Trophic Niche Partitioning between Sympatric Naja naja and Ptyas mucosa: Crowdsourced Data in Application to Community Ecology

Authors: Weiss, Merlin, and Kalki, Yatin

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MERLIN WEISS[1,4] AND YATIN KALKI[2,3]

[1]*Department of Wildlife Management, Van Hall Larenstein University of Applied Sciences, Leeuwarden, The Netherlands 8934 CJ*
[2]*Madras Crocodile Bank Trust & Center for Herpetology, Mamallapuram, Tamil Nadu, India 603104*
[3]*Department of Ecology, Evolution, and Organismal Biology, Kennesaw State University, Kennesaw, Georgia, 30144, USA*

ABSTRACT.—Spectacled Cobras (*Naja naja*) and Oriental Ratsnakes (*Ptyas mucosa*) frequently share habitats and presumably occupy a similar trophic niche. We present a dietary synopsis of both species as well as niche metrics based on feeding events retrieved from crowdsourced data. Our analysis suggests a high importance of ophiophagy in the diet of *N. naja*, which occasionally feeds on mammals and frogs, but rarely on other taxa. *Ptyas mucosa* preyed most frequently on frogs and occasionally on snakes and mammals. The relative importance of shared prey items was generally high and confirmed overlap of their trophic niches. Interspecific trophic competition could serve as a noninvasive conservation tool. In particular, adult *N. naja* may avoid areas in which size-equivalent or size-superior *P. mucosa* are present, potentially offering new perspectives on common conservation practices for this medically significant snake. Methodological biases because of low detection probability of subterranean predation events and a bias in ophiophagous events in data retrieved from social media cannot be ruled out. Two key issues need to be considered when using crowdsourced data to assess trophic niche partitioning: 1) choosing an appropriate level of prey identification as a base for meaningful comparison and 2) ensuring relative spatial homogeneity of data origins over the common range. When considering the trade-off between data quality and quantity for comparative analysis, crowdsourcing is a valuable but supplementary resource for studies of niche partitioning in sympatric species. The presented data expand the known dietary spectrum of both snake species by 42 previously unpublished trophic interactions.

Coexistence of similar species occupying similar niches has always challenged our understanding of the organization of ecological communities (Macarthur and Levins, 1967; Peterson et al., 2011). Limited resources commonly get used differently among species because of differences in morphological, physiological, or behavioral traits (Schoener, 1974; Tilman, 1987). Consequently, the partitioning of niches mitigates the effect of interspecific competition on the performance of competing species (Chesson, 2000; Levine and HilleRisLambers, 2009). Reptile and amphibian communities tend to be structured by resource partitioning in habitat, food, and time (Toft, 1985). Ecological differences of sympatric species are typically measured on the dimensions of micro- and macrohabitat, food type, and size as well as diel and seasonal rhythm (Schoener, 1974). Although research in the late 20th century primarily focused on frog and lizard communities (Pianka and Parker, 1975; Toft, 1985), an increased ecological interest in snakes (Shine and Bonnet, 2000) has revealed great differences in coexisting patterns of snake species among different geographic regions and within communities (Luiselli, 2006; Durso et al., 2013). Dietary behavior and composition consistently prove to be a core dimension in studies on niche partitioning. Emphasizing the trophic position of animals to investigate potential competition on a local level, commonly referred to as the Eltonian niche concept (Soberón, 2007; Dehling and Stouffer, 2018), is a robust and straightforward way to quantify deterministic aspects of niches (Rahman et al., 2014; Staniewicz et al., 2018). Hence, approximated descriptive metrics such as niche breadth and niche overlap provide valuable insights into the relationships of sympatric species and help to understand their community organization (Colwell and Futuyma, 1971). Studies on feeding ecology and resource consumption of snakes are often the result of a trapping procedure and analysis of stomach contents (Mushinsky and Hebrard, 1977; Luiselli and Rugiero, 1991; Himes, 2003; Halstead et al., 2008) or stable isotopes (Willson et al., 2010; Durso and Mullin, 2017; Perkins et al., 2020; Rebelato et al., 2020). However, trapping procedures involve stress when data are collected by forcing snakes to regurgitate prey items (Fitch, 1987), and they may be biased by activity patterns of snakes (Siers et al., 2018). Because stable isotope studies also have their limitations (Cresson et al., 2014; Shipley and Matich, 2020), a combination of dissimilarly retrieved data often provides the best insights into feeding ecology of species or communities (Nielsen et al., 2017; Durso et al., 2022).

Increasing popularity of citizen science platforms and social networks has created yet another opportunity to mine natural history data of species across broad spatial and temporal scales at unprecedented rates (Kalki and Weiss, 2020; Maritz and Maritz, 2020; Bhatnagar and Kalki, 2021). Crowdsourced data are already a powerful tool in conservation work (Pimm et al., 2015; Brown et al., 2018) and research on the distribution and ecology of various species (Fink et al., 2014; Marshall and Strine, 2019; Iankoshvili and Tarkhnishvili, 2021). A novel approach to feeding ecology is to summarize the diet composition of species, particularly carnivores, by using photographed in situ feeding events shared on citizen science platforms and social networks (Layloo et al., 2017; Kalki and Weiss, 2020). Such natural history observations and their value for understanding feeding behavior and ecology and evolution of species (Greene, 1983; Hoso et al., 2007) are becoming increasingly appreciated in the scientific community, especially in herpetology (Maritz et al., 2021). If the predator and its prey can be identified successfully, metadata and reference objects often allow for further insights such as location or size approximation. However, variables such as habitat characteristics, time of day, and sex can only be addressed rarely and are hardly statistically representative because of typically small sample sizes. Poor image quality (Panter and Amar, 2021), a tremendous underrepresentation of particularly secretive species (Marshall and Strine, 2019), and the potential overrepresentation of subjectively more spectacular predation events (e.g., cannibalism) are also common

problems. Therefore, raw trophic interactions prove to be the most robust information retrievable from a crowdsourced dataset to understand aspects of the ecology of a focal species (Maritz and Maritz, 2020). Although trapping procedures have repeatedly been used to assess trophic niche partitioning between two or more sympatric species (Lelièvre et al., 2012; Rahman et al., 2014), a crowdsourced dataset remains to be applied to a problem in community ecology. This approach poses two key challenges: 1) choosing an appropriate level of prey identification (LPI) to accurately represent niche relationships without increasing the number of samples lost because of a lower taxonomic level and the impact of potential misidentification bias and 2) ensuring a relatively even spread of origin points of samples to minimize the impact that differences among local populations may have on the representation of niche relationships. The former issue of how the LPI effects niche metrics has been discussed by Greene and Jaksic (1983), affirming the importance of using a high LPI. A low LPI (e.g., at the ordinal level) arguably underestimates niche breadth and overestimates niche overlap (Greene and Jaksic, 1983). Because the quality of crowdsourced data (and thus the highest LPI reasonably possible) varies greatly, a high LPI comes at the cost of potentially losing samples that fall below a taxonomic threshold that, in turn, may misrepresent the true relationships. At the same time, intraspecific geographic variation in diet composition is common in snake species (Dix, 1968; Arnold, 1977; Kephart, 1982). Crowdsourced data (as well as examination of stomach contents of museum-preserved specimens) cover a much wider geographic range and thus variation than traditional field studies (Rodrìguez-Robles, 1998). A meaningful comparsion of sympatric species must therefore ensure a comparable spread of data points and their macrohabitat characteristics within the range of both competing predators. Provided that these criteria are taken into consideration, crowdsourcing may prove a valuable resource in studying snake communities. Herein, we describe the dietary composition of two sympatric snake species and use crowdsourced data to evaluate their potential dietary overlap by approximating meaningful niche metrics.

Spectacled Cobras (*Naja naja* Linnaeus 1758) and Oriental Ratsnakes (*Ptyas mucosa* Linnaeus 1758) are two common and frequently observed species on the Indian subcontinent. Both are believed to be generalist predators and frequently share agricultural and (sub)urban landscapes (Srinivasulu and Das, 2008). Literature suggests that *P. mucosa* is primarily a diurnal predator (Wall, 1921; Mao et al., 2008; Saha and Chaudhuri, 2017; Chowdhury, 2018) occasionally also foraging at night (Ghosh et al., 2020). *Naja* shows both nocturnal and diurnal activity (Whitaker and Captain, 2004), a trend also observed in African species of the *Naja* complex (Shine et al., 2007). As with *P. mucosa*, activity patterns and habitat use of *N. naja* regularly overlap with those of humans, often leading to fatal bite accidents (Suraweera et al., 2020). A better understanding of trophic niche partitioning between venomous snakes that are typically associated with human-dominated environments (i.e., hemerophiles) and their nonvenomous competitors may also provide valuable insights on how to improve conflict management between humans and snakes, for example, regarding snake translocation. We expected that both species would be generalist predators with similar diets and relatively high trophic niche overlap (Whitaker and Captain, 2004).

Materials and Methods

We retrieved feeding events of *N. naja* and *P. mucosa* from search engines, social media, citizen science platforms, validated personal observations, and published literature. We searched for social media (Facebook, Instagram, Flickr, YouTube) and search engine (Google, Yahoo) records by using the keywords "[Species name] feeding," "[Species name] kills," or "[Species name] predation." We visually validated the predator species and identified the prey animal to the finest taxonomic level possible based on morphological traits. We disregarded observations in captive settings and whenever predator or prey species could not be determined at least to the class level. If possible, we categorized each snake into one of three size classes, i.e., small, medium, or large, based on measurements provided in the source or a visual size approximation by using reference objects in the pictures. Animals with approximated snout–vent-length (SVL) of <30 cm were classified as small, SVL between 30 and 150 cm as medium, and SVL of >150 cm as large. Although *P. mucosa* generally grows larger than *N. naja*, we applied the same size classification to both species, allowing us to consider interspecific competition between animals of similar sizes.

If possible, we recorded the location of each event along with latitude and longitude of the closest spatial point known, the name of the observer, and the website link. We did not use a neutral IP address because many feeding events were published in private Facebook groups that are only accessible by joining the group. Feeding events published in citizen science platforms were retrieved from iNaturalist (www.inaturalist.org), India Nature Watch (www.indianaturewatch.net), and Reptiles of India (www.indianreptiles.org). Furthermore, we added feeding events from credible personal observations as well as from the published literature. The latter also included novel observations stored in SquamataBase (Grundler, 2020). The data used in this study are available in the supplementary data file.

We calculated the number of records retrieved from different sources (i.e., citizen science, literature, personal observations, search engines, and social media) and the percentage that each source contributed to the database of each snake species. We then disregarded duplicated observations of a distinct feeding event shared by a single observer on multiple platforms, i.e., data points that merely differed in the type of source from which they were retrieved. Dietary composition of *N. naja* and *P. mucosa* was first expressed as a percentage to the levels of Anura, Aves, Mammalia, Sauria, and Serpentes. Niche breadth and overlap were calculated on four different levels of prey identification: order (suborder for Squamata), family, genus, and species. For every taxonomic threshold, we recorded the percentage of available data points per snake species. We calculated niche breadth by using Levins' index following the equation $B = 1/\sum p_i^2$, where B is Levins' index and p_i is the proportion of individuals consuming a particular prey item (Levins, 2020). We standardized this value by using $B_\alpha = (B-1)/(n-1)$, where B_α is the standardized niche breadth and I is the total number of prey items consumed. B_α places species on a range from 0 to 1, most specialized to most generalized, respectively (Krebs, 1989). We compared all niche breadths per snake species of different sizes for sample sizes ≥ 5. Trophic niche overlap was calculated using Pianka's index (Pianka, 1973) following the equation $O_{jk} = \sum_i^n p_{ij}p_{ik}/\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}$, where O_{jk} is Pianka's index for niche overlap between species j and k, p_{ij} the proportion of the ith prey item in the diet of species j, p_{ik} the

TABLE 1. Niche metrics at different LPIs: *B* (Levins' index for niche breadth) and B_a (standardized), Pianka's index for niche overlap, the percentage of available data points, and the sample size (*n*) per LPI.

	Order LPI	Family LPI	Genus LPI	Species LPI
B (*N. naja*)	4.18	10.45	12.63	12.97
B_a (*N. naja*)	0.32	0.5	0.42	0.43
% (*N. naja*)	100	95.05	92.08	92.08
n (*N. naja*)	101	96	93	93
B (*P. mucosa*)	4.97	10.09	13.36	15.07
B_a (*P. mucosa*)	0.31	0.43	0.48	0.49
% (*P. mucosa*)	97.62	85.71	75	70.24
n (*P. mucosa*)	82	72	63	59
Overlap	0.81	0.71	0.66	0.64

proportion of the *i*th prey item in the diet of species *k*, and *n* the total number of prey items. Niche overlap was calculated at four levels of prey identification. All niche metrics were calculated based on the number of individuals consuming a certain prey rather than the quantity of prey items consumed because multiple prey items consumed by the same individual predator would be pseudoreplicates (Krebs, 1989). We thus disregarded the number of prey items consumed at a distinct occasion and did not assume two or more distinct observations to feature the same predator. All calculations assume equal accessibility of prey items for *N. naja* and *P. mucosa*, given the data did not allow for a consideration of resource availability. We rejected a species being a specialist or the two species having no strong trophic overlap if values of B_A and O_{jk} exceeded a threshold of 0.4 and considered them clear generalists or strongly overlapping if B_α and O_{jk} were >0.6 (Grossman, 1986; Novakowski et al., 2008). In addition, we calculated the standard deviation between values of B_α and O_{jk} at different LPIs to reflect the range of spread between different taxonomic thresholds. To investigate whether data points of both species had a comparatively even geographic origin (i.e., did not originate in radically different locations), we plotted points with available coordinates on a map and displayed a two-dimensional kernel density estimation. Finally, we calculated the difference of both density estimations over the common range and plotted this result with a color gradient indicating areas of equal or skewed observation density per species. All analyses and visualizations were carried out in R v.4.0.5 (R Core Team, 2015) with the packages tidyverse (Wickham et al., 2019), spaa (Zhang, 2016), sp (Pebesma and Bivand, 2005), and sf (Pebesma and Bivand, 2018).

RESULTS

We collected 105 feeding events of *N. naja*, 101 of which were distinct observations, and 93 prey animals were identified to species level, 3 were to family level, and 5 to (sub)order level. The most frequently recorded prey class of *N. naja* were snakes (*n* = 42, 41.6%), followed by mammals (*n* = 21, 20.8%), frogs (*n* = 19, 18.8%), birds (*n* = 11, 10.9%), and lizards (*n* = 8, 7.9%). For all four LPIs, at least 92% of data points were available for calculating niche metrics, i.e., they could be determined to species level. Levins' index of niche breadth increased steadily toward higher LPIs (Table 1), and a standardization revealed the greatest LPI at family level (B_a = 0.5). The B_a values of *N. naja* varied at SD = 0.07. *Naja naja* was a generalist predator when prey items are identified to the family level, whereas an ordinal LPI indicates a preference for feeding on snakes. From 42

TABLE 2. Niche metrics of *Naja* of different sizes at different LPIs: *B* (Levin's index for niche breadth) and *B*α (standardized), Pianka's index for niche overlap, the percentage of available data points, and the sample size (*n*) per LPI.

	Order LPI	Family LPI	Genus LPI	Species LPI
B (large)	2.33	8.14	9.87	9.66
B_α (large)	0.22	0.55	0.49	0.54
% (large)	100	100	100	100
n (large)	52	52	52	52
B (medium)	4.55	5	5.17	5.17
B_α (medium)	0.51	0.4	0.35	0.35
% (medium)	100	86.21	86.21	86.21
n (medium)	29	25	25	25
B (small)	2.27	2.27	3.57	3.57
B_α (small)	0.64	0.64	0.86	0.86
% (small)	100	100	100	100
n (small)	5	5	5	5

ophiophagic events, particularly large individuals (*n* = 52, 51.5%) were observed to feed on snakes (78.6% of ophiophagic events), making up 63.5% (*n* = 33) of their diet. With an ordinal LPI, a narrow niche breadth was shown (Table 2) that shifts toward generalist-like values at higher LPIs. All feeding events featuring large individuals allowed for a determination up to species level. The B_α values of large individuals were most variable, with SD = 0.16. Medium-sized individuals (*n* = 29, 28.7%) appeared to have a narrower niche breadth when using high LPIs (B_α = 0.35 at species level; Table 2), with a preference for frogs (*n* = 10, 34.5%). In contrast to large *N. naja*, medium-sized animals appear only on an ordinal LPI as generalist predators and steadily decrease in their dietary flexibility at increasing LPIs. Below ordinal level, 86.21% (*n* = 25) were available for analysis per respective taxonomic threshold. Medium-sized individuals yielded values varying at SD = 0.08. Small individuals consistently show the most generalist feeding strategy, which is misleading because of the small sample size (*n* = 5) containing just four different prey species. We report at least 30 different prey species in the diet spectrum of *N. naja*. Twenty-two of the trophic interactions were previously unpublished.

For *P. mucosa*, we determined 86 feeding events with 84 distinct observations, and 59 prey animals were identified to species, 4 to genus, 9 to family, 10 to order, and 2 to class. Frogs made up the largest part of observations (*n* = 29, 34.5%), followed by snakes (*n* = 18, 21.4%), mammals (*n* = 16, 19%), lizards (*n* = 12, 14.3%), and birds (*n* = 9, 10.7%). For *N. naja*, *P. mucosa* was a generalist at higher LPIs (Table 1), whereas an ordinal LPI suggests a specialization on anurans. The availability of data points decreased at high LPIs, leaving only 70.24% for an analysis at species level. Values of B_α varied among different LPIs at SD = 0.08. Analysis by size for *P. mucosa* revealed the same trend for higher B_α estimates at higher LPIs for large- and medium-sized individuals (Table 3). We refrained from interpreting values for small individuals because of a low sample size (*n* = 2). Medium-sized *P. mucosa* (*n* = 19, 22.6%) appeared to be generalists as reflected by $B_\alpha \geq 0.8$ for generic and species LPIs based on at least 89% of available data points. Large *P. mucosa* (*n* = 35, 41.7%) were less flexible in their diet and were found to have a B_α of 0.56 at generic and species LPIs. However, slightly fewer data points were used to estimate this value (74.3% on species LPI and 80% on generic LPI). We report at least 31 different prey species in the diet spectrum of *P. mucosa* containing 20 previously unpublished trophic interactions.

TABLE 3. Niche metrics of *Ptyas mucosa* of different sizes at different LPIs: B (Levin's index for niche breadth) and B_a (standardized, Pianka's index for niche overlap), the percentage of available data points, and the sample size (*n*) for each LPI.

	Order LPI	Family LPI	Genus LPI	Species LPI
B (large)	4.8	6.84	9.33	9.39
B_α (large)	0.42	0.49	0.56	0.56
% (large)	100	82.86	80	74.29
n (large)	35	29	28	26
B (medium)	4.25	8.1	11.57	10.7
B_α (medium)	0.54	0.71	0.81	0.81
% (medium)	100	94.74	94.74	89.47
n (medium)	19	18	18	17

Throughout all LPIs, both species showed overlap in their dietary niche (Table 1) and consistently exceeded $O_{jk} = 0.64$. Estimates of niche overlap decreased with a higher LPI and thus peaked at an ordinal LPI with $O_{jk} = 0.81$. The O_{jk} value varied by SD = 0.07. Range-wide, the dietary niche of the two species thus appeared to overlap, but depended on the LPI. When only considering niche overlap between individuals of equal size classes, large-sized *N. naja* and *P. mucosa* have a slightly higher trophic niche overlap, decreasing from $O_{jk} = 0.72$ at ordinal LPI to $O_{jk} = 0.52$ at species LPI. In medium-sized individuals, values range from $O_{jk} = 0.82$ at ordinal LPI to $O_{jk} = 0.43$ at species LPI. Accordingly, a relevant trophic niche overlap cannot be ruled out, but its magnitude depends on the LPI. Of a total of 51 different prey items identified to species level (from 67 total prey items), we identified at least 12 that were in the diet spectrum of both *N. naja* and *P. mucosa* (Fig. 1). Those shared prey species make up 55.5% of feeding events by *N. naja* and 50% of *P. mucosa*.

We found that 71.3% of *N. naja* (*n* = 72) and 71.4% of *P. mucosa* (*n* = 60) observations had available coordinates of origin. Kernel density estimations of data points from both species (Fig. 2) revealed a cluster of *N. naja* feeding events in southern India around Bangalore and along the Western Ghats. *Ptyas mucosa* records also were clustered in the south, but were slightly less frequent along the Western Ghats. Few records of either species were found in northern and central India. Although the overall distribution of locations represented in this study appears similar, the relative density remained skewed (Fig. 3), with areas of equal density being rare. However, exceptionally strong underrepresentation was only found in the Western Ghats (for *P. mucosa*) and regions of northern and northeastern India (for *N. naja*).

Overall, social media platforms were the largest source of observations for *N. naja* and the second largest for *P. mucosa* (*N. naja*: *n* = 46, 43.8%; *P. mucosa*: *n* = 35, 40.7%). Literature yielded the second largest source type for *N. naja* and the largest part for *P. mucosa* (*N. naja*: *n* = 30, 28.6%; *P. mucosa*: *n* = 41, 47.7%). Personal observations were the third largest source type for *N. naja* (*n* = 12, 11.4%) and contributed 3.5% (*n* = 3) of records to *P. mucosa*. Approximately 8.6% (*n* = 9) of *N. naja* and 3.4% of *P. mucosa* (*n* = 3) observations were directly retrieved from search engines. Lastly, 7.6% of *N. naja* (*n* = 8) and 4.7% of *P. mucosa* (*n* = 4) observations were retrieved from citizen science platforms.

DISCUSSION

Through the crowdsourced approach, we found that *N. naja* and *P. mucosa* both share a similar niche breadth that does not endorse a generalist feeding strategy as firmly as the literature may suggest (Whitaker and Captain, 2004). In fact, an LPI beyond the ordinal level is needed to be able to reject both species having clear specialist tendencies. An ordinal LPI presumably underestimates dietary flexibility (Greene and Jaksic, 1983). The data for *N. naja* allowed for higher LPI while still using a satisfying portion of the data, making the niche breadth estimate at species level resulting from 92.1% of records arguably the most reliable approximation. By contrast, the high LPI for *P. mucosa* required disregarding a substantial amount of data. The appropriate LPI for a sheer descriptive purpose may be chosen independently for each unique species. It is not necessary for two or more species to match, so a mutual LPI for comparative purposes should be chosen considering both the highest LPI possible while including as much data as possible. Therefore, analyzing diet composition on a family level satisfies both demands because an ordinal LPI is exceeded and at least 85% of available data per snake species can be included in calculations.

N. naja showed a surprisingly high number of snakes in its diet throughout all LPIs. Various studies have shown a high degree of ophiophagy in African *Naja* species (Haagner et al., 1990; Maritz et al., 2019). Close relatives to the *Naja* complex, such as species of the genus *Bungarus* and *Elapsoidea*, particularly *Ophiophagus hannah*, have long been known to be ophiophagous specialists (Ashe, 1965; Branch et al., 1992; Nishank and Swain, 2019). Although *N. naja* has been reported to prey on snakes (Wall, 1921; Mukherjee and Bhupathy, 2004; Maheta et al., 2020), our data suggest an understated importance of ophiophagy because snake prey comprised nearly half of the overall diet composition at the class level. However, ophiophagy and particularly cannibalism seem to become more frequent when *N. naja* reaches a larger size. Arguably, prey size could limit the consumption of some potential prey animals, and Greene (1983) emphasized the use of a ratio between predator and prey mass (weight ratio [WR]). Elapids are in fact considered to have a high WR in which larger individuals forage on a variety of prey animals and occasionally consume snakes that exceed their own mass (Greene, 1983; Shine and Wall, 2007). Snake species that are commonly associated with human-dominated environments (Barhadiya and Ghosh, 2021; Kalki et al., 2021) showed a high relative importance in the diet of *N. naja* (*N. naja*, 31%; *Daboia russelii*, 23.8%; and *Ptyas mucosa*, 11.9%). Whether the high proportion of ophiophagy results from actual preference or simply from *N. naja* feeding more often on particularly common animals in an urban environment remains unknown. The disproportionate presence of snakes in the diet of *N. naja* compared with equally common human-associated species such as rodents may have several explanations. Subterranean predation events have a virtually nonexistent chance of being observed. Accordingly, burrowing prey such as rodents are most likely to be severely underrepresented and would likely temper the magnitude of ophiophagy, if included. Also, the time required to swallow a prey item likely increases with prey size (Shine, 1991; Vincent et al., 2006), and particularly ophiophagy requires a prolonged phase of prey intake (Jackson et al., 2004). The probability that a predation event is visually detected should thus also depend on prey size and type and be lower for smaller rodents than for snakes. An overrepresentation of ophiophagic events may also be a general trend in records retrieved from social media (Kalki and Weiss, 2020; Maritz and Maritz, 2020), which contributed 56.8% of ophiophagic events of *N. naja* in this study. Prey preference for snakes also is not reflected in the venom
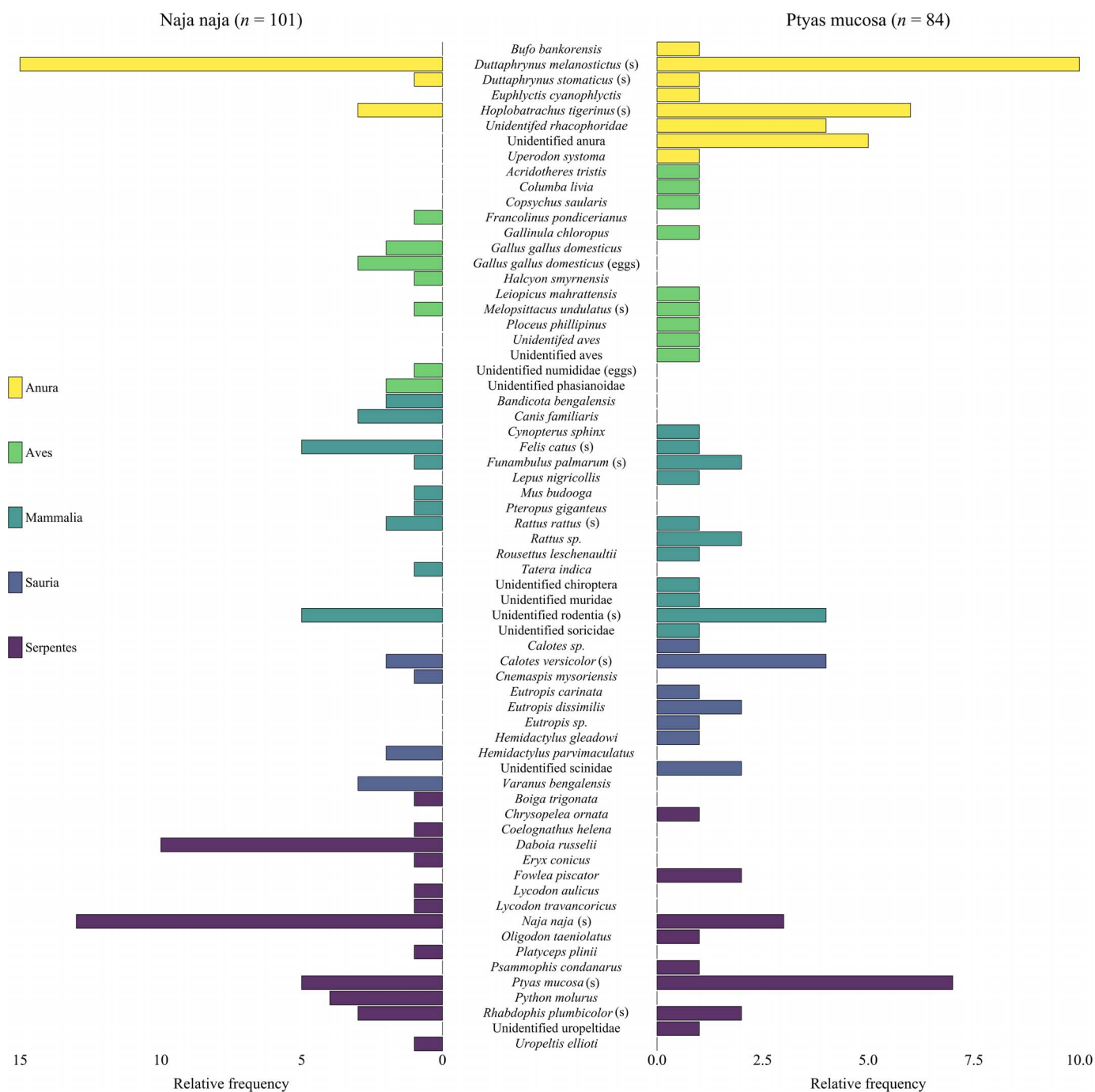
FIG. 1. Prey items recorded in the diet of *Naja naja* (left) and *Ptyas mucosa* (right) and their relative frequencies. Shared prey items are labeled as (s).

composition of *N. naja* because its α-neurotoxins showed the strongest response in amphibians (Harris et al., 2020). Snake venom composition is however not considered to remain constant throughout a snake's lifespan (Meier, 1986; Gibbs et al., 2011; Madrigal et al., 2012). When comparing diet composition on a species level, particularly medium-sized *N. naja* more frequently consumed *Duttaphrynus melanosticus* than any other prey item. The relative frequency of dietary amphibians declined in larger individuals, implying the possibility of a change in venom composition favoring ophiophagy. The true importance of ophiophagy remains to

be validated along with dietary breadth information that is based on a broader range of collection inventories for *N. naja*.

Like *N. naja*, we found that *P. mucosa* frequently fed on other snakes. Ophiophagic events were most commonly cannibalistic, and *P. mucosa* occasionally fed on *N. naja* and various colubrids. Frogs comprised a large fraction of the diet of *P. mucosa*, as for *N. naja*. We view a single feeding event on a softshell turtle reported by Wall (1921) to be an anomaly.

Our estimates of trophic niche overlap show that *N. naja* and *P. mucosa* exhibit substantial overlap, especially with LPIs of order and family. When using high LPIs (genus or species), *N. naja* and *P. mucosa* seem to compete most when both are of large

(A) Feeding events of *Naja naja* (*n* = 72)   (B) Feeding events of *Ptyas mucosa* (*n* = 60)
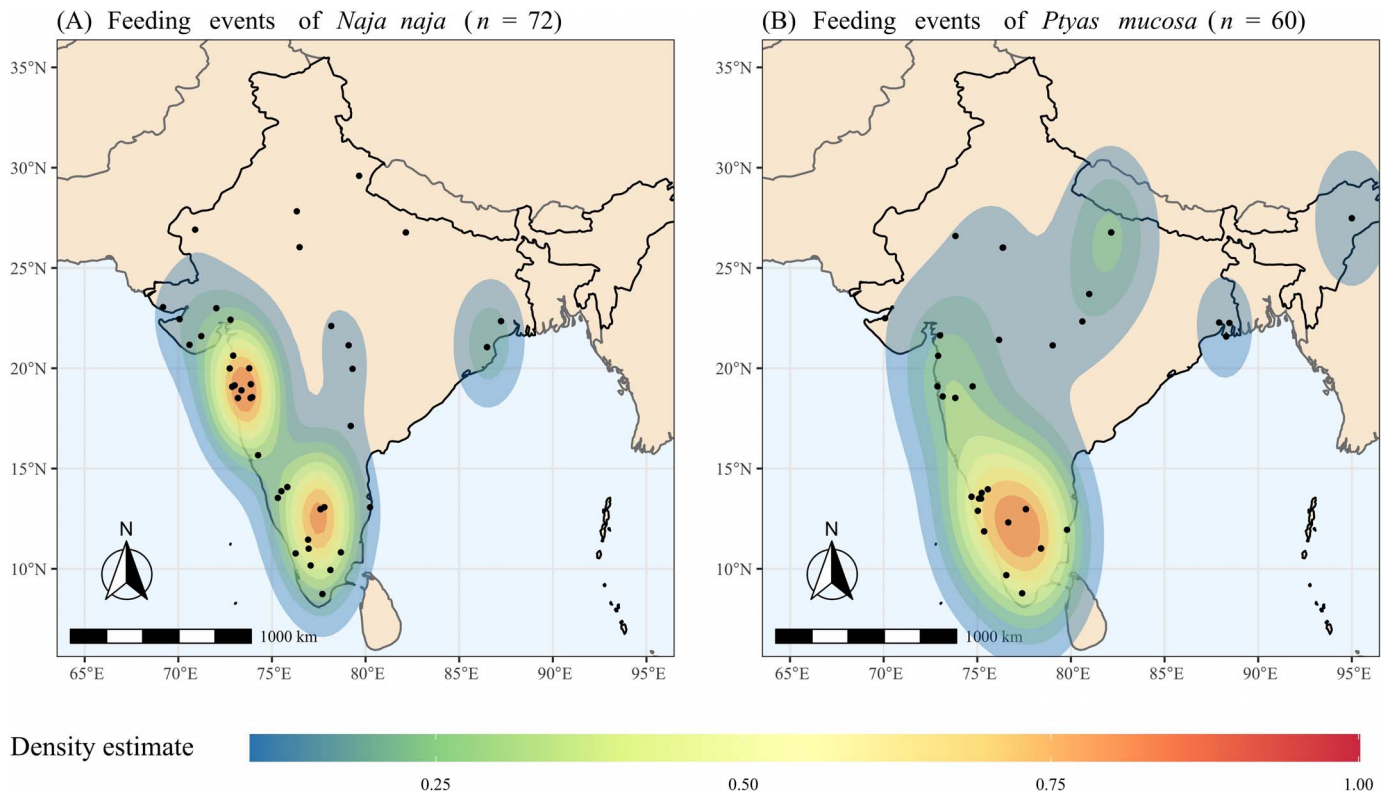
FIG. 2.   Kernel density estimates of feeding events with available coordinates (WGS 84) from (A) *Naja naja* and (B) *Ptyas mucosa*.
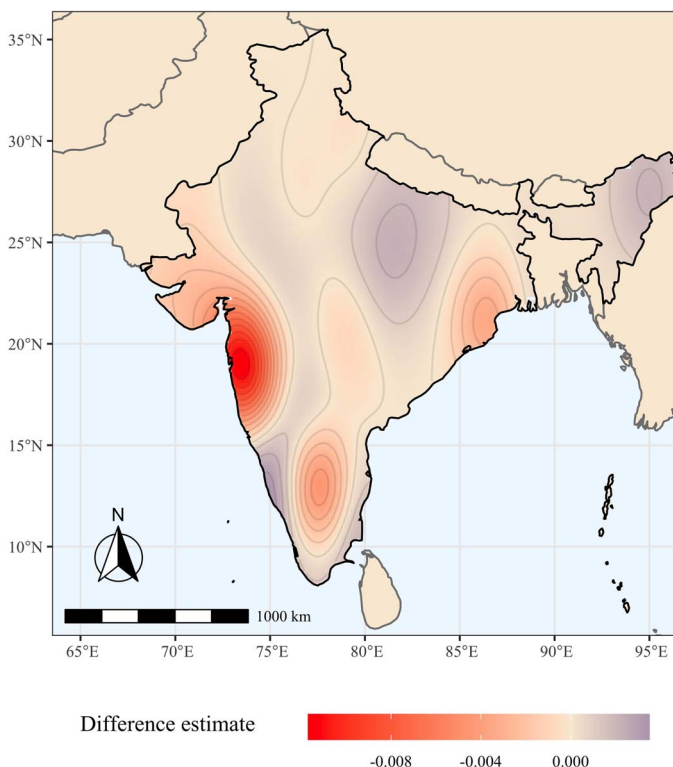
FIG. 3.   Density difference between areas with a higher density of *Naja* records (red) and *Ptyas mucosa* records (blue). Coordinates are referenced to WGS 84.

size (i.e., >150 cm). Medium-sized individuals overlap slightly less in their dietary niche, but still might be considered trophic competitors. Analogous to niche breadth, the most appropriate LPI to assess niche overlap is determined by a trade-off between high LPI and potential data loss. In this case, several literature-based predation events by *P. mucosa* did not allow for size classification and reduced the value of a size-subset approach to niche overlap (Maritz et al., 2021). When comparing the relative frequency of predation events on prey in the diet spectra of both snakes, species of the genera *Duttaphrynus* and *Hoplobatrachus* as well as various rodents arguably have the greatest importance. In total, *N. naja* and *P. mucosa* are direct competitors for just 34.3 and 27.9% of recorded prey items in the dietary range, respectively. When considering all observed predation events, these shared prey items make up more than half (55.4% for *N. naja* and 50% for *P. mucosa*) of all events recorded in each predator species.

Individual *N. naja* and *P. mucosa* were found to prey on one another. However, *P. mucosa* had a much larger relative importance in the diet spectrum of *N. naja* than *N. naja* did in the diet of *P. mucosa*. Presumably, trophic competition has a more severe impact on *P. mucosa*. Niche partitioning involves niche axes other than diet, and further insights on activity patterns and space use are required to fully elucidate how both species coexist (Schoener, 1974). We may assume frequent nocturnal predation activities in both species, as *Duttaphrynus*, *Hoplobatrachus*, and many rodents typically are nocturnal. As for shared prey species, niche partitioning in time is unlikely because shared prey animals also share activity patterns. Differences in habitat use along various spatial scales may also influence abundance and coexistence of *N. naja* and *P. mucosa* (Laurent and Kingsbury, 2003; Luiselli, 2006). Sympatric species may adjust dietary preferences between different-sized groups

to avoid interspecific competition (Toft, 1985; Luiselli et al., 1998; Luiselli, 2006) that might be reflected by shifts in the relative predation frequencies on different taxa between medium- and large-sized *N. naja*. Given a rather high LPI, medium-sized *N. naja* pursue a much more specialized feeding strategy than their larger relatives (also supported by a large portion of available data). Changes in niche breadth for small *N. naja* could not be addressed herein and seem challenging considering the drastic underrepresentation of juveniles. We did not detect any shifts in diet composition between large- and medium-sized *P. mucosa*, but we observed a reversed trend in niche breadth between large- and medium-sized *N. naja*. Large *P. mucosa* mostly were observed to prey on mammals, and both size classes showed a high number of frogs in their diet. Interestingly, *P. mucosa* and medium-sized *N. naja* both frequently consumed frogs, and relatively large *P. mucosa* have been shown to consume medium-sized *N. naja*. Therefore, the presence of large- and medium-sized *P. mucosa* might negatively affect the likelihood that medium-sized or smaller *N. naja* can occupy the same geographic area. Although the relationship between large *N. naja* and smaller *P. mucosa* seems to be more predator-prey than competitive, it is possible that *N. naja* might avoid areas in which equal-sized or larger *P. mucosa* are already present. That, in turn, would suggest a crucial implication for conflict management in areas with a high rate of bite accidents with *N. naja*. Translocation of snakes is a common practice to avoid such accidents and is not necessarily limited exclusively to venomous species (Reinert, 1991; Ramesh and Nehru, 2019). Translocation of medium-sized and relatively large *P. mucosa* could potentially increase the chance of size-inferior *N. naja* occupying an area after the removal of its direct competitor, consequently achieving an opposite effect than initially intended. By contrast, the presence of smaller *P. mucosa* may also attract particularly large *N. naja*, although presumably not as strongly as the presence of frogs or rodents. Further insight on niche partitioning at different dimensions, microhabitat use, home range size, and metapopulation dynamics (i.e., colonization probability) is required to fully understand organizational processes involving *N. naja* and its nonvenomous competitors and to eventually derive reasonable considerations for conservation measures.

As opposed to most niche studies, our data did not originate from a single location, but rather from several localities throughout the Indian subcontinent. Allopatric differences between spatially separated populations cannot be accounted for and therefore play a subordinate role, resulting in our study offering a more global reflection of species dietary characteristics. The location of areas with a high frequency of observations from social networks and citizen science is mainly determined by their popularity with people rather than by the focal species themselves. If such areas are within the range of all species of interest (and if they are equally common), the availability of retrievable data points should not be drastically skewed. For *N. naja* and *P. mucosa*, we found relatively similar densities of data throughout the geographic region except that the Western Ghats favored *N. naja*. Although a perfectly even distribution of feeding events for two or more species is highly unlikely, strongly over- and underrepresented areas turned out to be more uncommon than anticipated. Accordingly, a comparison based on crowdsourced data seems reasonable and meaningful. A considerable amount of data for both species did however not feature spatial information, naturally weakening assumptions of spatial homogeneity. As with data points having an LPI

restricted to an ordinal level, records with unavailable coordinates are to be expected when crowdsourcing feeding events. Careful consideration should be given to the spatial distribution of data points before comparisons between species are made. In addition, this yields information about areas with underrepresented natural history data that could be addressed to improve data quality.

To minimize the issue of choosing an appropriate LPI and to avoid severe spatial biases, it is advisable to define clear thresholds. On the one hand, a minimum percentage of data per LPI is required to accept or reject a species as a generalist or specialist and overlap in trophic niche of two species (>85% in this study). On the other hand, a minimum percentage of data with known spatial origin is required to assess relative spatial homogeneity (>70% in this study). If these criteria are met, crowdsourced data provide an extensive, fast, and cost-efficient resource for dietary breadth studies. Furthermore, crowdsourced data serve as a valuable supplement for understanding community organization of sympatric species, especially those species that are highly cryptic and difficult to sample.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at http://dx.doi.org/10.1670/22-013.S1.