POINTS OF VIEW

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Challenges and Opportunities in the Study of Snake Diets

The importance of feeding in the evolution and ecology of snakes is difficult to overstate. Feeding and diet have had profound influences on phylogenetic diversification (Greene 1983), promoted morphological (Hoso et al. 2007; Sherratt et al. 2018) and behavioral diversification (Greene and Burghardt 1978; Hoso et al. 2007; Glaudas and Alexander 2017), and have driven the evolution of extreme physiology (Secor and Diamond 1998). It is through feeding that snakes have the potential to influence faunal communities dramatically (Savidge 1987; Dorcas et al. 2012). Feeding is also an important driver of venom biochemistry (Daltry et al. 1996; Barlow et al. 2009; Modahl et al. 2018; Holding et al. 2021) with evidence suggesting that, generally, venoms are more likely to have evolved for predation purposes than for defense (Ward-Smith et al. 2020; but see Kazandjian et al. 2021). However, the fact that venom is also used defensively has devastating impacts on humanity through the global burden of snakebite (Gutiérrez et al. 2017; Williams et al. 2019). The risk of a defensive bite from a venomous snake, or even falling prey to a giant snake (Headland and Greene 2011), has also influenced our own evolution in important ways (Isbell 2009) and is likely the reason that snakes play such a central role in much of human mythology (Stanley 2008) and psychology (Davey 1994).

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Accordingly, one might expect that the study of snake diets—a key element in the diversification of snakes, possibly the primary mechanism by which snakes interact with ecosystems, and a likely selective pressure in venom evolution—would be robust and relatively complete. Remarkably, this is not obviously true.

Because of the complex, multidimensional nature of animal diets (Nielsen et al. 2018), quantifying the completeness of our understanding of snake diets is challenging. However, two recent studies illustrate the limits of our knowledge. In the first, Grundler (2020) published a catalogue of feeding records for snakes—dubbed SquamataBase. Although still in development, it represents the first attempted quantitative synthesis of snake diets globally. However, it includes information from only 1248 species of snakes (ca. 32% of all species), 733 (58.7%) of which are represented by ten or fewer records. In the second, Maritz and Maritz (2020) examined the diets of southern African snakes and revealed the ease with which 327 novel feeding records were reported on social media in fewer than five years. The lack of representation of many species in the available literature, and the outlandish ease with which novel prey types can be detected in even "well-known" species highlights the incomplete nature of the global catalogue of snake feeding records, raising concerns for the basis for our understanding of snake feeding outside of a few well-studied systems.

The availability of species-specific information about diets unsurprisingly varies dramatically across the snake tree of life. Generally speaking, snake species can be assigned to one of four classes based on what is known about their diets. For a small number of species, detailed studies have used large numbers of feeding records from multiple populations to examine diverse topics including interspecific, geographic, interpopulation, seasonal, sexual, and ontogenetic variation in diet (e.g., Daltry et al. 1996; Shine et al. 1998; Luiselli et al. 2001; Luiselli 2006a, b; Shine and Wall 2007; Smith et al. 2019; Wiseman et al. 2019). For these species, robust catalogues of feeding records facilitate important intraspecific contrasts that have significant inferential power and form the basis of our theoretical understanding of snake feeding and diets. For many other species, the literature reports a moderate number of prey items in a way that allows the diet of the species to be described in generalized terms. These generalized descriptions are informative for making interspecific comparisons and are useful for contextualizing species in public outreach initiatives, but often rely heavily on taxonomic aggregation of prey types (e.g., Maritz et al. 2019; Portillo et al. 2019), simplifying important dietary complexity, and, ultimately, limiting the inference that can be drawn from detailed intra- and

Table 1. Information ideally recorded from in situ observations of feeding, or the examination of stomach contents so as to maximize later utility to a range of inquiries. In most instances, not all of this information will be available, but for the majority of observations, some of it is available but rarely recorded/reported.

Information	Description
Predator ID	Species-level identification of the snake predator with photo and/or museum specimen voucher number(s), and/or confirmation of ID by experts. Identification should be supplemented with reasoning.
Prey ID	Species-level identification of the prey with photo and/or museum specimen voucher number(s), and/or confirmation of ID by experts. Identification should be supplemented with reasoning.
Time and place	Time, place, and microhabitat description of the event. Locality information should include both GPS coordinates and locality and microhabitat descriptions. Date and time to be provided at best available resolution.
Predator characteristics	Predator characteristics including linear measurements (snout–vent length, tail length, head width and length), mass, sex, apparent body condition, reproductive state, and presence of pre-shed cloudy eyes.
Prey characteristics	Prey characteristics including linear measurements (specifics depend on prey type), mass, sex, condition (e.g., for lizards, whether tail freshly autotomized).
Ingestion notes	Direction (e.g., prey swallowed head-first vs. tail-first vs. bent-double), order (e.g., number of prey present in stomach and sequence of consumption), and behavior (including post-ingestion behaviors e.g., wiping the mucosa on the substrate) of ingestion.
Digestion notes	Extent of digestion (e.g., tail and hind feet only present, intact but viscera exposed) of prey items observed in the guts of preserved or freshly-killed snakes.
Behavior notes	Behavioral aspects including prey subjugation behavior (e.g., strike-induced chemosensory searching, pinning the prey using a coil, use of venom or constriction), time to prey quiescence, prey ingestion behavior (e.g., pterygoid walking), notes on damage to predator and/or prey (e.g., tooth marks), seemingly incidental stomach contents (e.g., plant material, ants and other arthropods perhaps indicative of secondary ingestion or carrion consumption), and the potential influence of observers on behavior.
Authenticity notes	Notes reflecting any reasons to suspect that feeding event took place in captivity (e.g., specimen tags sometimes record animal had been captive; presence of albino lab rodents, or extralimital prey in stomachs). Photographic evidence with appropriate context and provenance.
Sample notes	For studies where multiple specimens examined report: total number of specimens examined; number of specimens with and without food in the stomach; total number of prey items; distribution of prey items among stomachs. Ideally it should be possible to assign every prey item to the individual snake it came from to facilitate post-hoc analyses. If stomachs, intestines, and/or faeces are examined separately, report as such. If live, wild snakes are recaptured and checked for food multiple times, report individual study IDs and dates checked (including when food was absent). Report whether or not any data have been previously published.

inter-specific comparisons. Globally, the majority of species fall into a third class: species for which the extent of our knowledge regarding diet is either known from only a few published records and/or supplemented by inference of diet from closely related or ecologically similar species. Lastly, there remain some newly described or rarely encountered species for which no information, detailed or otherwise, is available. Given the numerical distribution of species within these four classes, we know lots about a few species, a little bit about many species, and nothing about some species. Certainly, our suite of well-studied species can act as model systems from which we derive a more widely applicable understanding. Unfortunately, how representative those species are for snakes as a whole remains to be seen. Moreover, the ability of robust dietary information to inform understanding of venom biochemistry and its effect on humans is only likely to arise with species-specific (or even population-specific) dietary information, and not from an understanding of feeding by snakes in model systems.

What needs to change to improve this status quo? The following is our perspective on changes that we, as the herpetological community, can implement to start filling some of the obvious gaps in our knowledge and shifting snake feeding and dietary ecology beyond the anecdotal. These suggestions relate to: 1) maximizing the utility of observations by gathering appropriate information from each, 2) how systematic studies of snake diets are conducted and used, 3) the mechanisms for reporting once-off feeding observations and records, and 4) the development of a centralized repository for feeding records.

1. Maximizing the utility of observations by gathering and reporting valuable metadata.—An obvious manner to advance the study of snake diets and feeding is to ensure that the appropriate information regarding each record is gathered and reported. For some purposes, predator and prey identification might suffice, but other information (Table 1) can be critical for functional morphologists or behavioral ecologists. These data are often available but never recorded or reported. This challenge could be overcome with the development of standardized data collection sheets freely available from society websites.

2. Systematic studies of snake diets must be prioritized for poorly-known species, must always be preferentially cited over field guides, and must acknowledge method-specific biases.—Systematic studies of snake diets—primarily through the dissection of museum specimen gut contents, but also through extensive field studies with direct observation and palpation of stomachs (Fitch 1963, 1965), fixed videography (Clark 2006; Glaudas et al. 2017), or with molecular techniques aimed at either identifying prey species using fecal DNA (Brown et al. 2014) or stable isotope analyses (Durso and Mullin 2017; Rebelato et al. 2020; Durso et al. 2021)—form the cornerstone of what is known about snake feeding. In an effort to shift the global understanding of snake feeding forward, studies like these must be prioritized, especially in poorly studied regions. Unfortunately, descriptive dietary studies are often unpopular research ventures because the secretive nature of snakes makes them difficult focal organisms to study, requiring large time and resource investments that often only yield small sample sizes. Moreover, descriptive dietary studies are unlikely to be published in high-impact journals (Chavan and Penev 2011) and when published, are rarely cited, with many authors preferring to cite generalized, sometimes poorly-substantiated dietary descriptions from field guides instead. As producers and consumers of this kind of natural history data, we have an ethical obligation to cite descriptive, empirical dietary studies, thus giving credit where credit is due (van den Burg 2020). We also have a role to play as reviewers and editors by requesting authors to cite original natural history studies over field guides. At the outset of their work, researchers attempting systematic studies of snake diets should be aware of method-specific biases which might influence the utility of the collected data. Several studies reveal the remarkable magnitude by which dietary records within systematic studies differ depending on the collection method adopted (Rodríguez-Robles 1998; Glaudas et al. 2017; Maritz and Maritz 2020). Moreover, methods vary not only in the specificity with which prey items can be identified, but also the diversity of potentially useful information that can be gathered. For example, identification of prey DNA can provide highly specific identification, but provides no information about other aspects of the predator prey interaction such as relative prey size or direction of ingestion.

3. Community science can facilitate collection of redundant once-off feeding observations, but these need to be cautiously synthesized and integrated into the literature.—There are currently two mechanisms available to report a once-off observation of a snake feeding. If the record is novel, i.e., that prey animal has not been previously recorded in the diet of that snake, then the observer(s) can publish a description of the observation in a herpetological natural history outlet (including, but not limited to, *Herpetological Review*, *Herpetology Notes*, *African Herp News*, *Revista Latinoamericana de Herpetología*, etc.). These natural history notes are important initial elements of properly quantified snake diets and often act as important gateway publications for aspiring herpetologists. Their synthesis and curation can also make important contributions to the field (e.g., Schalk and Cove 2018). But, the lack of standardization and an absence of a indexing system within the outlets that carry these feeding records makes it challenging to know if an observation is truly novel (and therefore publishable) or to be confident that a literature search for a given trophic interaction is exhaustive (van den Burg 2020). Taken alone, these natural history notes work well to quantify dietary breadth, but have the potential to mischaracterize relative prey utilization—a characteristic often used to assess dietary specialization (Alencar et al. 2013)—if sparse data are used uncritically to characterized snake diets. The second mechanism available for reporting once-off feeding observations is a community science framework, which is also the only way an observer can catalogue a redundant feeding record. Despite being susceptible to biases in which feeding records get observed, these redundant records are perhaps the best available measures of the frequency with which different prey taxonomic types are consumed by snakes because of the remarkable observational power derived from armies of camera-carrying community scientists. However, critically, we currently lack a mechanism that provides synthesized feedback between the various community science platforms and the primary literature. One potential solution is for interested researchers to start publishing peer-reviewed systematic summaries of community science records (with archived observation identifiers) in the primary literature (e.g., Maritz and Maritz 2020; Putman et al. 2021).

4. We must develop a centralized global database for snake feeding records to act as a repository for once-off records, to index literature, and facilitate comparative studies.—An alternative solution to deal with the chaos of scattered natural history notes and community science records would be the development and maintenance of a central repository for snake feeding records. Herpetology has precedents for this, with many of us using The Reptile Database, AmphibiaWeb, and GenBank on a regular basis. The recently published SquamataBase (Grundler 2020) offers an obvious nucleus on which to build such a repository, albeit with increased accessibility (especially for untrained users including community scientists). Not only could obscure records that are published in difficult-to-access outlets become searchable upon addition to the database, but the results of regular systematic surveys of community science platforms could also be catalogued. The repository could also provide a secure virtual museum for storing feeding records shared on social media—an emerging variation on the community science theme that has seen researchers gather records at unprecedented rates (Kalki and Weiss 2020; Maritz and Maritz 2020), but that currently lacks data storage security because of the complex interaction of social media with privacy rights and copyright laws. Moreover, editors who oversee the publication of traditional once-off observations or systematic studies of diet could require that authors log all records into the repository in much the same way that they require that genetic sequences are accessioned to GenBank.

The challenges mentioned above are not the only issues we face in our endeavor for more robust snake feeding data. Several major obstacles (for which we have no suggested solutions) also need to be actively addressed. Primarily, we need to work out appropriate ways of aggregating sources of information, especially when examining proportional use of prey types. Secondary sources of information, such as field guides, lack the details required for most analyses. But given the data-sparse nature of snake feeding information, any robust solution is going to have to integrate information from systematic studies of diet and a range of once-off observation sources (van den Burg 2020). Going forward, we will also require novel analytical tools. Promisingly, Grundler and Rabosky (2020) recently developed an analytical tool that assigns species to functional feeding clusters on the basis of their phylogenetic relatedness and similarities in their dietary records, explicitly accounting for their potential incompleteness. Tools such as these continue to advance our understanding of snake diets and how they evolve (Grundler an Rabosky 2021), but we also will need to co-opt or develop other analytical tools to deal with issues of method-based differential detectability of certain prey types and improved mechanisms to aggregate prey types into functional (rather than taxonomic) groups. We will also need to grapple with how to appropriately credit community scientists (Ward-Fear et al. 2020), authors of once-off observations, authors of systematic and review studies (McMahan and McFarland 2021), and, ultimately, data deposited into a central repository. Finally, the threat of snake and prey systematic instability looms large. Undeniably, we need the systematics underlying our understanding of snake and prey diversity to be robust. However, the adjustment of historical feeding records in a centralized repository to reflect updated systematics will be incredibly onerous, placing even more pressure on systematists to ensure that newly published systematic arrangements are robust.

The availability of detailed dietary information for snakes globally would have a range of benefits. Because snakes are predators, feeding is central in how we view them, how they interact with their ecosystems, and how they interact with us. Despite the challenges posed by an integrative, global understanding of snake diets, a few structural changes in how we, as herpetologists, engage with snake feeding records and studies will allow us to take a large step in the right direction. Let's publish more systematic diet studies (especially for poorly known lineages and in poorly studied regions), and let's cite those studies rather than reaching for our field guides. Let's escalate the collection of once-off observations including redundant records, and let's find mechanisms for integrating syntheses of these into the primary literature. Let's actively develop and support a centralized repository for feeding records, and let's use it to explore and expand analytical tools for the robust analysis of dietary data. Murray et al. (2020) called for a better understanding of snake biology to better address the global snakebite crisis. The study of snake diets must be one of the leading avenues of research in that regard, but we need to make some important changes to how we gather and use snake feeding records to improve the contextualization of venom biochemistry. If not for that noble cause, then do it for the reason that so many of you are reading this very perspective—because the animals that we study are just plain fascinating.

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Response to Criticisms of an Updated Subspecies Concept

In an attempt to resolve some contemporary controversies about the taxonomy of incompletely separated lineages, I recently proposed an updated concept of subspecies (de Queiroz 2020). According to that updated concept, subspecies are entities of the same fundamental kind as species (separately evolving metapopulation lineages) that differ from other entities considered species only in that they are incompletely separated from one another and therefore are parts of a more inclusive species (lineage). This updated concept of subspecies not only resolves various controversies about the taxonomy of incompletely separated lineages, it also brings the concept of subspecies into congruence with a unified concept of species, gives the concept of subspecies a biologically meaningful definition, and ends the treatment of the subspecies category as an artificial taxonomic rank. Despite these benefits, this new concept of subspecies is at odds with certain taxonomic traditions, and therefore I anticipated that it would meet resistance. In this context, it is not surprising that a criticism of my proposal has recently been published by Hillis (2021). Here I respond to that criticism to clarify both the nature of my proposal and why it is preferable to retaining a more traditional concept of subspecies.

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