus, requirements for, rather than gains from, water associated with feeding might be a more general phenomenon than was previously supposed (with exception of herbivores feeding on plants of high water content).

The physiological controls involved in body fluid homeostasis are complex and interactive, involving signals that are clearly influenced by factors related to eating and digestion (McKinley and Johnson, 2004). Given the physiological variation that research has documented in a wide range of animals (French, 1956; McMillen and Lee, 1967; Wright et al., 2013; Lillywhite, 2016), more precise understanding of water requirements related to feeding will depend on the detailed examination of parameters that are relevant to water balance in individual species. Nonetheless, the present study adds a new perspective to a growing body of literature pointing to some generality that eating can have negative, rather than positive, consequences for fluid homeostasis in dehydrating animals — including species living in xeric habitats. Various species have been noted to reduce their food intake when water is restricted (e.g., French, 1956), and comparatively water-sensitive amphibians have been noted to increase cutaneous drinking of water in response to feeding (Jørgensen, 1993). Further studies might usefully examine thirst or patterns of water consumption that are related to feeding in context of net water exchange attributable to the process. Detailed studies of the physiological underpinnings of water budgets and the importance of dietary vs. free water in the environment will also be of interest.

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Competing interests

No competing interests declared

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Figures



Fig. 1. A Florida cottonmouth (*Agkistrodon conanti*) with head over a water bowl just after drinking a considerable volume of water. Expansion of the anterior body is evident and attributable to the volume of water that is in the anterior portion of the gut. This drinking occurred about five days following consumption of a meal.

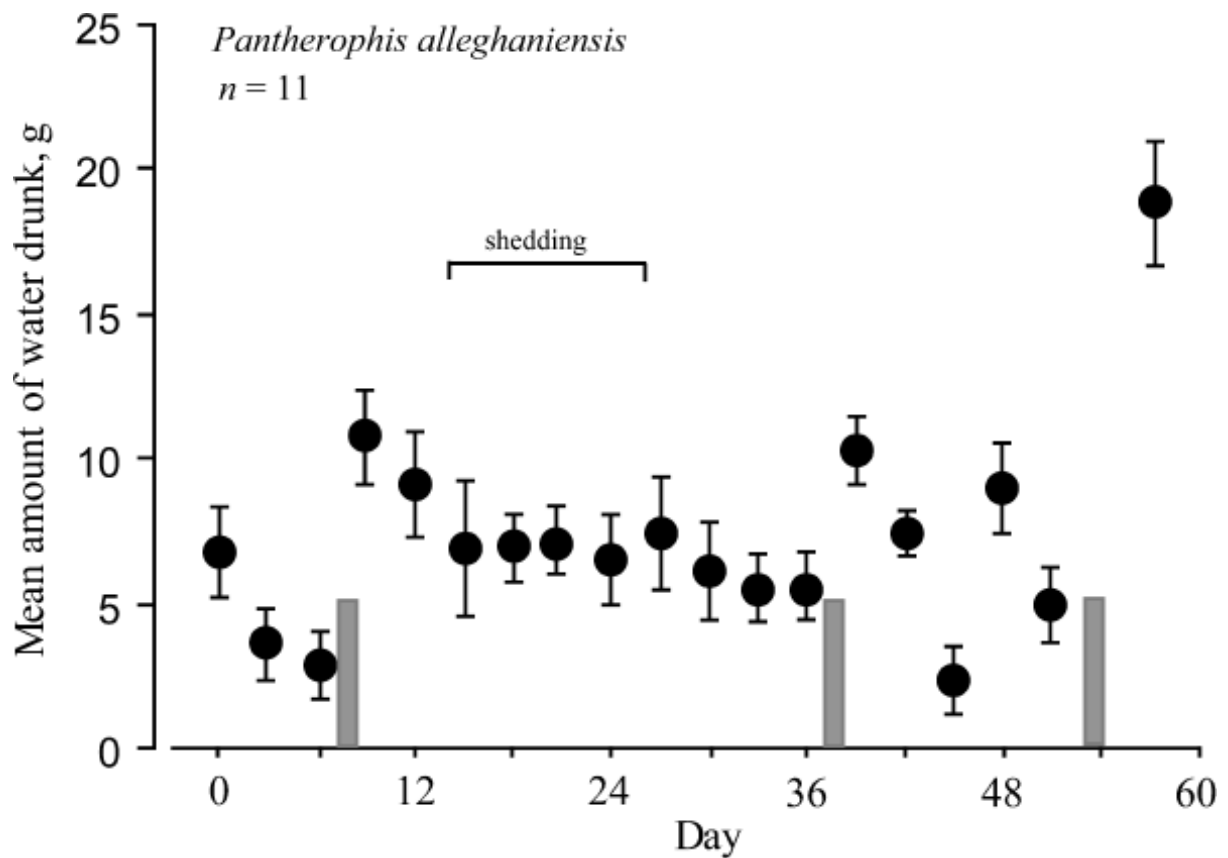


Figure 2. Water consumption in relation to feeding events in adult yellow rat snakes, *Pantherophis alleghaniensis*. Snakes were offered water or food at intervals shown, and data points represent mean \pm s.e.m. Feeding events are indicated by the vertical gray bars. Snakes were not fed during a period when they were in terminal stages of ecdysis, bracketed between days 14 and 26.

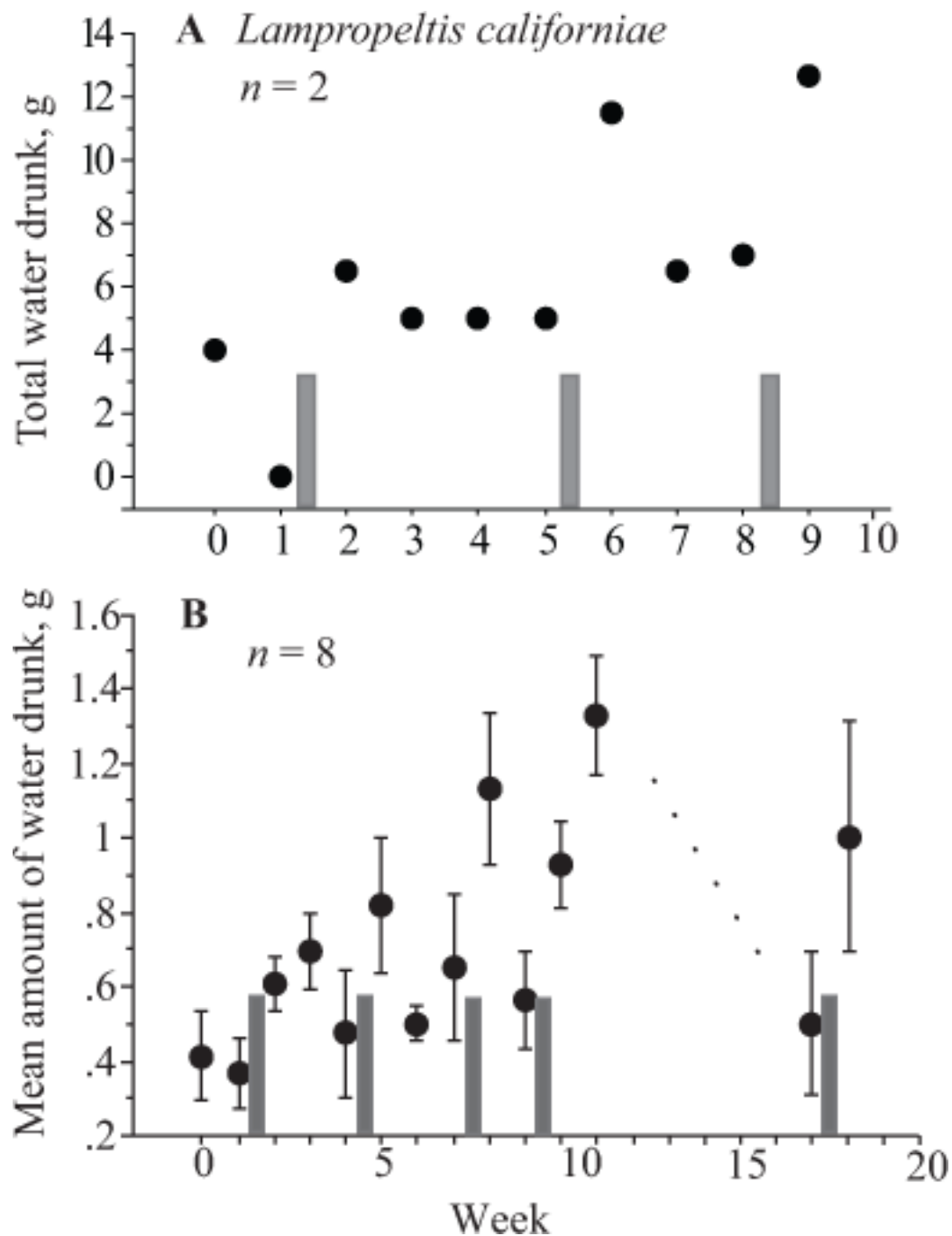


Figure 3. Water consumption in relation to feeding events in two adult (a) and eight baby (b) California king snakes, *Lampropeltis californiae*. Snakes were offered water or food at intervals shown, and data points for baby snakes (b) represent mean \pm s.e.m. Feeding events are indicated by the vertical gray bars. The array of dots on the graph shown in B represent days when the drinking protocol continued but water consumption was not quantified.

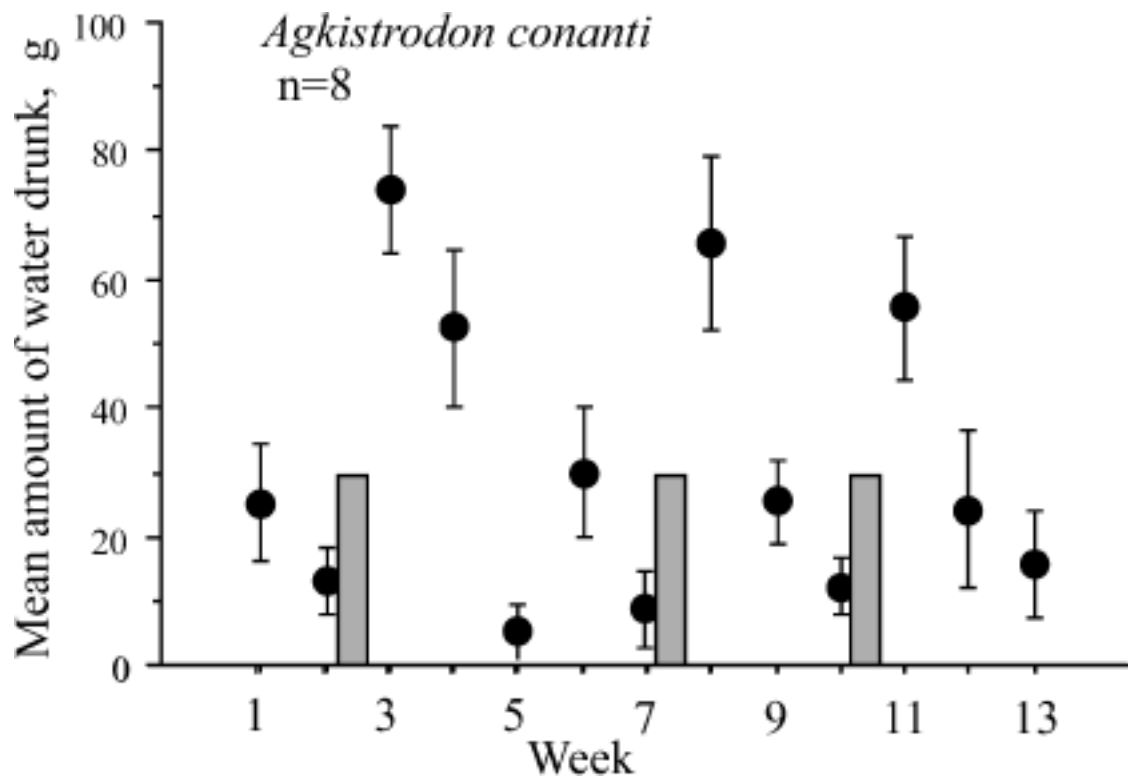


Figure 4. Water consumption in relation to feeding events in eight adult Florida cottonmouths, *Agkistrodon conanti*. Vertical gray bars represent days when snakes were fed.

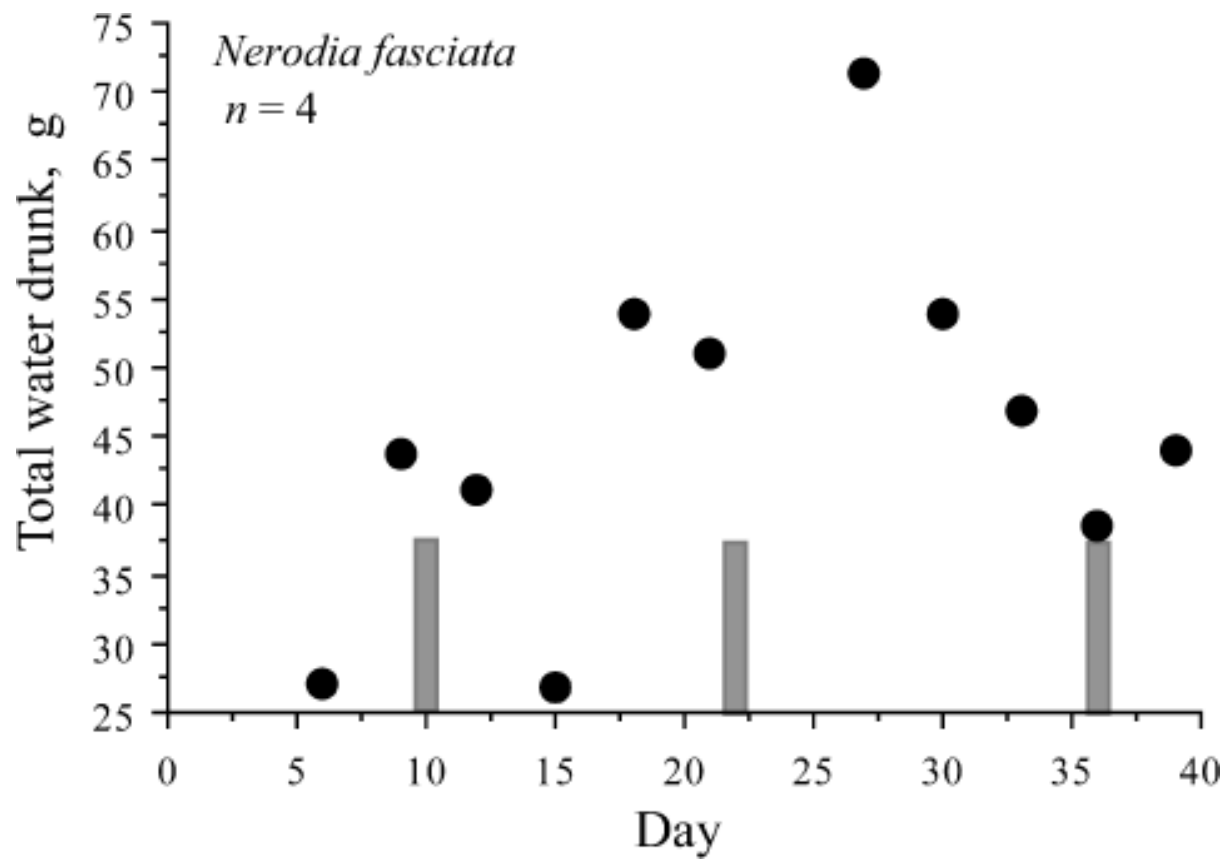


Figure 5. Water consumption in relation to feeding events in four adult banded water snakes, *Nerodia fasciata*. The vertical gray bars represent days when snakes were fed.

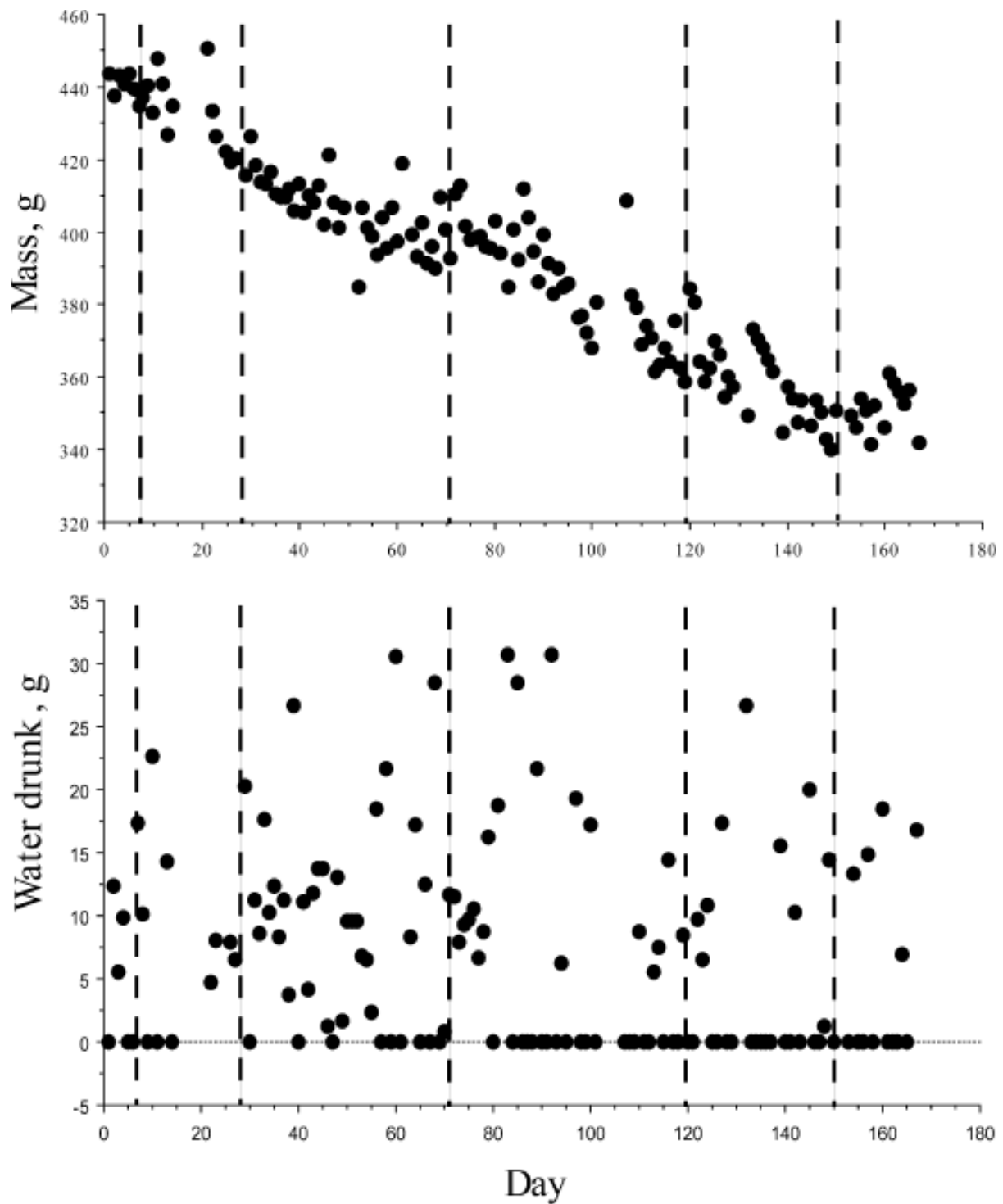


Figure 6. Daily measurements of mass and water ingested by drinking in an individual banded water snake (*Nerodia fasciata*) that was fed at variable intervals (vertical dashed lines). No data points are shown for a small number of days when the investigator was absent.