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# Heavy, Bulky, or Both: What Does “Large Prey” Mean to Snakes?

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**ABSTRACT.—We lay out mass-bulk theory (MBT)—relationships for gape-limited predators among relative prey mass (RPM), relative prey bulk (RPB), prey shape, prey taxon, and feeding frequency. Elongate reptiles with narrow mouths eat tiny items; chunks of prey; or, as with many snakes, “large” animals ingested intact. RPM and RPB define item size, with implications for costs and benefits of feeding. Prey are heavy, bulky, both, or neither, only relative to consumers. Type I items are not heavy or bulky; they require minimal handling and gape, but many must be eaten. High RPM, high RPB, or both characterize types II, elongate (e.g., eels); III, fusiform to ovoid (e.g., mice); and IV, nonuniform in cross-sectional dimensions (e.g., some fishes), density (e.g., birds), and/or deformability (e.g., crustaceans). High handling costs and payoffs characterize types II and III; III and IV require wider gape, but IV comes with lower RPM, costs, and payoffs. RPM and RPB have implications for biology and conservation, such that heavy, bulky, or heavy and bulky—but not large—usefully describe prey size. We explore MBT with 1) natural history vignettes and graphical integration of RPM, RPB, prey shapes, and feeding frequency; 2) nonvenomous colubrids that vary in gape and diet; (3) front-fanged colubroids that consume lizards, centipedes, or earthworms; and (4) bird-eating snakes. Further testing of MBT is hampered by logistical and cultural challenges. Our explorations are bookended by reflections of a herpetologist enjoying his eighth decade, emphasizing how an early-career publication stemmed from youthful experiences and led to this review.**

**RESUMEN.—HWG reflexiona sobre como una publicación en los inicios de una carrera académica se originó de experiencias juveniles y derivó en la vida de un herpetólogo disfrutando su octava década. Relacionado con ello, definimos la teoría masa-volumen (TMV)—la relación para predadores limitados por el tamaño de su boca entre la masa relativa de su presa (MRP), el volúmen relativo de la presa (VRP), la forma de la presa, el taxon de la presa, y la frecuencia de alimentación. Los reptiles de cuerpos alargados y bocas estrechas obtienen su alimento de porciones o presas pequeñas, de partes pequeñas de presas grandes, o de presas “grandes” ingeridas completas, como lo hacen muchas serpientes. MRP y VRP definen el tamaño de la porción, y tienen implicaciones en los costos y beneficios de la alimentación. Las presas pueden ser pesadas, voluminosas, ambas o ninguna, en relación con su depredador. Las presas de tipo I, no son pesadas ni voluminosas; son fáciles de manipular y no requieren bocas grandes, pero deben consumirse muchas. MRP alta, VRP alta, o ambas, definien a las presas tipo II, alargadas, como las anguilas; tipo III, esferoides a ovoides, como los ratones; y tipo IV, no uniformes en sección transversal, como algunos peces, o no uniformes en densidad, como las aves. Costos de manipulación y beneficios nutricionales altos caracterizan a los tipos II y III; los tipos III y IV requieren bocas más grandes, pero el tipo IV implica una MRP baja, y costos y beneficios nutricionales más bajos. MRP y VRP tienen implicaciones biológicas y de conservación, de manera que es útil describir la presa como pesada, voluminosa, o pesada y voluminosa—pero no grande. Aquí exploramos la TMV con 1) viñetas de historia natural e ingración gráfica de MRP, VRP, tipos de formas de presas, y frecuencia de alimentación; 2) colúbridos no venenosos, que varían en tamaño de boca y en dieta; 3) colubroideos con colmillos frontales que consumen lagartijas, ciempiés, o gusanos de tierra; y 4) serpientes que consumen aves. Pruebas adicionales de la Teoría Masa-Volúmen son obstaculizadas por retos logísticos y culturales.**

> “[The *Python sebae*’s stretched] skin when dry was 25 feet 2 inches [7.7 m] long . . . stomach of the snake contained not less than one peck [approximately nine liters] of brass, copper, and iron rings, such as the natives wear on the arms and legs . . . A snake of that size would swallow an antelope as large as a cow, horns and all.” (Johnston, 1908:270)

> “Natural history is replete with observations of feeding, yet only recently have investigators begun to treat feeding as a device whose performance—as measured in net energy yield/feeding time or some other units assumed commensurate with fitness—may be maximized by natural selection.” (Schoener, 1971:369)

> “Too many workers continue to publish lists of prey species eaten, without regard to the size and seasonal energetic requirements of the snake or to the availability and nutritional content of prey in the environment.” (Godley, 1980:411)

Observations of serpents ingesting humans and other “large” animals in one piece must be far older than written history (e.g., Isbell, 2009; Headland and Greene, 2011), although what prey size means in this context often has been vague, even among herpetologists—a 15-kg venison medallion or salmon fillet, immense by our standards, would be small if scaled to the masses of many snakes and their meals (Figs. 1, 2). These limbless reptiles generally feed infrequently, and their diets have been revealed by field observations (e.g., Trail, 1987; Ribble and Rathbun, 2018; Groen et al., 2020), necropsies and regurgitations (e.g., Fitch, 1960; Luiselli and Akani, 2003; Boback et al., 2016), and museum specimen stomach contents (e.g., Werner, 1909; Schmidt, 1932; Klauber, 1956). Now, data also flow from stable isotopes (e.g., Willson et al., 2010; Durso and Mullin, 2017), fecal DNA (e.g., Brown et al., 2014; Durso et al., 2022), roadkill (Hoefer et al., 2021), remote cameras (e.g., Robinson et al., 2005; Putman and Clark, 2015; Glaudas et al., 2017a), and community science (e.g., Maritz and Maritz, 2020; Durso et al., 2021; Putman et al., 2021). Following that brief preface, this coauthored perspective begins and ends in first person

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FIG. 1. Mammals can be heavy and bulky prey—"large" in handling costs, nutritional payoffs, and required gape—as illustrated by Boa Constrictors (*Boa constrictor* sensu lato) that ate White-tailed Deer (*Odocoileus virginianus*) in Sector Santa Rosa, Guanacaste Conservation Area, Guanacaste Province, Costa Rica (data and photos: D. H. Janzen and W. Hallwachs). (A) During and (B) shortly after ingestion of a 4-kg fawn by a 10-kg boa, 5 April 2013 (masses estimated from similar-sized conspecifics). (C) Forced regurgitation of a 3.5-kg fawn by a 3-kg boa, 1983 (weighed in the field; right, D. H. Janzen; left, E. Carrillo). They are fusiform prey with relative prey mass (RPM) of ~0.4 (A, B), which is not unusual for snake meals, and RPM of ~1.17 (C), which is heavier than typically consumed by snakes other than boids, pythonids, and front-fanged species.

singular, whereby HWG details how an early-career publication on the evolution of feeding in snakes (Greene, 1983a) grew out of youthful experiences and then reflects on life for a herpetologist enjoying his eighth decade. In between, we (HWG and KDW) review research that helps better elucidate relationships among relative prey mass (RPM), relative prey bulk (RPB), prey shape, prey taxonomic identity (ID), and feeding frequency—what we call mass-bulk theory (MBT).

I (HWG) first thought about snakes eating large meals as a recent high school graduate interning with Henry Fitch and Charles "Jay" Cole at the University of Kansas Museum of Natural History. My assignment that summer of 1963 was to dissect preserved skinks and assay their breeding cycles (Fitch and Greene, 1965; Greene, 1969), but accounts of snake prey (e.g., Schmidt, 1932; Klauber, 1956; Fitch, 1960) and field encounters with Western Massasauga Rattlesnakes (*Sistrurus tergeminus*) led me to also assess that species' diet with museum specimens (Greene and Oliver, 1965). Then, while off-duty in the military, I recorded scars on amphisbaenians and snakes in European museums to test hypotheses about their defensive tail displays (Greene, 1973a). For an M.A. at the University of Texas at Arlington (UTA), advised by William F. Pyburn, I studied feeding in venomous New World coralsnakes (*Micruroides* and *Micrurus*), again with museum specimens (Greene, 1973b, 1976, 1984). For my Ph.D. at the University of Tennessee, Knoxville, supervised by Gordon M. Burghardt, I used observations of defense and constriction to address homology, convergence, and the origins of novel behavior in snakes (H.W. Greene, 1977, 1979, 1994, 1999; Greene and Burghardt, 1978). Upon completion of graduate work, I had pondered hundreds of natural prey items and more than a thousand captive feeding events, based on phylogenetically basal (e.g., pipesnakes [*Cylindrophis*, Uropeltidae], Mexican Burrowing Pythons [*Loxocemus bicolor*, Loxocemidae], and dwarf boas [*Tropidophis*, Tropidophiidae]) to highly derived taxa (e.g., stilettosnakes [*Atractaspis*, Atractaspididae], king cobras [*Ophiophagus*, Elapidae], and mock vipers [*Psammodynastes*, Lamprophiidae]). Those experiences, along with foundational papers on diet (Fitch, 1941; Fitch and Twining, 1946), functional morphology (e.g., Gans, 1961; Boltt and Ewer, 1964), phylogenetics of character variation (Rabb and Marx, 1973), and optimal foraging (MacArthur and Pianka, 1966; Schoener, 1971), led me to wonder why snakes eat some prey but not others.

FIG. 2. Aquatic chordate prey of natricine colubrids range from elongate to fusiform or bulky and from light to heavy. (A) Northern Watersnake (*Nerodia sipedon*) grasping a Chestnut Lamprey (*Ichthyomyzon castaneus*; identified by B. H. Bauer), 30 April 2021, Wolf River, Fayette County, Tennessee (data and photo: D. P. Hailey). (B) Terrestrial Gartersnake (*Thamnophis elegans*; TL ~43 cm) grasping a Mottled Sculpin (*Cottus bairdii*), late afternoon, 25 July 2019, Warm Springs Creek, Sun Valley, Blaine County, Idaho (data and photo: M. and J. W. Fitzpatrick). (C) Diamond-Backed Watersnake (*Nerodia rhombifer*; TL ~75 cm) ingesting a Gizzard Shad (*Dorosoma cepedianum*; identified by D. S. Hendrickson; evidently carrion, TL ~22 cm), 29 July 2009, Village Creek Heritage Park, Arlington, Tarrant County, Texas (data and photo: T. D. Hibbitts). (D) Mississippi Green Watersnake (*Nerodia cyclopion*) ingesting a sunfish (*Lepomis* sp.; identified by A. A. Echelle); Cane Bayou, Lacombe, St. Tammany Parish, Louisiana (data and photo: J. Schauer). Completed predation was not witnessed in these incidents. For (A), (C), and (D), the first likely had high relative prey mass (RPM) and low relative prey bulk (RPB), the latter two likely had low RPM and high RPB; (B) likely was intermediate in RPM and RPB, although the pectoral fins might have enhanced RPB.

At the 1977 American Society of Ichthyologists and Herpetologists meeting, I nervously presented "Behavioral, ecological, and morphological aspects of adaptive radiation in snakes" (Collette, 1977:814). My so-called "preliminary working model" specified item size with prey/predator mass ("weight ratio" [WR]) and prey diameter/predator head diameter ("ingestion ratio" [IR]). I expected handling costs and payoffs would increase with higher WR and gape with higher IR; prey types were described as small and any shape (low WR, low IR), elongate (high WR, low IR), ovoid (high WR and IR), irregular (low WR, high IR), or fusiform (moderate WR and IR). Pilot comparisons supported the model's predictions about the evolution of methods for subduing prey, gape, and foraging trade-offs, of which later explorations were published (Greene, 1983a, 1984, 1986a, 1992, 1997, 2013; Losos and Greene, 1988; Rodríguez-Robles et al., 1999a; Cundall and Greene, 2000; Wiseman et al., 2019). Meanwhile, early on, Shine (1977) and Godley (1980) had used mass to assess prey for six snake species and foraging trade-offs between prey ID within a species, respectively, and Voris and Voris (1983) examined prey shapes and gapes in Seasnakes.

Subsequent decades have entailed an explosion of interest in snake biology, within which we (HWG and KDW) conclude that MBT has had significant but patchy effects. Beyond the studies cited in the previous paragraph, the deconstruction of prey size (Figs. 3, 4) into RPM (previously WR) and RPB (previously IR) have influenced some discussions of snake biology (exemplified by references cited in Appendix 1). However, often research on snakes has not used them or has done so ambiguously (Appendix 2). Referring to snake prey, for example, Brecko et al. (2011) assumed fish are less bulky than frogs regardless of mass; Mociño-Deloya et al. (2015) treated all lizards as "small" and mammals as "large"; and Moon et al. (2019) in a comprehensive review frequently alluded to "large" prey, usually without reference to RPM or RPB. Likewise, some taxon-focused reports have provided data pertinent to MBT, typically prey ID and RPM (Appendices 3–5), but many other diet studies mention neither RPM nor RPB (Appendix 6).

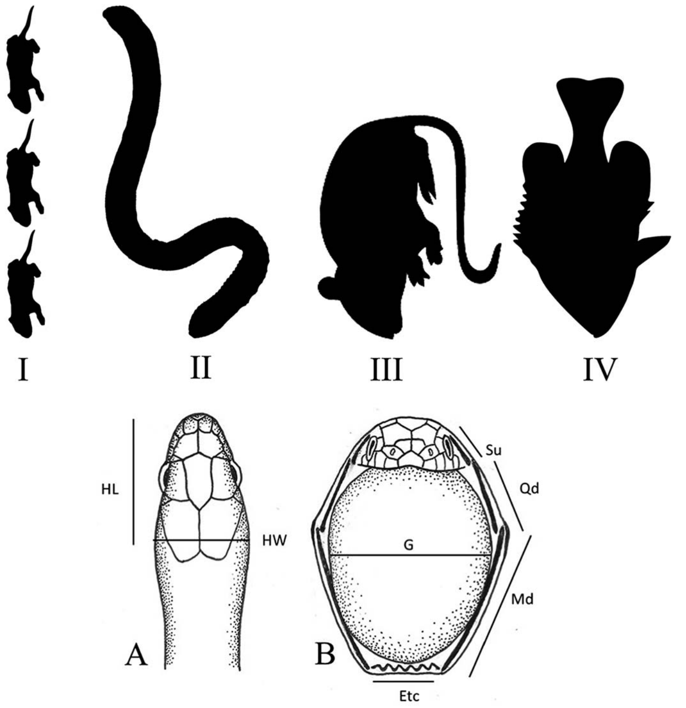

FIG. 3. Idealized prey size and shape types and the components of gape. Small type I prey are not heavy or bulky, regardless of shape and taxonomy; type II prey are elongate (e.g., eels); type III prey are fusiform to ovoid (e.g., rodents); and type IV prey are noncircular in cross-section (e.g., some fishes), nonuniform in density (birds), or both. (A) Dorsal view of a generalized snake with simple external measurements that might reflect gape; HL = head length from snout to retroarticular process of the quadrate, HW = head width at widest point. (B) Simplified view of some bony elements in a snake that might influence gape (G), illustrating supratemporals (Su), quadrates (Qd), and mandibles (Md), as well as the elastic tissue connection (Etc) where most amniotes have a firm mandibular symphysis (modified from Arnold, 1983; animal silhouettes in this and Fig. 4 were adapted from phylopic [http://phylopic.org/]).

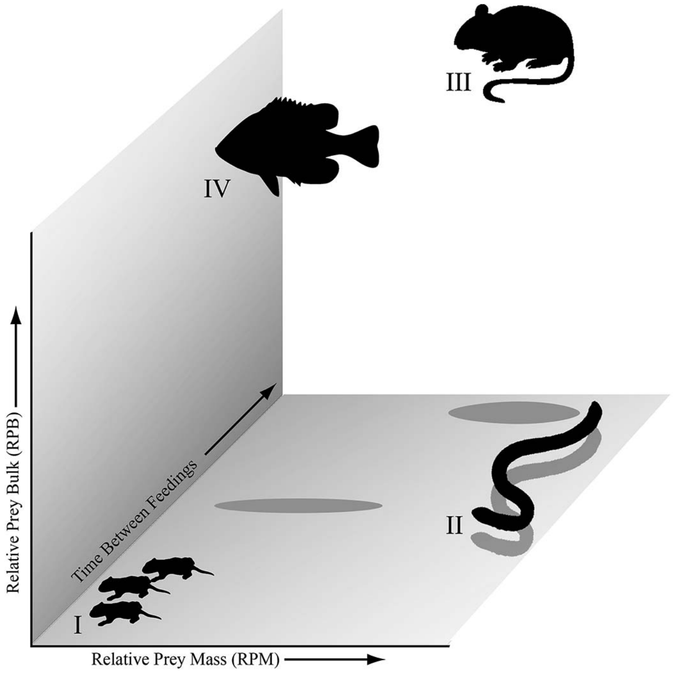

FIG. 4. Graphical model illustrating the relationship between prey types I–IV in terms of relative prey mass (x-axis), relative prey bulk (y-axis), and time between feedings (z-axis). See text for additional explanation.

Among "Natural History Notes" we surveyed in the first 2021 issue of Herpetological Review, 39 diet records for 33 snake species (27 genera) include 6 (15%) with RPM data; for 33 other prey (85%), RPM could have been recorded for at least 3 and perhaps 5 more because specimens were deposited in museums, so the total could have been 14 (36%). None of the 39 records addressed RPB.

Several goals justify gathering diet data, from answering questions about morphology, physiology, ecology, ethology, evolution, and conservation to furthering nature appreciation with public outreach. Moreover, different applications might prioritize certain information—prey ID for ecological questions (e.g., Greene and Jaksic, 1983; Luiselli, 2006a; Pinto-Cuelho et al., 2021), RPM for foraging behavior (e.g., Arnold, 1993; Andreadis and Burghardt, 2005; Loughran et al., 2013; Glaudas et al., 2019), RPM and RPB for evolutionary and functional morphology (Cundall and Greene, 2000; Vincent et al., 2006a; Cundall et al., 2014; Moon et al., 2019; Gripshover and Jayne, 2021; Cundall and Irish, 2022; Jayne et al., 2022), and all of them for conservation and education (e.g., Greene, 1997, 2003, 2013; Clayton and Myers, 2015; Mehta et al., 2020). MBT is clearly germane to many aspects of snake biology, and yet its key parameters often have gone unmeasured, perhaps in part because Greene (1983a) ineffectively portrayed them. Although diet records and broader studies absent MBT can be useful, Godley's complaint (1980; quoted above) still rings true—many accounts of snake diets are simply prey ID lists or are based upon them.

We believe in core roles for natural history within biology and art in clarifying science (e.g., Greene, 2005a, 2005b, 2013; Wiseman and Bettaso, 2007; Wiseman, 2018). This paper, therefore, first explores verbally and visually "large prey" and its implications for MBT. In three following sections, we illustrate MBT with nonvenomous colubrids that vary in diet and gape; front-fanged colubroids that feed on lizards, centipedes, and earthworms; and snakes that eat birds. We next emphasize gathering data for RPM and RPB in taxon-focused and broader studies and then comment on logistical and cultural impediments to that task. Throughout this paper, we detail specific predator-prey interactions to promote acquiring useful information for future syntheses; we provide extensive literature citations to support our conclusions, rather than as an exhaustive review of snake feeding biology (but see, e.g., Moon et al., 2019; Cundall and Greene, 2000; Grundler, 2020; Cundall and Irish, 2022).

Abbreviations refer to California Academy of Sciences (CAS); Museum of Vertebrates, Cornell University (CUMV); Robert W. Hansen field catalog (RWH); Harry W. Greene field catalog (HWG); Museum of Comparative Zoology, Harvard University (MCZ); Robert L. Seib field catalog (RLS); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Texas Natural History Collection, University of Texas at Austin (TNHC); snout–vent length (SVL); total length (TL); and carapace length (CL). Among the taxa discussed here (see Pough et al., 2016), Scolecophidia (including Typhlopidae) and Alethinophidia are treated as basal lineages of Serpentes ("snakes"; Head et al., 2020). Within Alethinophidia, Colubroidea is successively more distantly related to Acrochordidae, Boidae plus Pythonidae, Loxocemidae, Uropeltidae (including

FIG. 5. A dozen or more ant larvae regurgitated by a Bibron's Blindsnake (*Afrotyphlops bibronii*), 16 December 2022, KwaSani, Underberg, KwaZulu-Natal, South Africa (photo: M. da Fonseca). Assuming these insects were encountered as a single meal, overall RPM would have been >10× that of each individual type I prey item; approximately the same gape would have been required for an elongate type II prey item with the same diameter as each larva.

*Cylindrophis*), and Aniliidae plus Tropidophiidae. Colubroidea encompasses Atractaspididae, Colubridae (including Colubrinae, Dipsadinae, Natricinae), Elapidae, Homalopsidae, Lamprophiidae, and Viperidae. Front-fanged colubroids include atractaspidids *Atractaspis* and *Homoroselaps*, elapids, and viperids.

## LONG BODIES, SMALL MOUTHS, AND MASS-BULK THEORY

Body elongation repeatedly preceded limb loss in tetrapod evolution (Mann et al., 2022), and reduced diameter entails a narrower mouth (Gans, 1961). Other than by lowering metabolic rates, attenuate squamates compensate for a narrow mouth by eating many tiny organisms (e.g., >50 ants/stomach in some typhlopids, Webb and Shine, 1993a; "nibblers," Andreadis and Burghardt, 2005; Fig. 5), parts of bigger ones (Appendix 7), or "spectacularly large prey" (Gans, 1961:217; "gorgers," Andreadis and Burghardt, 2005), as do many snakes (e.g., Moon et al., 2019; Cundall and Greene, 2000; Cundall and Irish, 2022) and a near-limbless gekkotan (Burton's Flap-footed Lizard, *Lialis burtonis*; Patchell and Shine, 1986). Conversely, most limbed lizards (including many varanids; Shine and Thomas, 2005; see Losos and Greene, 1988) frequently consume small items—the mean number of prey per stomach was 6.0–75.8 for six North American species (Pianka, 1970; Pianka and Parker, 1972; Parker and Pianka, 1973; Parker and Pianka, 1974; Pianka and Parker, 1975); means were 1.07–2.16 for five colubrid species from the same region, as predicted by MBT (see below), and mean RPMs were 0.19–0.33 (Table 1).

Gans (1961), by posing the small mouth problem in terms of food item value, implicitly identified RPM as crucial to understanding large prey. However, he construed biomechanical solutions (e.g., mandibular liberation, kinetic palatomaxillary arches, and unilateral feeding) in terms of prey "cross-sectional area" (Gans, 1961:220), a component of RPB. The scene

TABLE 1. Dietary attributes for the following six species of North American colubrids (sources in parentheses): Glossy Snakes (*Arizona elegans*; Rodríguez-Robles et al., 1999a), California Kingsnakes (*Lampropeltis getula californiae*; Wiseman et al., 2019; taxonomy follows Hillis, 2020), Scarlet Kingsnakes (*L. elapsoides*; Greene et al., 2010), California Mountain Kingsnakes (*L. zonata*; Greene and Rodríguez-Robles, 2003), Gopher Snakes (*Pituophis catenifer*; Rodríguez-Robles, 2002), and Long-nosed Snakes (*Rhinocheilus lecontei*; Rodríguez-Robles and Greene, 1999). *See text for comments on this maximum RPM value.

| | *A. elegans* | *L. getula californiae* | *L. elapsoides* | *L. zonata* | *P. catenifer* | *R. lecontei* |
|---|---|---|---|---|---|---|
| Predator SVL (cm) | 21–95 | 23–115 | 20–50 | 24–71 | 26–160 | 21–93 |
| Snakes with prey | 100 | 396 | 32 | 47 | 417 | 116 |
| Prey items | 107 | 447 | 34 | 51 | 1066 | 135 |
| Proportion of diet: reptiles, mammals, birds | 0.50, 0.44, 0.04 | 0.59, 0.29, 0.11 | 0.97, 0.03, 0.0 | 0.84, 0.12, 0.04 | 0.03, 0.75, 0.20 | 0.73, 0.26, 0.0 |
| Prey species | 16 | 75 | 9 | 10 | 99 | 17 |
| Prey items/stomach | 1–3 ($\bar{x} = 1.07$) | 1–3 ($\bar{x} = 1.13$) | 1–2 ($\bar{x} = 1.1$) | 1–3 | 1–35 ($\bar{x} = 2.6$) | 1–2 ($\bar{x} = 1.16$) |
| RPM | 0.04–0.77 ($\bar{x} = 0.33$) | 0.01–0.73 ($\bar{x} = 0.24$) | 0.11–0.38 ($\bar{x} = 0.19$) | 0.11–0.62 ($\bar{x} = 0.33$) | 0.01–1.36* ($\bar{x} = 0.21$) | 0.03–0.63 ($\bar{x} = 0.23$) |
| RPB discussed? | Yes | Yes | No | No | Yes | Yes |
| Proportion of head-first ingestion | 1.0 | 0.95 | 1.0 | 0.88 | 0.89 | 1.0 |
| Geographic variation | Not studied | Yes | No | No | Yes | Yes |
| Seasonal variation | Not studied | Yes | Not studied | Yes | Not studied | Not studied |
| Ontogenetic diet shift | Partial | Partial | No | Partial | Yes | Partial |

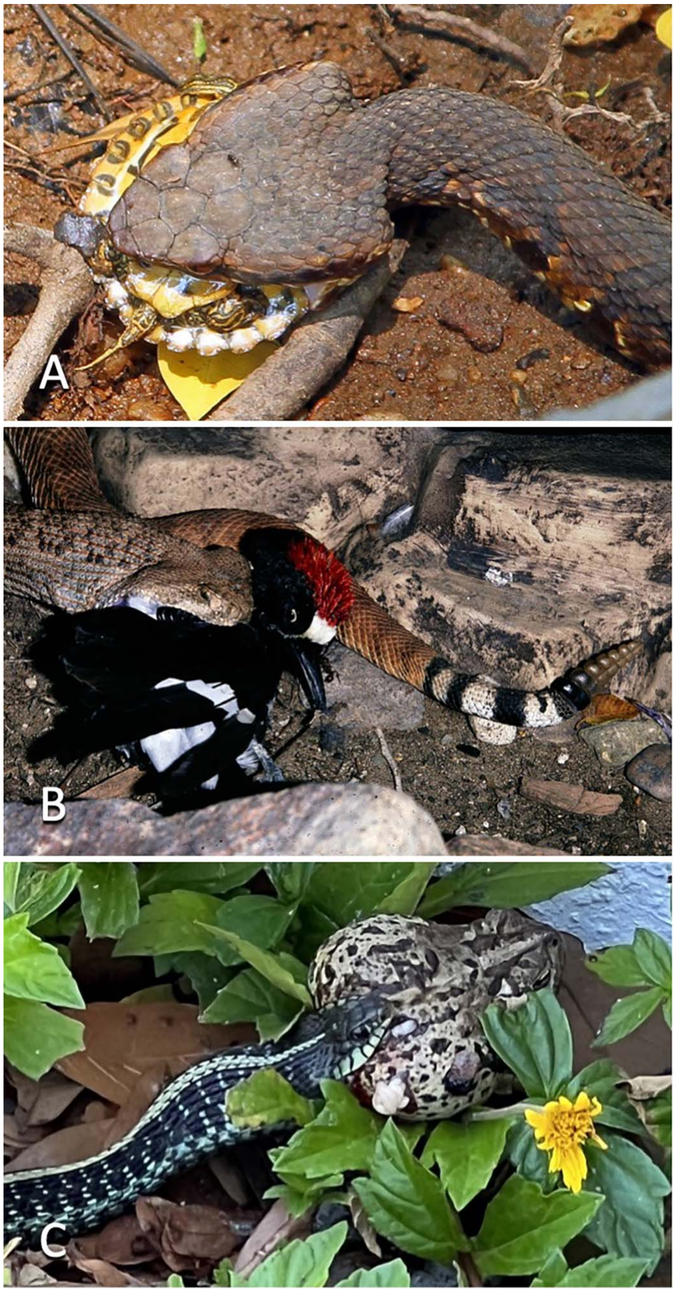

FIG. 6. Ways to be a type IV prey, with low relative prey mass (RPM) and high relative prey bulk. (A) Nonuniform cross-sectional dimensions because of nondeformable shell: adult Cottonmouth (*Agkistrodon piscivorus*) eating a juvenile Slider (*Trachemys scripta*), Maxwell Air Force Base, Montgomery County, Alabama, 1102 h, 26 May 2014; snake TL, ∼75–90 cm; turtle CL, ∼7.5 cm; ingestion required ∼30 minutes and RPM likely <0.1 (data and photo: R. Dowling). (B) Nonuniform cross-sectional dimensions because of wings and nonuniform density because of feathers: young adult female Western Diamond-backed Rattlesnake (*Crotalus atrox*) grasping adult male Acorn Woodpecker (*Melanerpes formicivorus*; identification, age, sex, and estimated mass of 80 g by W. D. Koenig), ingestion required ∼180 min, Portal, Cochise County, Arizona, 2 August 1999; TL, 79 cm; mass, 380 g including prey; RPM, ∼0.27 (CUMV 13952; photo: H. W. Greene). (C) Facultative increase in cross-sectional dimensions and decrease in density because of lung inflation: adult Common Gartersnake (*Thamnophis sirtalis*) grasping a Southern Toad (*Anaxyrus terrestris*), St. Augustine, St. Johns County, Florida, 7 May 2022; completed ingestion was not observed (data and photo: K. Glaser).

was, thus, set for ongoing confusion of two distinct and yet interactive size parameters, despite efforts to clarify these relationships (e.g., Greene, 1983a; Arnold, 1993; Greene, 1997:71–73; Cundall and Greene, 2000; King, 2002; Vincent et al., 2006a; Greene 2013:151–155). As an example of conflating mass and bulk subsequent to Gans (1961), “the largest prey item recorded for any snake is a 59 kg impala consumed by a 4.72 m African python [*Python sebae*] . . . The shoulders of an adult man when collapsed forward may measure only 35–40 cm wide, and could probably be engulfed by pythons in excess of 5 m” (Branch and Hacke, 1980:306).

Prey size should be defined by RPM and RPB because, as detailed below, they have different implications for costs and benefits of feeding. Prey can be “large” in one, both, or neither parameter (Figs. 1–5) but only relative to masses and gapes of individual snakes who subdue, consume, and process them or not. Prey taxa are not intrinsically heavy or bulky but can be described in terms of four types. Type I items with low RPM and RPB are not heavy or bulky, regardless of shape; their masses and cross-sectional areas are trivial to predators, so they require neither subduing nor big gapes to be swallowed; and they must be eaten often to provide adequate nutrition (Figs. 3–5). “Large” prey with high RPM, high RPB, or both define the following three additional idealized shape types: II, elongate (e.g., eels; Figs. 2–4, 9); III, fusiform to ovoid (e.g., mammals; Figs. 1, 3, 4); and IV, noncircular in cross-section, density, and/or deformability (e.g., many fishes and birds; Figs. 2–4, 6, 7). Among these shape types, with all else equal, high handling costs (e.g., Arnold, 1993; Andreadis and Burghardt, 2005; Mukerjee and Heithaus, 2013; Kornilev et al., 2022), high payoffs, and low feeding frequency characterize II and III. Types III and IV require wide gape to surmount high RPB; type IV items also come with lower meal payoff because of nonuniform cross-sectional dimensions or density and, thus, require increased feeding frequency or other compensation, e.g., low energy demands.

All else is rarely equal, and prey can vary in taxon-typical attributes such as retaliatory bite force (e.g., amphisbaenians, Barbo and Marques, 2003), nutritional content (e.g., Krause et al., 2003; Wiseman et al., 2019), and surface features (e.g., Godley, 1980; Savitzky, 1983; Voris and Voris, 1983; Arnold, 1993; Willson and Hopkins, 2011; Bringsøe, 2019; Wiseman et al., 2019; Hamanaka and Mori, 2020; Cleuren et al., 2021). They also might differ in ways evident only at high RPM, high RPB, or both, including toxicity (e.g., some amphibians, Feldman et al., 2012, 2020), social defense (e.g., carnivores, Janzen, 1970; primates, Gardner et al., 2015), and shape changes (e.g., lizard ring-forming, Fitch, 1935; Bowker, 1987; anuran body inflation, Ferreira et al., 2019). Even tiny RPM and RPB prey items can vary in ways that matter—Black Mambas (*Dendroaspis polylepis*, TL > 2 m, mass ∼1.5 kg) eat lipid-rich termites (∼2 mg each, RPM ∼0.001) but not toxic ants (Dial and Vaughan, 1987; Branch, 1991; Branch et al., 1995; but see Evans and Alexander, 2021). Likewise, weasels (*Mustela*) might be more formidable prey than rodents for Old World ratsnakes (*Elaphe*; Prötzel et al., 2018), Bullsnakes (*Pituophis catenifer sayi*; Mulaik, 1938), and adders (*Vipera*; López Jurado and Caballero, 1981; Bringsøe, 2019), but data on RPM and handling times will be required to explore costs and benefits of eating those carnivores. We conclude that the term large prey is always ambiguous and should be replaced with the words heavy, bulky, or both, which in common parlance signify just what they mean here; Arnold’s (1993:103–111) discussion of

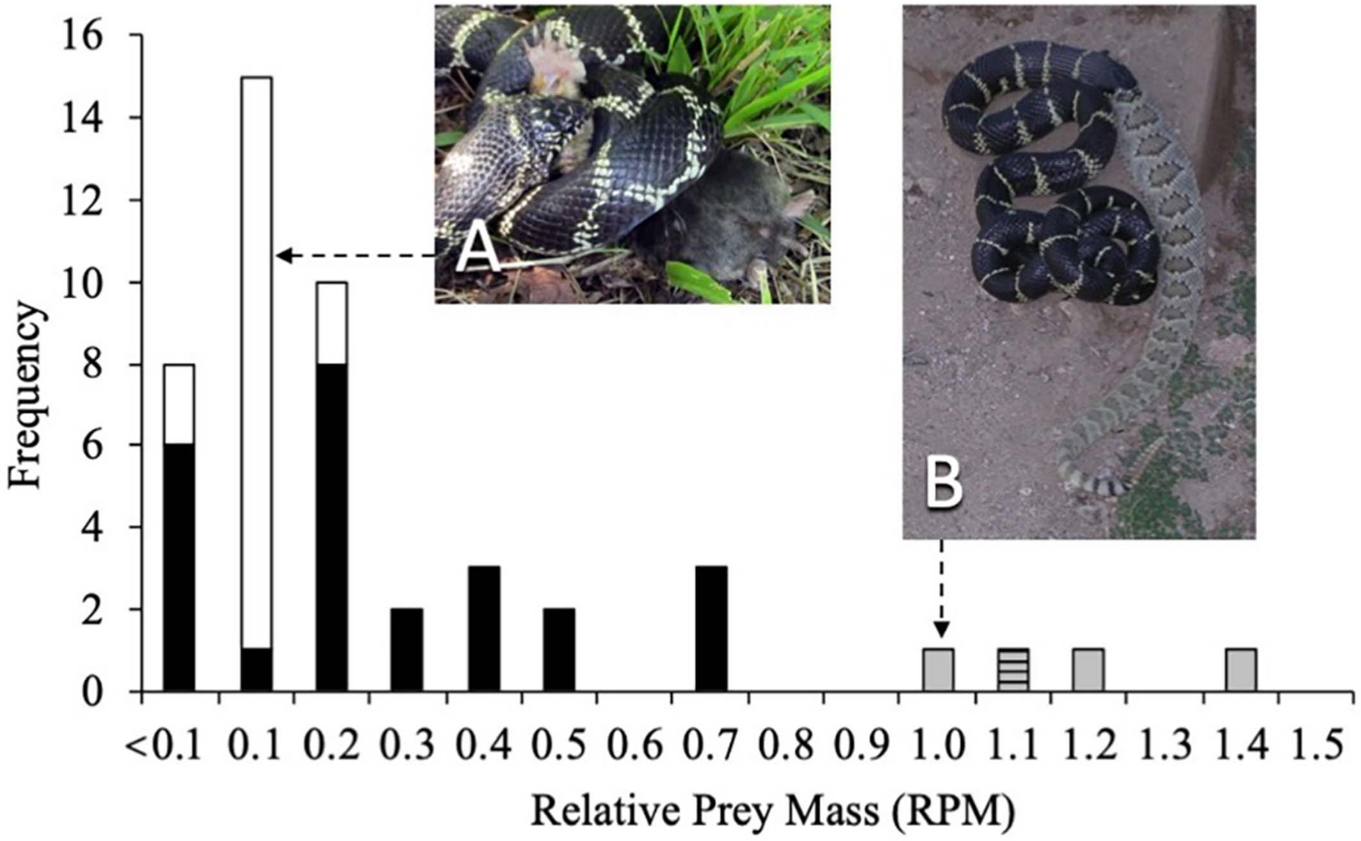

FIG. 7. Frequency distribution of relative prey mass (RPM) for different prey shapes from 43 California Kingsnakes (*Lampropeltis getula californiae*; modified from Wiseman et al., 2019). Black bars = snake prey (type II), white bars = nonsnake prey (types III and IV); banded gray bar = digested captive snake prey and solid gray bars = regurgitated captive snake prey, from Jackson et al. (2004). Inset (A): Eastern Kingsnake (*L. g. getula*; mass, ~300 g) attempting to ingest a Eastern Mole (*Scalopus aquaticus*; adult mass, ~50 g), RPM of ~0.17, Beaufort, Carteret County, North Carolina, 1327 h, 21 July 2017 (data and photo: F. S. Boyce). Inset (B): *L. g. californiae* ingesting Mojave Rattlesnake (*Crotalus scutulatus*; RPM, ~0.80–1.0), Pima, Graham County, Arizona, 17 August 2006 (data and photo: R. White).

"varieties of useless prey" remains pertinent, as is Kornilev et al.'s (2022) review of snakes failing to survive ingesting harmful prey.

Besides foraging theory and other conceptual realms, MBT might be applicable to additional gape-limited predators. Possible examples include frogfishes (Antennariidae; Pietsch and Arnold, 2020:451), lizardfishes (Synodontidae; Soares et al., 2003), venomous deep-sea eels (Monognathidae; Bertelsen and Nielsen, 1987), morays (Muraenidae; Diluzio et al., 2017; Higgins et al., 2018; Mehta et al., 2020), some frogs (e.g., *Ceratophrys*; Duellman and Lizana, 1994), certain varanids and helodermatids (Greene, 1986a; Repp and Schuett, 2009), and some birds (e.g., Roadrunner [*Geococcyx californianus*]; Holte and Houck, 2000).

*Relative Prey Mass.*—Greene's (1983a) WR and IR suffered from the use of ratios (Atchley et al., 1976) and imprecisions of "weight" and "ingestion." RPM instead specifies equivalent aspects of predators and prey, which are measurable with simple tools (e.g., field-portable balances) in the same units (e.g., grams) and amenable to diverse comparisons (e.g., analyses of covariance on log-transformed data for hypothesis testing and percentages for outreach). Moreover, RPM has long been used for snakes (e.g., Fitch and Twining, 1946; Brown, 1958; Rodríguez-Robles and Greene, 1999; King, 2002; Andreadis and Burghardt, 2005; Vincent et al., 2006a) and is more directly related to costs and benefits than linear dimensions or volume (e.g., Henderson, 1993; Greene et al., 1994; Machio et al., 2010; Enge et al., 2022). Predator mass scales variably with length among species (e.g., Jayne et al., 2022) but also differs within species, even within an individual seasonally, depending on physiological condition (e.g., Fitch, 1949; Dobson, 1992; Cundall, 2000; Rivas, 2020:92). Finally, RPM measurements are subject to other errors and biases, particularly with preserved specimens and proxy estimates of live weights (for a careful example, Boback et al., 2016; for subsampling stomachs with hundreds of tiny prey items, Araújo et al., 2008).

Multiple similar items in a stomach could represent single meals in terms of search costs. Clumped prey eaten in rapid succession at one site might include schooling fishes (B. Greene et al., 1994), insect larvae (Webb et al., 2000; Fig. 5), reptile eggs (e.g., Rodríguez-Robles and Greene, 1999; Barends and Maritz, 2022a; Durso et al., 2022), roosting bats (Sorrell et al., 2011), nestling birds and mammals (e.g., Rodríguez-Robles et al., 1999b; Quick et al., 2005; Barends and Maritz, 2022b), and suckling mammals ingested with their mothers (e.g., Lanchi et al., 2012). As exemplars of payoffs from prey taken in one foraging bout, for a 50-g California Mountain Kingsnake (*Lampropeltis zonata*) that ate five 1-g nestling mice, RPM was 0.02/item and 0.1 combined; a 5-g rodent with the latter RPM would have entailed greater RPB and perhaps overall higher handling costs. For a 45-g *L. zonata* that ate 10 1-g squamate eggs, RPM was 0.022 per item and 0.222 combined; a single egg of equivalent value would require wider gape but not higher costs to subdue (data from Greene and Rodríguez-Robles, 2003). Note, however, that intact and well-digested young rabbits in the stomach of a Trans-Pecos Ratsnake (*Bogertophis subocularis*) could have been taken from separate nests (Moon and Rabatsky, 2004); likewise, a Reticulated Python (*Malayopython reticulatus*) simultaneously located and killed two children (Headland and Greene, 2011), but repeated predation by *P. sebae* on adult humans (as implied by Johnston, 1908) likely occurred over months or years. In each of these examples, the costs and benefits of ingestion might best be assessed for individual prey.

Above complexities notwithstanding, measuring RPM is straightforward compared to RPB, and perhaps its greatest challenge is to account for predator mass variation over time relative to length (e.g., Fitch, 1949; for length-mass relationships in snakes, Feldman and Meiri, 2013; Rivas, 2020:92; Jayne et al., 2022). A core importance of RPM is that higher values imply higher handling costs (heavier adversaries struggle harder) and higher payoffs (more grams of prey means more nutrition). Two predictions of MBT thus are that high RPM comes with the benefit of less frequent foraging—yielding fewer risks and time for other activities—but entails the cost of subduing heavier prey by brute force, constriction, and/or venom.

*Relative Prey Bulk.*—Beyond error and bias, RPB is conceptually and empirically more problematic than RPM; Fabre et al. (2016:635), for example, wrote of "large and bulky prey . . ." as "heavy and/or . . . relatively wide or tall for their length . . . ." Challenges arise because RPB might reflect a prey's cross-sectional dimensions (e.g., mouse versus shad; Fig. 2c), cross-sectional density (e.g., mouse versus bird; Fig. 6b), deformability (e.g., mouse versus turtle; Fig. 6a), or a combination of those variables, as well as structural components of predator gape (e.g., cranial bones, soft tissues; Fig. 3)—attributes difficult to measure for both prey and predators in ways that are functionally relevant, variable across taxa and methods, and controversial (e.g., King, 2002; Martins et al., 2002; Close and Cundall, 2012; Hampton and Moon, 2013; Hampton, 2018; Cundall, 2019; Moon et al. 2019; Gripshover and Jayne, 2021; Cundall and Irish, 2022; Jayne et al., 2022). Nonetheless, qualitative comparisons and experimental studies indicate significant relationships between RPB and structural correlates of gape (e.g., Cundall and Greene, 2000:324; Close and Cundall, 2012; Gripshover and Jayne, 2021; Cundall and Irish, 2022; Jayne et al., 2022).

Having struggled with these intricacies when studying snake diets (e.g., Rodríguez-Robles et al. 1999a; Wiseman et al., 2019), we anticipate their clarification by other researchers (see below) and simply refer here to RPB because bulk is defined as "a lot of size or heft, though not necessarily heavy . . . Pillows are bulky . . . big in an inconvenient way" (www.vocabulary.com, accessed June 1, 2021). Bulk describes a key aspect of snake feeding and has been used in this sense (e.g., Marques et al., 2010; Passos et al., 2019:9; Barends and Maritz, 2022a; Solórzano and Sasa, 2022) and yet provides an umbrella for more precise terms and elaborations (e.g., Close and Cundall, 2012; Cundall, 2019; Moon et al., 2019; Gripshover and Jayne, 2021; Jayne et al., 2022); moreover, this overarching descriptor is useful in realms as different as functional morphology and public outreach (a child alerted us to the pillow example). High RPB implies high handling costs (more time and energy for ingestion and concomitant risks from other predators), separate from but interacting with those imposed by high RPM (King, 2002; see especially Close and Cundall, 2012; Jayne et al., 2022; Kornilev et al., 2022). Another core prediction of MBT is that snakes feeding on high RPB prey are specialized for enhanced gape regardless of RPM, whereas feeding frequencies depend on eating type III (high RPM, less often) versus IV prey (low RPM, more often).

*RPM, RPB, and Prey Shapes.*—Prey shapes are defined by linear dimensions and geometry, which are often taxon specific; at high RPM and/or RPB, they have consequences for costs and benefits of feeding (e.g., Greene, 1983a; Voris and Voris, 1983; Gripshover and Jayne, 2021; Cundall and Irish, 2022; Jayne et al., 2022). As discussed below, all else equal and at a given gape, type II prey (Figs. 2a, 7b, 9) will entail the highest handling costs and payoffs; heavy bulky type III prey (Fig. 1) will have high costs from RPM and RPB, as well as high payoffs from RPM. At constant RPM, however, items that are fusiform, ovoid, or asymmetric in cross-section (III and IV, Figs. 1, 6), rather than uniform and elongate (II), require increased gapes—so generalists should drop these from their diet at lower RPM than type II prey (potentially testable, e.g., with a South American Watersnake [*Erythrolamprus miliaris*] eating fishes, frogs, and caecilians, Eisfeld et al., 2021; see next section on colubrids).

In terms of prey ID and shape, earthworms, centipedes, and some chordates are elongate (type II); limbed squamates and mammals span fusiform to ovoid, and some amniote eggs are spherical (type III). Type IV prey vary in overall dimensions, density, and/or deformability relative to mass but are defined by a need for wide predator gape at lower RPM—note that fusiform or roundish prey can differ in density and/or deformability, such that a bird or a tortoise would yield lower RPM than a rodent with equivalent cross-sectional area (Close and Cundall, 2012; Jayne et al., 2022; see below). Thus, although high RPB is obvious for shad and many other fishes because of disparate major and minor cross-sectional axes (Fig. 2c; Voris and Voris, 1983), some other prey taxa have high RPB because of rigid or dangerous structures, including turtle shells (Fig. 6a), bird beaks and long feathered limbs (Fig. 6b), mole forefeet (Fig. 7a), porcupine quills (Duarte, 2003), deer antlers (e.g., Sunquist, 1982; Rivas, 2020:91-92), and inflatable lungs of anurans (Fig. 6c; Ferreira et al., 2019).

As another example of linking RPB with RPM, relevant to human-snake relationships and thus conservation (Pooley, 2022), some herpetologists have claimed our shoulders prevent ingestion by all but the longest snakes—but people coexisting with giant constrictors usually weigh less than adult Caucasians (at 90 kg, HWG has twice the mass of an adult male Indigenous Philippine Agta) and occasionally are attacked and eaten by these snakes (Branch and Hacke, 1980; Headland and Greene, 2011; Rivas, 2020:99–103; Natusch et al., 2021). Moreover, snakes can reduce RPB for at least some mammals by alternately deforming a prey item's shoulders during ingestion, such that they are swallowed sequentially rather than simultaneously (Close and Cundall, 2012).

*MBT and Fossils.*—Greene (1983a) estimated TL (∼1.8 m and ∼0.5 m, respectively) and RPM (∼0.42) for an Eocene boid (*Eoconstrictor fischeri*, Georgalis et al., 2021) and its crocodilian prey. Subsequent researchers described the fossilized stomach contents of other arguably crown group snakes (e.g., *Pachyrhachis problematicus*; Scanlon et al., 1999; Greene and Cundall, 2000), and we anticipate further integration of paleontological evidence for RPM and RPB with data from extant taxa. A stem serpent that plausibly ate clumped nestling dinosaurs (Zaher et al., 2022), an *E. fischeri* (SVL ~90 cm) containing a freshly ingested lizard (SVL ~8 cm, torso diameter ~17 mm; Smith and Scanferla, 2016), and a giant Pliocene adder (*Bitis* cf. *olduvaiensis*, TL ~1.45 m) that ate an immature hare (Rage and Bailon, 2011:473–476) exemplify possibilities for applying MBT to ancient prey-predator interactions in snakes and their closest extinct relatives.

## Mass-Bulk Theory and Nonvenomous Colubrid Snakes

Refining MBT could entail holding RPM, RPB, prey shape, or ID constant to test predictions of how other variables respond across a diverse range of snakes and prey. Ideally, this approach includes evaluating individual, ontogenetic, sexual, seasonal, and geographic variation before addressing specific questions (e.g., Greene, 1984; Bea et al., 1992; Luiselli, 2006b; Wiseman et al., 2019) in a phylogenetic framework (e.g., Greene, 1983a; Vincent et al., 2006a; Barends and Maritz, 2022b). For those reasons, and because it has a broad diet and is well represented in museum collections, California Kingsnakes (*Lampropeltis getula californiae*) provided special potential for testing MBT. We began a study of these serpents while KDW was in HWG's Berkeley herpetology course (Wiseman et al., 2019), of which the results are integrated here with research on certain other colubrids—collectively 1,840 prey items from 1,108 snakes (Table 1; for relationships, Zaher et al., 2019). We partly used data from museum specimen stomach contents (e.g., 55% of 447 *L. g. californiae* records) and attempted to address redundancy, bias, and sources of variation (e.g., Rodríguez-Robles and Greene, 1999:490). Our smallest samples were for Scarlet Kingsnakes (*Lampropeltis elapsoides*) and *L. zonata*, attractive snakes that collectors might not kill immediately, such that stomach contents were not preserved. *Lampropeltis elapsoides*, *P. catenifer*, and Long-nosed Snakes (*Rhinocheilus lecontei*) eat mostly skinks (*Plestiodon*), mammals, or whip-tailed lizards (*Aspidoscelis*), respectively; Glossy Snakes (*Arizona elegans*) and *L. g. californiae* have broader diets, encompassing squamates, birds, and rodents. For heuristic purposes, we subjectively characterize gapes as narrow or wide, with hopes that differences (or lack thereof) eventually will be quantified.

Several results from comparisons among these colubrids are consistent with predictions from MBT:

(1) *Lampropeltis g. californiae*, with a narrower gape than *A. elegans* and *P. catenifer*, drops high RPB prey types III and IV from the diet at much smaller RPM (~0.2) than for type II; *L. g. californiae* eats high RPM meals only in the form of snakes, and stout *Crotalus* provide the highest value (Fig. 7b). RPM thus helps explain how eating rattlesnakes, only 7% of prey by frequency, might select for immunity against viper venom.

(2) *Lampropeltis g. californiae*, *A. elegans*, and *P. catenifer* have a maximum RPM ~0.7–1.0, but the broader gaped *A. elegans* and *P. catenifer* achieve higher values with bulky type III instead of elongate type II prey (Rodríguez-Robles, 2002:173; Wiseman et al., 2019:20). At distributional extremes, RPM was 0.01–0.73 for *L. g. californiae* and 0.02–0.86 for Eastern Kingsnakes (*L. g. getula*; Godley et al., 2017); captives regurgitated prey with RPM 1.17 and 1.35 but digested one with RPM 1.06 (Jackson et al., 2004). These observations imply a maximum RPM ("upper breaking point" of Arnold, 1993) of ~1.0 (Fig. 7) for that species, which is rarely achieved in nature and only with type II prey. Likewise, two *P. catenifer* died during or shortly after ingesting type III rodents with RPMs of 0.82 and 1.36 (Rodríguez-Robles, 2002). Whether such success-failure bracketing can work for other species depends upon an adequate sample of field-based RPM data and the logistics of providing especially heavy prey to captive animals: Mole Snakes (*Pseudaspis cana*) likely would require a huge enclosure to seize an antelope (B. Maritz et al., 2020), for example, as might Gaboon Adders (*Bitis gabonica*) to ambush an ungulate or primate (Foerster, 2008; Warner and Alexander, 2011).

(3) *Arizona elegans* and *L. zonata* that consume type IV birds are longer than other snakes that eat type III mammals, and the latter are longer, on average, than snakes taking less bulky types II and III lizards. Total length is correlated with gape within species (Jayne et al., 2022), and a similar relationship between snake TL and lizard, bird, or mammal prey also characterizes some other colubrids (e.g., Milksnakes [*Lampropeltis triangulum* sensu lato] Rodríguez and Drummond, 2000; Barten, 2010; Greene et al., 2010).

(4) *Arizona elegans* has a wider gape than *R. lecontei* and consumes mammals at a smaller TL; among limbed squamate prey, the former mainly consumes stout-bodied type III phrynosomatids and the latter elongate type II whiptails.

(5) *Lampropeltis elapsoides* and *R. lecontei* are slender, sharp-snouted diggers, with narrow gapes and diets that emphasize type II lizards in their diets. Longer *L. elapsoides* rarely add higher RPM and RPB items (among 34 individuals with prey, the longest individual's TL was 50 cm; a 44-cm TL snake ate the only rodent), whereas southerly *R. lecontei* with TLs of 38–97 cm occasionally eat type III mammals.

(6) Head-first ingestion is typical for most snakes, perhaps because legs, scales, and other protuberances more easily fold that way (for taxa in which tail-first prevails see, e.g., Greene, 1976; Cobb, 2004). For a given gape, tail-first should be easier as RPB decreases at lower RPM (e.g., Greene, 1976; Pleguezuelos et al., 1994; Mehta, 2003). Among 187 *L. g. californiae* prey, 10 swallowed tail-first were "relatively small or attenuate" (e.g., nestling rodents; Wiseman et al. 2019:8). Of 25 *L. zonata* prey, "three neonate mammals, probably relatively small items, were eaten tail first" (Greene and Rodríguez-Robles, 2003:309). Thirty-seven of 321 *P. catenifer* prey were swallowed tail-first or bent double, with "a trend for smaller animals (i.e., nestlings) to be swallowed tail-first with a higher frequency than juvenile[s] or adult[s]" (Rodríguez-Robles, 2002:168). *Lampropeltis elapsoides* and *R. lecontei* have narrow gapes and always eat prey head-first.

(7) HWG and collaborators scarcely addressed RPB because of uncertainties regarding what to measure (e.g., Rodríguez-Robles et al., 1999a; Rodríguez-Robles, 2002; Wiseman et al., 2019). MBT nonetheless predicts that small individuals exclude high RPB items from their diets and longer snakes eat those same prey taxa when low RPB correlates with low RPM. The following two kinds of type IV prey demonstrate opportunities for future studies of these trade-offs. (a) Among 447 items for *L. g. californiae*, ingestion of the only horned lizard (*Phrynosoma*) was fatal to predator and prey (Wiseman et al., 2019:14). Conversely, less than a fourth as many diet items for the wider-gaped *A. elegans*

included two fatal and two successful consumptions of *Phrynosoma* (Rodríguez-Robles et al., 1999a). Among other colubrids, Coachwhips (*Masticophis flagellum*) eats items as heavy and bulky as rabbits (Whiting et al., 1992), and yet RPM for *Phrynosoma* was low ($\bar{x} = 0.04$) and averaged half that of type II whiptails ($\bar{x} = 0.08$; Appendix 8). Consistent with MBT, however, a Desert Night Snake (*Hypsiglena chlorophaea*) ate an essentially hornless Pigmy Short-horned Lizard (*Phrynosoma douglasii*) with an RPM ~0.5 (O'Connor et al., 2010). (b) Moles (Talpidae) have semirigid, outward-turned forelimbs with stout claws (Lin et al., 2019), to which snakes have responded as follows: a *L. g. getula* failed to ingest one with an RPM less than the predicted maximum for types III and IV prey (Fig. 7a); shorter Copperheads (*Agkistrodon contortrix*), with wider viperid gapes, ate adult moles (Uhler et al., 1939; Graves, 2002); and a Rubber Boa (*Charina bottae*) consumed three nestlings with an RPM of ~0.1, such that their combined RPM was ~0.3 (Rodríguez-Robles et al., 1999b).

## MASS-BULK THEORY AND THE EVOLUTION OF VENOMOUS SNAKES

Preliminary assessments are consistent with MBT's prediction that snakes with high RPM will be adapted for subduing high-cost prey. Scolecophidians are nonconstrictors, are nonvenomous, and generally take tiny type I items (e.g., Shine and Webb, 1990; Webb and Shine, 1993a,b; Webb et al., 2000; Fig. 5). Constricting basal alethinophidians—aniliids, uropeltids, boids, and pythonids—often eat types II or III prey with RPM > 0.5, and individuals of the latter two taxa occasionally eat type III prey with RPM > 1.0 (Fig. 1c; Appendix 4). An acrochordid contained an "enormous" fish with RPM of 0.3 (Shine, 1986:427). Nonconstricting, non-front-fanged colubroids typically take types I–IV with RPM < 0.5 (Fig. 2; for an exception, see Linares and Eterovick, 2012), and constricting colubrids rarely exceed RPM of 1.0 (Fig. 7, Table 1, Appendix 3). Only elapids and viperids with some frequency have an RPM of ~1.0–1.7 (Figs. 8–10; Appendix 5). These patterns exist despite biases that might obscure them and have not been evaluated for the energetic effect of rarely eaten but unusually heavy or otherwise nutritious prey (e.g., Greene, 1986a; Wiseman et al., 2019).

Cundall and Greene (2000) further suggested that front-fanged snakes with tranquilizing toxins (e.g., most elapids) often consume type II prey (Fig. 9), whereas those that tranquilize and tenderize (e.g., many viperids; Figs. 8b, 10) emphasize type III items (toxin terminology from Mackessy, 2010); they inferred this reflects lower surface area relative to mass for heavy bulky meals, such that tenderizers facilitate digestion, especially in cold climates (e.g., Greene, 1992; Lutterschmidt et al., 1996). Here, we show how MBT can elucidate the roles of diet in venomous snake evolution and emphasize that although prey ID matters (e.g., Daltry et al., 1996; Gibbs and Rossiter, 2008; Barlow et al., 2009; Modahl et al., 2018; Davies and Arbuckle, 2019; Zancolli et al., 2019; Lyons et al., 2020; Holding et al., 2021), RPM and RPB are central to this topic (see also, e.g., Hayes et al., 2002; Bringsøe, 2019; Hamanaka and Mori, 2020).

*Assessing RPM While Controlling for Other Variables.*—If venoms tranquilize and tenderize especially dangerous and heavy prey, venomous snakes should take higher RPM items than nonvenomous species. Broad comparisons, however, as summarized above, risk confounding venom effects with the availability of equivalent RPM prey (Tsai et al., 2016) and vulnerability of particular prey taxa (e.g., Arnold, 1993). With respect to availability, RPM for sympatric aquatic nonvenomous Banded Watersnakes (*Nerodia fasciata*; 0.01–0.39, $\bar{x} = 0.11$) and venomous Cottonmouths (*Agkistrodon piscivorus*; 0.19–0.53, $\bar{x} = 0.16$) indeed differed as predicted by MBT (data from Camper, 2022). To control for vulnerability, we compared pairs of sympatric nonvenomous and venomous snakes and found that when colubrids (*Masticophis*) and rattlesnakes (*Crotalus*) eat the same lizard species, mean RPMs are four to five times higher for the latter (Fig. 8, Appendix 9). Future applications of this approach could encompass nonconstrictors, constrictors, non-front-fanged, and front-fanged snakes (for categories, see Sullivan and Weinstein, 2017), comparing RPM and RPB for multiple prey types in different habitats and at local to global scales.

*Elongate Nonvertebrates as Diversely Different Prey.*—Centipedes, despite their conveniently attenuate shape, are never eaten by most snakes, presumably because of sharp-legged struggling abilities and venomous forcipules. Exceptions include several Old and New World viperids (e.g., Clark, 1967; Bea and Braña, 1988; Revault, 1996; Holycross et al., 2002; Hamanaka and Mori, 2020), black-headed and crowned snakes (*Tantilla*), and certain other rear-fanged New World colubrids (e.g., Solórzano et al. 2012; Rorabaugh et al., 2020; Enge et al., 2022) and one clade of African rear-fanged lamprophiids (centipede-eaters [*Aparallactus*]; Maritz et al., 2021a). If RPM and RPB were available for diverse centipede-eaters—e.g., generalists versus specialists, front-fanged versus not—one might test hypotheses about convergent evolution and adaptive significance of venom delivery systems (e.g., Hofmann et al., 2021). For example, among vipers, Terciopelos (*Bothrops asper*) have consumed centipedes with RPMs of 0.07 and 0.65 (Greene, 1992; Boada et al., 2005), whereas *Aparallactus* and *Tantilla* evidently cannot match that latter value (RPM for a Rim Rock Crowned Snake [*Tantilla oolitica*] that died eating a centipede was ~0.3, assuming equal densities of predator and prey; Enge et al., 2022); Plains Black-headed Snakes (*Tantilla nigriceps*), however, subdue centipedes faster than Rock Rattlesnakes (*C. Lepidus*; Rodríguez-Robles, 1994; Greene, 1997:81) and Mamushi Pitvipers (*Gloydius blomhoffii*; Hamanaka and Mori, 2020).

Defensive abilities of centipedes are obvious to humans who handle them, whereas earthworms are slimy but seemingly harmless. Among relatively basal snakes, although most scolecophidians feed only on small social insects, one species of Australasian Blindsnake (*Acutotyphlops subocularis*) eats annelids (Shine and Webb, 1990), as do uropeltids other than *Cylindrophis* (Rajendran, 1985). Species in several nonfanged colubrid lineages, usually with TL < 0.3 m, consume earthworms (e.g., *Atractus* [e.g., Dixon et al., 1976; Cunha and Nascimento, 1978; Martins and Oliveira, 1998; Camper and Zart, 2014; Passos et al., 2019]; wormsnakes [*Carphophis*; Barbour, 1960; Clark, 1970; Quinn and Carmody, 2021]; coffeesnakes [*Ninia*; Greene, 1975], and some other goo-eaters [*Dipsas*, *Sibon*; Ray et al., 2012]). Moreover, eating annelids is correlated with secondary fang loss in *Aparallactus modestus* (Portillo et al., 2019) and the homalopsid *Brachyorrhos* (Murphy et al., 2012); among front-fanged snakes, only one bizarre viper (*Atheris barbouri*; Rasmussen and Howell, 1998) and a few Australasian elapids (e.g., *Ogmodon vitianus*; Zug and Ineich, 1993) eat them. Cundall and Greene (2000:323–324) stated that worm-eaters

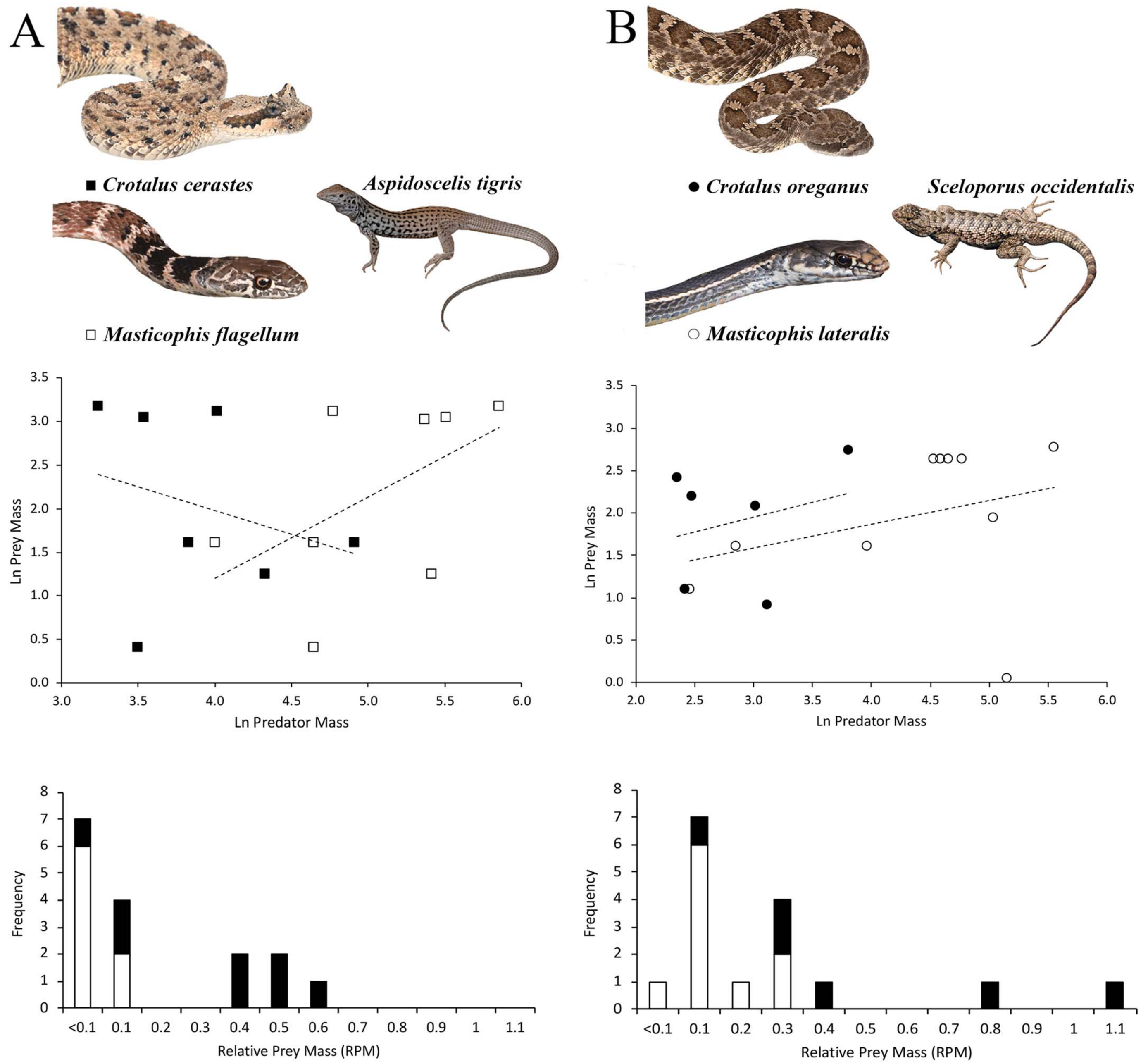

FIG. 8. Relative prey mass (RPM) differs between venomous crotalines and nonvenomous, nonconstricting colubrines feeding on the same prey types in western North America. (A) Sidewinder Rattlesnakes (*Crotalus cerastes*) and Coachwhips (*Masticophis flagellum*) that ate Western Whip-tailed Lizards (*Aspidoscelis tigris*). (B) Northern Pacific Rattlesnakes (*Crotalus oreganus*) and California Striped Whipsnakes (*Masticophis lateralis*) that ate sceloporines (*Sceloporus occidentalis* and *Uta stansburiana*). Animal images (top) by R. W. Hansen; log-transformed comparisons (middle) and frequency distributions (bottom) provide "moderate evidence" that RPM is "positively associated" with venom use by pitvipers (for methods, data, and clarifications, see Appendix 9).

are "nonconstrictors and nonvenomous, whereas those taking elongate vertebrates constrict (e.g., *Cylindrophis* and *Lampropeltis getula*) or are venomous (e.g., various fossorial elapids), suggesting... differences between annelids...and vertebrates... in mass-specific struggling abilities." Earthworms, however, might not always be easy to handle, as "Loss of the diastema [gap between fangs and other teeth] in *Toxicocalamus* could thus be interpreted as...for feeding on soft-bodied invertebrates that must be teased into the gullet because of the lack of any vertebral column or exoskeleton to resist longitudinal compression" (McDowell, 1969:507).

Certain New Guinea elapids (*Toxicocalamus*) that eat annelids (Shine and Keogh, 1996) have long puzzled herpetologists, either because venom is presumed unnecessary to immobilize such prey (McDowell, 1969:465, 467; Calvete et al., 2012:4095; O'Shea et al., 2015:256, 2018:404), or because those snakes, despite powerful toxins, are inoffensive when handled (Strickland et al., 2016:665 doubted their "small gapes and fangs... [can envenom] humans"; Kraus, 2017:574). The venom of *Toxicocalamus* nonetheless might be used defensively, given that the bright coloration of *Toxicocalamus ernstmayri* could be aposematic and Indigenous people believe its bite is deadly

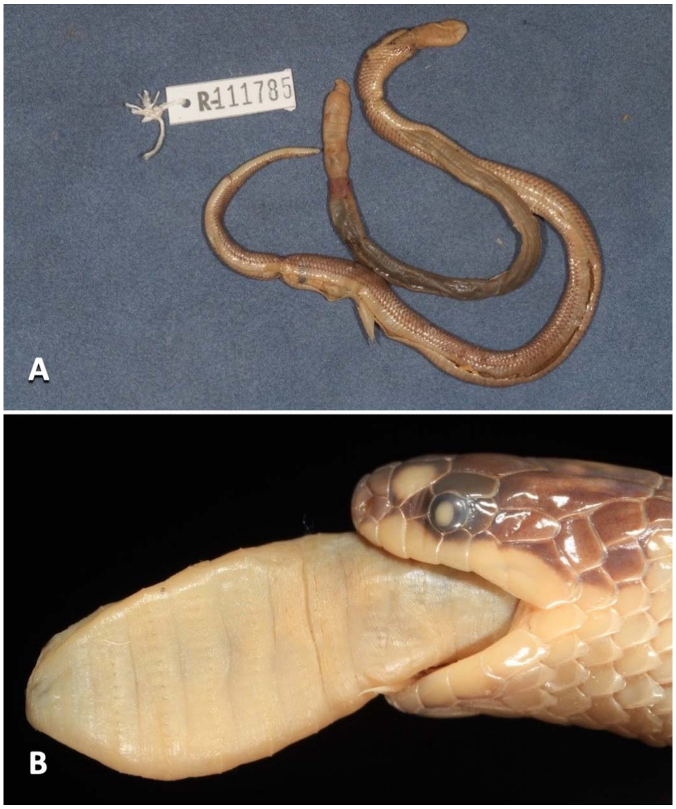

FIG. 9. (A) Venomous New Guinea worm-eating elapid, *Toxicocalamus loriae*, collected 23 December 1969, Kundiawa, Waghi Valley, Papua New Guinea (MCZ R-111785); total length (TL) of 178 mm, with recently ingested earthworm of roughly equal TL and relative prey mass of ~0.75—far heavier than quantified for any non-front-fanged worm-eating snakes; (B) snake's head with protruding earthworm posterior (see text for details; photos: M. O'Shea).

(O'Shea et al., 2018, 2020); moreover, other small elapids do kill people (e.g., Asian coralsnakes [*Sinomicrurus*; Kramer, 1977] and kraits [*Bungarus*; Moffett, 2002]).

We obtained data consistent with MBT's prediction that individual *Toxicocalamus* ingest earthworms with higher RPM than nonvenomous annelid-eaters. The holotype of *T. ernstmayri* (O'Shea et al., 2015), with an SVL of 1,100 mm and mass of 280 g, contained an earthworm with a TL of 436 mm (~40% snake SVL), mass of 85 g, and RPM of ~0.3. Assuming proportionality with those data, a *Toxicocalamus loriae*, with an SVL of 162 mm, contains an earthworm of a TL of ~160 mm and RPM of ~0.8 (Fig. 9; O'Shea et al., 2015); likewise, a *Toxicocalamus goodenoughensis* (Roberts and Austin, 2020), with an SVL of 271 mm, regurgitated an earthworm with a TL of ~200 mm and RPM of ~0.6. Those three snakes thus had an RPM of ~0.3–0.8 ($\bar{x} \sim 0.5$), compared to an RPM of 0.03–0.2 for worms eaten by three species of nonvenomous colubrids (Seib 1985a), a mean RPM of 0.07 for those eaten by Long-Tailed Alpine Gartersnakes (*Thamnophis scalaris*; Venegas-Barrera and Manjarrez, 2001), and a mean RPM of 0.3 for three eaten by *Atractus snethlageae* (Martins and Oliveira, 1998; Camper and Zart, 2014). Passos et al. (2019), however, illustrated two *Atractus* with perhaps high RPM annelid prey, suggesting that, like some other colubrids that eat soft-bodied invertebrates, they might have tranquilizing toxins (e.g., Carl, 1978; Salmão and Laporta-Ferreira, 1994; Zaher et al., 2014).

## MASS-BULK THEORY AND BIRDS AS SNAKE PREY

Birds epitomize high RPB at low RPM because of their beaks, long forelimbs, and feathers (e.g., Fitch and Twining, 1946; King, 1975; Mata-Silva et al., 2011; Camera et al., 2014; Jayne et al., 2022; Fig. 6b)—perhaps this is why so few snakes specialize on them, compared to hundreds of species that eat mainly amphibians, other reptiles, or mammals (e.g., Greene, 1997; Barends and Maritz, 2022a,b). Moreover, as detailed above for colubrids whose diets include prey types II–IV, often only longer individuals with wider gapes take birds (see also Rodríguez and Drummond, 2000). Nonetheless, serpent taxa for which feathered reptiles are dietary mainstays include anacondas (*Eunectes*; Rivas, 2020; Thomas and Allain, 2021), Asian catsnakes (*Boiga*; Greene, 1989a), African treesnakes (*Toxicodryas*; Greenbaum et al., 2021), Neotropical birdsnakes (*Phrynonax*; Robinson et al., 2005; Visco and Sherry, 2015; Zuluaga-Isaza et al., 2015), certain island vipers (e.g., Golden Lancehead [*Bothrops insularis*; Marques et al., 2012]), and Round Island Boas (*Casarea dussumieri*; Roesch et al., 2022); some of these same species or close relatives eat bats, another type IV prey (e.g., Esbérard and Vrcibradic, 2007; Szczygiel and Page, 2020). Future research thus could address whether ambushing versus searching snakes consume adults or nestlings and if birds and bats are functionally equivalent prey in terms of MBT. Ratsnakes (*Pantherophis*) and related colubrids discussed above warrant attention on both counts (e.g., Fitch, 1963; Plummer, 1977; Brown, 1979; Fitch, 1999; Rodríguez and Drummond, 2000; Rodríguez-Robles, 2002; Stake et al., 2005; DeGregorio et al., 2016; Wiseman et al., 2019; Barends and Maritz, 2022a,b).

Southwestern Speckled Rattlesnakes (*Crotalus pyrrhus*) eat birds more frequently than most other Pitvipers, and Cochran et al. (2021) insightfully explored geographic dietary variation in that context. Cochran et al. (2021) did not consider MBT, but two *C. pyrrhus* from California exemplify lower payoff for a House Sparrow (*Passer domesticus*; RPM 0.17, eaten by 107-g MVZ 229959) than a Desert Cottontail (*Sylvilagus audubonii*; RPM > 0.5, regurgitated by 991-g MVZ 229801). Ingestion times at constant RPM also are likely higher for type IV than the type II and III centipedes, lizards, and mammals that Rattlesnakes typically consume (Figs. 6b, 8; Fitch and Twining, 1946; Mata-Silva et al., 2011). Accordingly, are *C. pyrrhus* that emphasize birds in their diets behaviorally and/or morphologically specialized for high RPB and thus still obtain high payoff per meal, or do they compensate for lighter prey by more frequent feeding, slower growth, or lower fecundity?

Terrestrial, arboreal, and aquatic boids might also prove enlightening because although individuals of several species consume diverse types II and III prey with high RPM (Fig. 1, Appendix 4), some of them also eat birds. As predicted by MBT, island Boa Constrictors (*Boa constrictor* sensu lato) that consume passerines have lower RPM ($\bar{x} \sim 0.07$) than mainland individuals feeding with equal frequency on lizards, birds, and mammals ($\bar{x} \sim 0.44$; Boback, 2005). Among the longer mainland snakes—who also eat iguanas and mammals as diverse as carnivores and primates (Greene, 1983b)—the occasional Turkey Vulture (*Cathartes auratus*) is thus likely a low RPM-high RPB item (Boback, 2004; Platt et al., 2021).

### IS THERE A FUTURE FOR MASS-BULK THEORY IN SNAKE BIOLOGY?

To summarize, 1) MBT seeks to explain how RPM, RPB, prey shape, prey ID, and feeding frequency interact to influence the evolution, morphology, ecology, and behavior of snakes (see also Camper and Dixon, 2000; King, 2002; Vincent et al., 2006a,b; Close and Cundall, 2012; Loughran et al., 2013; Glaudas et al., 2019; Gripshover and Jayne, 2021; Barends and Maritz, 2022a,b; Cundall and Irish, 2022; Jayne et al., 2022; Kornilev et al., 2022). 2) Snakes encompass individual and phylogenetic differences in RPM, reflecting extensive taxonomic and shape diversity in their prey. An Australian Scrub Python (*Simalia kinghorni*) that ate a pademelon (*Thylogale*) with an RPM of 1.67 (Glaudas et al., 2019; S. Fearn, pers. com.) and a Sidewinder Rattlesnake (*Crotalus cerastes*) that contained a Western Whip-Tailed Lizard (*Aspidoscelis tigris*) with an RPM of 1.72 (Mulcahy et al., 2003) hold records for that parameter. *Dendroaspis polylepis* might exhibit the greatest RPM range, from ~0.001 for termites to ~1.0 or higher for duikers, galagos, and other mammals (Jackson, 1956; Branch et al., 1995; Phelps, 2002; Bourquin, 2021; Evans and Alexander, 2021). 3) RPB also shows great variation within and among species (Figs. 2, 8, 9; e.g., Voris and Voris, 1983; King, 2002; Martins et al., 2002; Close and Cundall, 2012; Hampton and Moon, 2013; Gripshover and Jayne, 2021; Jayne et al., 2022), although discerning patterns therein is daunting because of problems discussed above. 4) As for conservation, combining natural history with fanciful human parallels can enhance empathy for snakes among lay people; a 10.5-g Northern Pacific Rattlesnake's (*Crotalus oreganus*; MVZ 229849) likely first meal, an 11.2-g Western Fence Lizard (*Sceloporus occidentalis*; RPM 1.07), was roughly equivalent to HWG ingesting a 95-kg hotdog without using hands or cutlery.

*What is Needed?*—Scientific, logistical, and cultural factors are hampering snake research in ways that could not have been predicted decades ago. Greene (1986b, 2005a) identified a lack of publishing and archiving outlets as among impediments to natural history, but these problems now are minimized by journals devoted to individual observations (Teodoro et al., 2022), high-profile venues promoting descriptive studies (e.g., Maritz et al., 2021b; Enge et al., 2022), and public platforms for aggregating huge data sets (e.g., Grundler, 2020; Maritz and Maritz 2020; Putman et al., 2021). Moreover, theoretical considerations of biodiversity "knowledge short-falls" (Hortal et al., 2015), "next-gen natural history" (Tosa et al., 2021), and globalizing studies of snake diets (Maritz et al., 2021b) all portend a welcome increase in knowledge. The challenge for expanding MBT will be to gather more rich content and widely applicable data—but what would doing that look like, whence could they come, and what obstacles await?

Complete accounts of snakes feeding would include where and when; direction of ingestion and other behavioral contexts; ID, sex, linear measurements, and mass for predators and prey; and validating information, e.g., observer's name and contact, voucher photographs, and/or museum catalog numbers (Maritz et al., 2021b). If those data were available for taxonomically diverse samples of many snakes and meals, collected with multiple methods, we could better assess biases and measurement errors (e.g., Rodríguez-Robles, 1998; Glaudas et al., 2017a; Maritz and Maritz, 2020; Durso et al., 2022); with those data, we could examine individual, ontogenetic, sexual, seasonal, and geographic variation prior to posing other questions (e.g., Pleguezuelos et al., 1994; Luiselli, 2006b; Glaudas et al., 2019; Wiseman et al., 2019; Grundler and Rabosky, 2021; Durso et al., 2022). Likewise, we need RPM standardized for predator TL to transcend variation in reproductive, nutritional, and hydration status (Cundall, 2000; Rivas, 2020:92). We also hope that functional morphologists will fine-tune measuring RPB beyond lab conditions (e.g., Jayne et al., 2022), making their insights applicable to field observations and preserved specimens (see especially Close and Cundall, 2012:1046–1048). These are all technical matters, so gaining additional RPM and RPB data are, in principle, possible, although special considerations might sometimes prohibit some procedures (e.g., forced regurgitations; Reinert et al., 2008). Future projects could thus use massive, detailed datasets to explore MBT in terms of global patterns of snake evolution and ecology (e.g., Luiseilli, 2006a; Glaudas et al., 2019; Grundler and Rabosky, 2021; Cundall and Irish, 2022; Kornilev et al., 2022).

*Remaining Obstacles.*—Gathering MBT data from live and preserved snakes might prove ever more difficult, as regulatory overburdens for field biology threaten to prevent all methods except photography (e.g., Greene and Losos, 1988; Alexander et al., 2021). Exemplifying this trend, one herpetologist, after decades of permit and protocol approvals, quit teaching with live reptiles and collects occasional specimens with a hunting license; a young researcher concluded that beyond agency and institutional compliance, consequences of mistakenly breaking laws are so severe he no longer saves roadkill for museums. Now add in that those touting new methods often minimize their shortcomings (e.g., fecal DNA requires facilities and funds and yet yields limited data; Brown et al., 2014), focus on prey taxonomy (Hoefer et al., 2021; Durso et al., 2022), or emphasize problems with museum specimens ("the traditional method to gather snake diet data," Glaudas et al., 2019:758; but see, e.g., Fitch, 1960; Arnold, 1993; Luiselli and Akani, 2003). The negative effect of these trends is shown by a curator who denied our request to examine common species of *Lampropeltis* because "new imaging technologies can explore stomach contents without damaging valuable specimens, new generations of students rarely contribute museum specimens, and many recently common species are now rare or extinct and irreplaceable." Of course, we decry the last two realities, having prepped thousands of specimens and focused our careers on conservation. More importantly, museum specimens offer unique prospects for studying geographic variation in snake diets compared to other data sources (e.g., Sparks et al., 2015; Wiseman et al., 2019), so adopting that curator's attitude would lead to less learned about snakes and museums failing to meet their potential for studying biodiversity.

We also are not optimistic about community science contributing to MBT, despite its many positive aspects (Maritz and Maritz, 2020; Durso et al., 2021; Putman et al., 2021; see Cooper et al., 2021, for "community" versus "citizen" science). Recall that in our "Natural History Notes" survey described above, all 33 records lacking RPM (85% of 39 total) were from field observations. Obtaining additional data would have necessitated touching snakes, which is usually illegal without a permit as well as problematic because of animal welfare and, with venomous species, includes safety considerations (e.g., Ribble and Rathbun, 2018). Three records for which prey were available still would have required an instrument to provide RPM, so we wondered

Fig. 10. (A) Terciopelo (*Bothrops asper*) shortly after ingesting moderately heavy, bulky prey (perhaps a Tropical Cottontail [*Sylvilagus gabbi*] seen earlier at the site); 7 December 2021, Estación Biológica La Selva, Heredia Province, Costa Rica (photo: W. Lopez). (B) Rock was 18 cm wide, implying pitviper’s total length was ~1.26 m (data, interpretation, and photo: O. Vargas Ramírez).

whether lay naturalists might carry portable scales—costing and weighing less than cheap binoculars—but community science innovators told us that asking untrained, unlicensed people to touch live or dead animals would be poorly advised. Perhaps instead the most that can be promoted for community scientists to bolster MBT is putting scale bars in photos, such that linear dimensions and mass can be estimated by comparison with organisms of similar size, visible animal structures (e.g., a hindfoot), or objects (e.g., a rock, Fig. 10; see also Barten, 2010; Marques et al., 2010; Close and Cundall, 2012; Feldman and Meiri, 2013; McMartin, 2013; Schalk and Cove, 2018:2; Quinn and Carmody, 2021). Then again, if wild hummingbirds can weigh themselves (Carpenter et al., 1983), perhaps someday snakes will too.

We hope to have convinced readers that for many serpents, eating prey that are heavy, bulky, or both is at the core of their existence. If obstacles to data acquisition are not solved, however, Godley’s (1980) complaint about data quality will still apply 40 more years hence—biologists might well have 100,000 diet records, encompassing 75% of the world’s snake species and accessible with a few keystrokes (Grundler and Rabosky, 2021; Maritz et al., 2021b), but they mostly will document when, where, and what taxa were eaten. Much of that dietary information will be relevant to only a subset of potential applications, and MBT, however central to snake biology, will remain based mostly on data available now.

## Coda

Watching and writing about animals has blessed me (HWG), over the course of roughly seven decades—including during preparation of this paper—with a resilient sense of purpose as well as boundless pleasure and satisfaction. My childhood love of reptiles began in Texas at age 7, thanks to “dry-land terrapins” (Eastern Box Turtles [*Terrapene carolina*]) and “horned frogs” (Texas Horned Lizards [*Phrynosoma cornutum*]) on grandpa’s piney woods dirt farm. Within a few years, I met a Western Diamond-backed Rattlesnake (*Crotalus atrox*) at a camp for military brats in the Hill Country and was impressed that our soldier-counselors did not kill the rattlesnake. Since that first venomous serpent, there have been countless others in more than a dozen countries, along with many good times and some so bad they still haunt me. As a civilian first responder during college years, I helped many people survive violence, sudden illness, and emergency childbirth. By the age of 27, I had pulled a headless teenager out of a wreck, failed to save a toddler in anaphylactic shock while her mother sat screaming next to me, and lost a favorite professor and a lover to murders. Luckier breaks during my youth included as an army medic being sent to Germany instead of Vietnam, and, at a time when few academics thought snakes worthy of study, having William Pyburn and Gordon Burghardt as graduate advisors.

After earning a Ph.D., my good fortune has included for 20 years teaching herpetology and vertebrate natural history at the University of California, Berkeley, while serving as curator of herpetology in the MVZ. A 1999 move to Cornell University brought new challenges, as I lectured on evolution and ecology to thousands of mostly business majors and then fine-tuned “walking and talking the Tree of Life” for biology undergraduates (Ballen and Greene, 2017). Along the way, I penned two books that bridged science and art, with an emphasis on serpents of course (Greene, 1997, 2013). More than a decade ago, I veered into anthropology and shifted research emphasis to snake-primate interactions (e.g., Headland and Greene, 2011; Gardner et al., 2015; Greene, 2017, 2018, 2020; Kazandjian et al., 2021).

Some of my most rewarding activities as a field biologist have occurred since retirement. In 2019, I realized a longstanding dream of observing big elapids by helping former Cornellians Bryan and Robin Maritz, along with South African biologist Graham Alexander, during their research on Cape Cobras (*Naja nivea*) in the Kalahari Desert. Spying on those magnificent yellow snakes as they foraged on Puff Adders (*Bitis arietans*) and Sociable Weavers (*Philetairus socius*) did not disappoint (Fig. 11a–c; Maritz and Maritz, 2019). Meanwhile, Emily Taylor, an English major in my Berkeley classes, had become a distinguished professor at Cal Poly State University, San Luis Obispo, and elected president of the American Society of Ichthyologists and Herpetologists. Two decades after Emily first visited the Mojave Desert with my herpetology course, I joined her class’s trip there, overflowing with pride for the phenomenal enthusiasm she inspires in students (Fig. 11d). Mentors, mentees, and professional colleagues are not obligated to be friends, so I feel blessed to count these people, along with coauthor Kevin Wiseman, as among my dearest.

As 2019 ended, I began restoring a chunk of Hill Country, named Rancho Cascabel for its resident *C. atrox*. Among the many joys of rural existence is enhanced familiarity with a place and its biota, across seasons and years, as well as surprises. In 2020, for example, I encountered a pair of Texas Patch-nosed Snakes (*Salvadora lineata*) mating near my Longhorns’ water trough (Fig. 12)—and thereby confirmed in nature the male of this species’ head-biting behavior, which was previously documented only for captives (Burchfield et al., 1982). Strolling on down life’s road, I hope to observe many more serpents, including some consuming meals that are heavy, bulky, or both.

FIG. 11. Friends, field trips, and retirement. (A) HWG observing adult Cape Cobra (*Naja nivea*; left arrow) and adult female Puff Adder (*Bitis arietans*; right arrow) at Tswalu Kalahari Reserve, South Africa; 26 February 2019 (photo: R. A. and B. Maritz). (B) Same *N. nivea* inspects *B. arietans*, which it repeatedly envenomed and eventually ate (photo: H. W. Greene). (C) Another *N. nivea* looks down from Sociable Weaver (*Philetairus socius*) nest colony (photo: H. W. Greene). (D) Cal Poly State University, San Luis Obispo herpetology class at Pisgah Lava Flow, San Bernardino County, California; 12 May 2019; arrows indicate Professor Emily Taylor (left) and HWG (photo: E. N. Taylor).

*Acknowledgments.*—Special thanks to Erin Muths for inviting and so patiently editing this contribution, published half a century after the Society for the Study of Amphibians and Reptiles (SSAR) boosted an insecure Ph.D. candidate's confidence with its first Outstanding Student Paper Award (for Greene, 1973b). This is the final installment in the Journal of Herpetology's senior researchers' perspectives series, and we look forward to future pieces by younger, more diverse SSAR members. We appreciate the many museum curators who facilitated our studies, which have been supported primarily by the MVZ, the Lichen Fund, a Cornell University Stephen H. Weiss Presidential Fellowship, and the National Science Foundation (BSR 83-00346, OPUS 1354156). For curatorial assistance with this paper, we thank C. Austin and J. Roberts (Louisiana State University Museum of Zoology), C. Dardia and C. Dillman (CUMV), T. LaDuc (TNHC), E. Smith (UTA), and C. Spencer (MVZ); M. O'Shea, along with A. Baldinger, J. Hanken, and J. Rosado of MCZ, were especially helpful with the *Toxicocalamus* example. We are especially grateful for feedback on our manuscript from S. Boback, G. Burghardt, D. Cundall, L. Alencar, C. Feldman, B. Maritz, G. Pauly, K. Schwenk, and J. Sigala-Rodríguez. B. Halstead advised on statistics and J. Sigala-Rodríguez prepared the Resumen. For other assistance we thank K. Adler, G. Alexander, A. Bauer, B. Bauer, C. Bell, K. Bemis, E. Braker, H. Bringsøe, G. Burghardt, R. Dowling, A. Durso, A. Echelle, A. Echternacht, S. Fearn, J. Fitzpatrick, M. Fitzpatrick, K. Glaser, X. Glaudas, E. Greenbaum, D. Hailey, W. Hallwachs, R. Hansen, D. Hendrickson, T. Hibbitts, E. Hillman, R. Huey, D. Janzen, B. Jayne, D. Johnson, J. Jones, D. Kizirian, W. Koenig, J. Losos, T. Lott, L. Luiselli, R.

FIG. 12. Mating behavior of Texas Patch-nosed Snakes (*Salvadora lineata*) at Rancho Cascabel, Mason County, Texas; observations were made at a distance of 1–2 m from the pair and began a few minutes before 0953 h CDT, 5 May 2021 (photos: H. W. Greene). (A) Snakes remained within a ~1-$m^2$ patch of sparse low vegetation between corral gate post and light-colored rock, lower center in image. (B) When discovered and thereafter, the longer, thicker male had grasped the female's head in his jaws and their bodies were loosely aligned, in hairpin or irregularly semicircular coils; their cloacae initially were not juxtaposed (1010 h). (C) Male grasping female's head during copulation (0954 h). (D) Intromission involved the right hemipenis (here, at 1056 h).

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## APPENDIX 1.

References to aspects of MBT for snakes include Voris and Moffett (1981), Pough and Groves (1983), Herzog and Bailey (1987), Mushinsky (1987), Sazima and Martins (1990), Shine (1991), Arnold (1993), Forsman and Lindell (1993), Martins and Oliveira (1998), Rodríguez-Robles et al. (1999a,b), King (2002), Martins et al. (2002), Rodríguez-Robles (2002), Mehta (2003), Andreadis and Burghardt (2005), Boback (2005), Vincent et al. (2006a,b; 2007), Glaudas et al. (2008), Nowak et al. (2008), Vincent and Mori (2008), Willson and Hopkins (2011), Close and Cundall (2012), Hampton and Moon (2013), Loughran et al. (2013), Cundall et al. (2014), Maritz and Alexander (2014), Ribeiro et al. (2016), Banci et al. (2017), Glaudas et al. (2017a,b), Means (2017), Bartoszek et al. (2018), Jayne et al. (2018), Glaudas et al. (2019), Maritz et al. (2019), Gripshover and Jayne (2021), Marques and Sazima (2021), Natusch et al. (2021), Reinert et al. (2021), Barends and Maritz (2022a), Cundall and Irish (2022), and Jayne et al. (2022).

## APPENDIX 2.

References to general aspects of snake feeding biology without data on RPM or RPB include Bea et al. (1992), Webb and Shine (1993a), B. Greene et al. (1994), Dwyer and Kaiser (1997), Saviozzi and Zuffi (1997), Rodríguez-Robles (1998), Fitch (1999), Scanlon et al. (1999), Luiselli et al. (2001), Carreira Vidal (2002), Luiselli and Akani (2003), Quick et al. (2005), Luiselli (2006a,b), Esbérard and Vrcibradic (2007), Shine et al. (2007), Dugan and Hayes (2012), Natusch and Lyons (2012), Brown et al. (2014), Fabre et al. (2016), Klaczko et al. (2016), Sullivan and Weinstein (2017), da Silva et al. (2018), Portillo et al. (2019), van den Burg (2020), Cleuren et al. (2021), Grundler and Rabosky (2021), Naik et al. (2021), and Durso et al. (2022).

## APPENDIX 3.

References with RPM data from nature for non-front-fanged colubroids include Brown (1958), Tyler (1977), Seib (1984, 1985b), Hero and Magnusson (1987), Greene (1989a,b), Branch and Burger (1991), Greene and Jaksic (1992), Whiting et al. (1992), Pleguezuelos et al. (1994), Lacey et al. (1996), Shine et al. (1996), Capula et al. (1997), Reed (1997), Martins and Oliveira (1998), Rodríguez-Robles and Greene (1999), Rodríguez-Robles et al. (1999a,b,c), Feldman and Wilkinson (2000), Camper and Dixon (2000), LaBonte (2001), Venegas-Barrera and Manjarrez (2001), Rodríguez-Robles (2002), Greene and Rodríguez-Robles (2003), Cobb (2004), Moon and Rabatsky (2004), O'Connor et al. (2010), Greene et al. (2010), Dartez et al. (2011), Durso and Kiriaszis (2011), Vrcibradic et al. (2011), Wostl et al. (2012), Duarte (2012), Gatica-Colima and Córdoba-Reza (2012), Laspiur et al. (2012), Linares and Eterovick (2012), Solórzano and Greene (2012), Winck et al. (2012), Camper and Zart (2014), Mendelson and Adams (2014), Casper et al. (2015), Da Silva et al. (2015), Zuluaga-Isaza et al. (2015), Stender-Oliveira et al. (2016), Pizzatto et al. (2018), Oliveira et al. (2019), Wiseman et al. (2019), Valencia-Herverth et al. (2021), and Camper (2022).

## Appendix 4.

References with RPM data from nature for aniliids, uropeltids, boids, and pythonids include Hay and Martin (1966), Greene (1983a), Trail (1987), Slip and Shine (1988), Strussmann (1997), Martins and Oliveira (1998), Rivas (1998), Shine et al. (1998), Rodríguez-Robles et al. (1999b), Boback et al. (2000), Fearn (2002), Boback (2004, 2005), Fredriksson (2005), Pizzatto et al. (2009), Reed and Rodda (2009), Barros et al. (2011), Headland and Greene (2011), Boback et al. (2016), Ribeiro et al. (2016), Bartoszek et al. (2018), Glaudas et al. (2019), Rivas (2020), Natusch et al. (2021), Reinert et al. (2021), Cundall and Irish (2022), and Pommer-Barbosa et al. (2022).

## Appendix 5.

References with RPM data from nature for front-fanged colubroids include Fitch and Twining (1946), Fitch (1960), Abalos et al. (1964), Voris and Moffett (1981), Greene (1984, 1992), Haagner (1991), Branch et al. (1995), Lutterschmidt et al. (1996), Martins and Oliveira (1998), Fitch (1999), Hardy and Greene (1999), Cundall and Greene (2000), Correa-Sanchez et al. (2001), Taylor (2001), Branch et al. (2002), Martins et al. (2002), Pauly and Benard (2002), Rodríguez-Robles (2002), Schuett et al. (2002), Valdujo et al. (2002), Mulcahy et al. (2003), Nogueira et al. (2003), Oliveira and Martins (2003), Swannack and Forstner (2003), Moon et al. (2004), O'Shea et al. (2004), Shepard et al. (2004), Hartmann et al. (2005), Glaudas et al. (2008), Marques et al. (2010), Gavira and Loebmann (2011), Hampton (2011), Horan et al. (2011), Hovey and Comrack (2011), Mata-Silva et al. (2011), Santana (2011), Siler et al. (2011), Sorrell et al. (2011), Warner (2011), Warner and Alexander (2011), Maritz (2012), Loughran et al. (2013), Camera et al. (2014), Colbert et al. (2014), Maritz and Alexander (2014), Tetzlaff et al. (2014), Webber et al. (2016), Means (2017), Glaudas et al. (2019), Campbell and Hewlett (2021), Da Silva et al. (2021), Marques and Sazima (2021), Martínez-Vaca León and Morales-Mávil (2021), Camper (2022), and Carbajal-Márquez et al. (2022).

## Appendix 6.

References on snake taxa that do not mention RPM or RPB include López Jurado and Caballero (1981), Bea and Braña (1988), Bhupathy and Vijayan (1989), Jones and Whitford (1989), Zug and Ineich (1993), Revault (1996), Shine and Keogh (1996), Luiselli and Akani (1998), Luiselli and Angelici (1998), Rodríguez and Drummond (2000), Hill et al. (2001), Holycross et al. (2001), Platt et al. (2001), Shewchuk and Austin (2001), Clark (2002), Holycross et al. (2002), Gardner and Mendelson (2003), Monteiro et al. (2006), Machio et al. (2010), Gaiarsa et al. (2013), Prudente et al. (2014), Sparks et al. (2015), Carbajal-Márquez et al. (2016, 2020), Platt et al. (2016), Layloo et al. (2017), Prötzel et al. (2018), Bringsøe (2019), Berg et al. (2020), Bringsøe et al. (2020), Cabral et al (2020), Escalante and Acuña (2020), Feldman et al. (2020), R. Maritz et al. (2020), Vela et al. (2020), Vásquez-Cruz (2020), Cochran et al. (2021), Conradie and Pinto (2021), Eisfeld et al. (2021), Faraone et al. (2021), Hoefer et al. (2021), Maritz et al. (2021a), Mebarki et al. (2021), and Thomas and Allain (2021).

## Appendix 7.

That some snakes consume prey parts rather than intact animals scarcely could have been imagined at the time of Gans' (1961) landmark paper. Subsequent discoveries include Texas Blindsnakes (*Rena dulcis*) and Brahminy Blindsnakes (*Indotyphlops braminus*) removing termite heads prior to ingestion of their abdomens (Reid and Lott, 1963; Mizuno and Kojima, 2015), Northern Cat-eyed Snakes (*Leptodeira septentrionalis*) and Giant Parrot Snakes (*Leptophis ahaetulla*) tearing off portions of treefrog egg masses (Warkentin, 1995; Gomez-Mestre and Warkentin, 2007), Gerard's Watersnakes (*Gerarda prevostiana*) removing and ingesting crab legs (Jayne et al., 2002), Taiwan Kukri Snakes (*Oligodon formosanus*) slitting and swallowing contents of sea turtle eggs (Huang et al., 2011), Banded Kukri Snakes (*Oligodon fasciolatus*) slicing open and eating internal organs of Black-spined Toads (*Duttaphrynus melanostictus*; Bringsøe et al., 2020), Blunt-headed Slug-eaters (*Aplopeltura boa*) sawing off opercula before ingesting the bodies of snails (Kojima et al., 2020), and Queen Snakes (*Regina septemvittata*) eating appendages of crayfish (Gripshover and Jayne, 2021). In some of these examples, snakes perhaps consumed pieces to avoid toxic body parts (e.g., Mizuno and Kojima, 2015; Bringsøe et al., 2020), whereas a Cottonmouth (*Agkistrodon piscivorus*) pulling chunks off fish carrion (Campbell and Hewlett, 2021) is noteworthy because the intact RPM of ~3 was almost twice the recorded maximum for snakes.

## Appendix 8.

For five Coachwhips (*Masticophis flagellum*) that consumed five Texas Horned Lizards (*Phrynosoma cornutum*) and one Coast Horned Lizard (*Phrynosoma blainvilli*), RPMs were 0.028 (Tyler, 1977), 0.033 and 0.066 (Whiting et al., 1992), 0.041 (LaBonte, 2001), and 0.006 and 0.056 (TNHC 87848 contained two *P. cornutum*; T. LaDuc, pers. com.), thus a range of 0.006–0.056 ($\bar{x} = 0.038$). For eight *M. flagellum* that ate type II Western Whip-tailed Lizards (*Aspidoscelis tigris*; Appendix 9), RPMs were 0.015–0.191 ($\bar{x} = 0.078$). A conservatively two-tailed Mann-Whitney *U*-test implies this is "weak evidence" that the medians are different ($P = 0.14$; significance terminology of Muff et al., 2022:206).

## Appendix 9.

For six Northern Pacific Rattlesnakes (*Crotalus oreganus*) eating sceloporines (four Western Fence Lizards [*Sceloporus occidentalis*], two Side-blotched Lizards [*Uta stansburiana*]), masses (g) of prey and predator, respectively, followed by sources are as follows: 11.2, 10.05, MVZ 229849; 3.0, 11.2, MVZ 6842; 2.5, 22.5, MVZ 33913; 8.0, 20.5, MVZ 50213; 15.5, 45.0, HWG 1112; and 9.04, 11.91, Pauly and Benard (2002). For 10 California Striped Whipsnakes [*Masticophis lateralis*] eating sceloporines the values were as follows: 14.0, 118.1, MVZ 227; 14.0, 98.2, MVZ 5876; 14.0, 92.7, MVZ 60986; 7.0, 153.3, MVZ 43636; 16.0, 257.6, MVZ 21915; 14.0, 105.3, MVZ 26007; 5.0, 52.8, MVZ 36428; 1.0, 173.1, MVZ 35463; 5.0, 17.3, MVZ 93655; and 3.0, 11.7, MVZ 43638. For seven Sidewinder Rattlesnakes (*C. cerastes*) eating Western Whip-tailed Lizards (*Aspidoscelis tigris*), the results were as follows: 22.5, 55.6, MVZ 57606; 7.0, 75.8, MVZ 7458; 19.0, 34.5, HWG 851; 11.0, 135.5, HWG 967; 24.0, 46.2, MVZ 63664; 11.0, 25.5, RLS 6960; and 20.5, 33.0, RLS 8141. For eight Coachwhips (*M. flagellum*) eating *A. tigris* the values were as follows: 22.5, 118.0, RWH 942; 3.5, 224.2, MVZ 20394; 21.0, 247.0, CAS 10308; 5.0, 54.8, MVZ 6692; 5.0, 103.8, MVZ 13889; 24.0, 348.5, RWH 925; 1.5, 103.8, MVZ 13889; and 20.5, 215.1, MVZ 5546. We compared RPM medians with two-tailed Mann-Whitney *U*-tests and size effects with analyses of covariance on log-transformed masses; *P*-values were $<0.05$ (some $<0.02$) implying at least "moderate evidence" of differences (Muff et al., 2022). Note only small *C. oreganus* consumed lizards, whereas *C. cerastes* of all sizes ate them; both *Masticophis* species attain a TL of >1 m, such that lizard species with small adult masses cannot provide high RPM for adults of those snake species.