

## Giant Gartersnakes (*Thamnophis gigas*) Exploit Abundant Nonnative Prey While Maintaining Their Appetite for Native Anurans

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**ABSTRACT:** The introductions of nonnative species can cause great change in the trophic dynamics of native species. Giant Gartersnakes, endemic predators in the Central Valley of California, are listed as threatened because of the conversion of their once vast wetland habitat to agriculture. Further contributing to this snake's changing ecology is the introduction of many nonnative prey species, resulting in a diet that is almost completely composed of nonnative species. In order to determine whether these snakes actively select their prey or simply consume what is abundant, we examined prey selection by adult Giant Gartersnakes in the context of what prey was available to each individual. Giant Gartersnakes selected a native anuran over nonnative anuran and fish species despite these nonnatives dominating the available species composition. These results contribute to understanding the mechanisms underlying Giant Gartersnake diets in the contemporary landscape and can lead to improved management of prey communities for Giant Gartersnakes and other native predators.

**Key words:** Bullfrog; Conservation; Diet; Fish; Gartersnake; Prey selection; Threatened predator; Wetland management

MANY FACTORS ultimately influence prey selection (Sih and Moore 1990). In turn, prey selection has important consequences for understanding the relationships of predators with their environment and each other (Manly et al. 2002). Documenting the selection or avoidance of specific prey, including nonnatives, can help inform management tactics and therefore, conservation for rare predators. Furthermore, the availability of (preferred) prey is an important factor in forecasting the long-term persistence of a predator.

Prey availability is often changed by the introduction of nonnative prey species, which in turn could alter the foraging ecology and ultimately the fitness of predators (Franssen et al. 2007). Giant Gartersnakes (*Thamnophis gigas*) are semiaquatic snakes precinctive to the Central Valley of California and currently listed as a threatened species at state and federal levels (California Department of Fish and Game Commission 1971; U.S. Fish and Wildlife Service 2017) because of wetland habitat reductions and fragmentation (Halstead et al. 2010; Huber et al. 2010). Over the past several decades, in addition to habitat loss, Giant Gartersnakes also have experienced changes in their prey community with the introduction of numerous nonnative species (i.e., fish and anurans; Rossman 1996). In addition to one native anuran, Sierran Treefrogs (*Pseudacris sierra*), nonnative American Bullfrogs (*Lithobates catesbeianus*) also commonly occur in Giant Gartersnake habitats. Potential fish prey that co-occur with Giant Gartersnakes are almost exclusively nonnative, including several nonnative species in the sunfish family (Centrarchidae), such as Green Sunfish (*Lepomis cyanellus*), Bluegill (*Lepomis macrochirus*), and Largemouth Bass (*Micropterus salmoides*); both native and nonnative species in the minnow family (Cyprinidae); and other nonnative fish species, such as Mississippi Silverside (*Menidia beryllina*), Western Mosquitofish (*Gambusia affinis*), and Black Bullhead Catfish (*Ameiurus melas*; Rossman 1996; Stebbins and McGinnis 2012). Despite the dramatic

changes to their prey base, no studies to date have examined the diet or prey selection of Giant Gartersnakes, despite the potential effects of altered prey communities on Giant Gartersnake populations. Potential effects include interspecific competition with nonnative and native fish and frogs (Adams et al. 2003), risk to the snake of impalement injury and potential death from ingestion of fish (Alarcos et al. 2009; Šukalo et al. 2012), predation of young snakes by bullfrogs (Wylie et al. 2003), and increased parasite loads or disruption of normal parasite cycles (Reshetnikov et al. 2013).

Considering the changes in prey availability compared to the historical wetland communities of California's Central Valley, we hypothesized that Giant Gartersnakes preferentially select native prey, despite the numerical abundance of nonnatives. To explore this hypothesis, we compared Giant Gartersnake stomach contents to prey availability to estimate diet selection of the species. This study system, in which Giant Gartersnakes co-occur with almost exclusively nonnative prey, presents an opportunity to examine the implications of introduced species on prey selection of a threatened predator. Understanding the degree to which Giant Gartersnakes select native and nonnative prey will enable resource managers to better conserve this rare snake.

### MATERIALS AND METHODS

#### Field Methods

Sampling locations for this study were divided into four areas in the Sacramento Valley of California, USA: the American, Butte, Colusa, and Sutter basins (Fig. 1). In the American Basin, all sites were located within the Natomas Basin Preserve (a series of mitigation sites composed of restored marshes and rice fields) located in Sacramento and Sutter counties. In the Butte Basin, trapping occurred in canals adjacent to private rice fields in Butte County. In the Sutter Basin, trapping was conducted in canals adjacent to private rice fields in addition to the Gilsizer Slough Giant Gartersnake Conservation Complex (a mitigation site with preserved and restored wetlands) in Sutter County. In the

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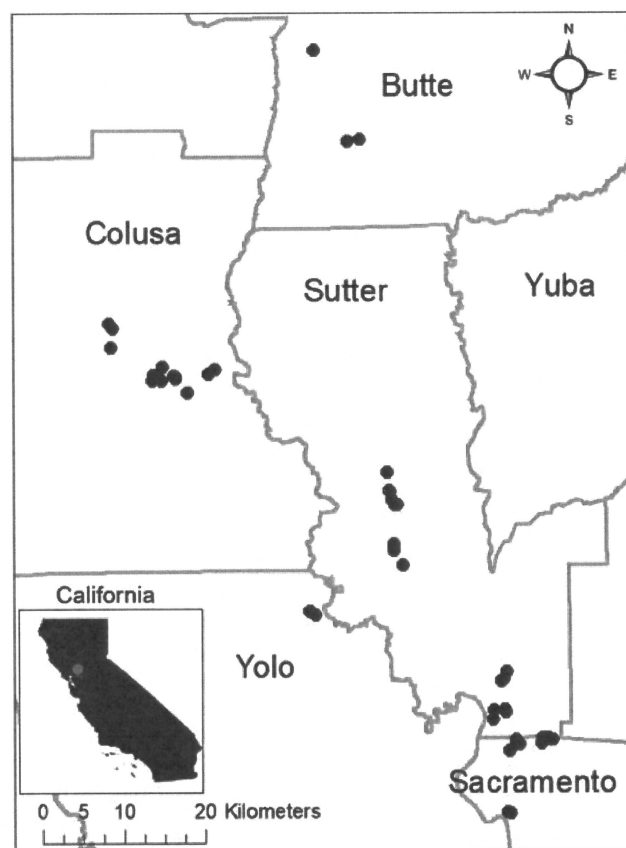


FIG. 1.—Locations of Giant Gartersnakes (*Thamnophis gigas*) containing prey in the Sacramento Valley, California (inset), USA, 2013–2014.

Colusa Basin, trapping was conducted in canals adjacent to private rice fields and in actively managed wetlands in the Colusa National Wildlife Refuge in Colusa County.

As part of routine protocols for occupancy and abundance surveys, snakes were captured from mid-April to mid-September in 2013 and 2014 using modified minnow traps, processed, and then released (Casazza et al. 2000; Halstead et al. 2013). Captured Giant Gartersnakes were marked with unique brands (Winne et al. 2006) and passive integrated transponder (PIT) tags and measured. Nongravid adult snakes in healthy condition were gently palpated to encourage regurgitation of stomach contents. Palpation to encourage regurgitation is a well-established and commonly practiced technique that has no long-term negative effect on the snake (Fauvel et al. 2012).

We measured prey availability separately for each capture of each individual snake with stomach contents from by-catch of prey species in snake traps. By-catch was identified to species, genus, or family, counted, and released daily in every fifth trap of traplines typically containing 50 traps. Prey availability was measured for each snake by summing the by-catch of the trapline where an individual snake was caught for a window that included 3 d prior to capture, the day of the snake's capture, and 3 d after the snake's capture.

## Analytical Methods

We estimated Giant Gartersnake prey selection using Bayesian analysis of hierarchical Poisson regression models with a log-link function (Manly et al. 2002). The models were hierarchical in that model coefficients were individual specific and allowed to vary around a population mean value, which places the individual as the sample unit and allows for individual variation in selection (Gillies et al. 2006). We specified counts of used or available prey as the response variable, and predictor variables in all models included an intercept, use (stomach contents coded as 1; available prey coded as 0), and prey type (categorical with dummy variable coding; a commonly available and consumed prey, American Bullfrog tadpoles, was the reference prey type), as well as other predictors and interactions of interest. The null model of no selection comprises the intercept and main effects for use and prey type. The model of constant selection (i.e., selection of prey does not vary among years, seasons, or with snake characteristics) adds an interaction between use and prey type, thus allowing the counts of consumed prey to be disproportionate to the counts of prey available to the snake. The coefficients for these interactions are log (selection ratios) relative to the reference prey category, so we calculated selection ratios ( $\hat{w}$ ) for each of the prey types as  $\hat{w}_i = e^{\beta_i}$ , where  $e$  is Euler's number and  $\beta_i$  is the population mean coefficient for the interaction of the use indicator with prey type  $i$ . We further calculated standardized selection ratios ( $B$ ), which can be interpreted as the probability that a snake with an average selection profile will select as its next prey item prey type  $i$ , given equal availability of all prey types, as

$$B_i = \frac{\hat{w}_i}{\sum_{i=1}^K \hat{w}_i},$$

where  $K$  is the number of prey types.

Because we were interested not only in the selection of prey by Giant Gartersnakes, but also whether selection varied over time, by habitat, and with individual characteristics, we expanded the constant selection model to include these effects on selection. To do so, we included main effects for the predictor of interest, all two-way interactions, and a three-way interaction between use, prey type, and the predictor of interest. In these cases, the coefficients for the three-way interactions represent the change in selection with a unit increase in the additional predictor variable. In total, we evaluated seven models to explain diet selection of Giant Gartersnakes. We selected among competing models using the widely applicable information criterion (WAIC; Watanabe 2010). The WAIC is related to the more common Akaike's information criterion (AIC; Burnham and Anderson 2002) and deviance information criterion (DIC; Spiegelhalter et al. 2002), but differs from them by (1) evaluating pointwise out-of-sample predictive ability of models, (2) being applicable to hierarchical models without a defined number of parameters, and (3) using the full posterior predictive distribution in keeping with the Bayesian paradigm (Hooten and Hobbs 2015). We selected all priors to be uninformative, with normal (0, 10) priors for mean coefficients and half-Cauchy (2.5) priors for standard deviations.

TABLE 1.—Counts of prey consumed by (measured by regurgitation, some snakes regurgitated multiple prey items) and available to (measured by modified minnow trap captures) Giant Gartersnakes in the Sacramento Valley, California, USA, 2013–2014.

Year	Prey type	Number of snakes that ate prey type	Number of snakes that had prey type available	Proportion of snakes with prey type available that consumed prey type
2013	American Bullfrog adult	34	38	0.89
	American Bullfrog (tadpole)	7	31	0.23
	Sierran Treefrog tadpole	2	3	0.67
	Mosquitofish	7	48	0.15
	Centrarchid	2	42	0.05
	Cyprinid	0	22	0
	Ictalurid	0	16	0
	Silverside	1	7	0.14
	48 individual snakes			
2014	American Bullfrog adult	28	56	0.5
	American Bullfrog (tadpole)	14	56	0.25
	Sierran Treefrog tadpole	8	8	1
	Mosquitofish	11	74	0.15
	Centrarchid	5	56	0.09
	Cyprinid	16	48	0.33
	Ictalurid	2	10	0.2
	Silverside	5	26	0.19
	82 individual snakes			

We analyzed each model using Hamiltonian Monte Carlo (HMC) sampling as implemented by the software Stan (Carpenter et al. 2017). We called Stan from R v3.4.3 (R Core Team 2017) using the package RStan v2.16.2 (Stan Development Team 2017). We calculated WAIC using the package loo v1.1.0 (Vehtari et al. 2017). We ran each model on five independent chains of 20,000 iterations each, after a warmup of 5000 iterations. We thinned output by a factor of 10, so that posterior inference was based on 10,000 samples from the posterior distribution. We assessed convergence by examining history plots and with the partial scale reduction factor (Gelman and Rubin 1992); we observed no evidence for lack of convergence. For models with the most posterior support, we ran them again using five independent chains of 40,000 iterations each, after warmup of 5000 iterations, and thinned the output by 20 to increase effective sample sizes. Unless otherwise noted, we summarized posterior distributions as mode (highest posterior density interval).

## RESULTS

We recorded prey items from 127 Giant Gartersnakes in 130 instances (three snakes regurgitated on two separate occasions). The most consumed prey type was adult American Bullfrogs, and the least consumed prey type was the Bullhead Catfish (Ictalurids). In contrast, the most available prey type was mosquitofish, and the least available prey type was Sierran Treefrog tadpoles (Table 1). Many prey items were partially digested to the point where mass readings would be inaccurate; however, a subset (which were in good condition) of prey weights are available in Table 2. Bullfrog adults averaged 15.0 g, whereas treefrog tadpoles averaged 1.6 g.

Model selection results indicated that all models except the null model of no prey selection and constant selection were competitive (Table 3). The model with selection varying with snake length was the best fit, with selection varying by date nearly equivalent ( $\Delta$ WAIC much less than its standard error; Table 3). In general, Giant Gartersnakes were more likely to select anurans than fishes as prey (Figs. 2 and 3). Selection of some prey types differed for snakes of different lengths (Fig. 2).

In particular, larger snakes selected Sierran Treefrog tadpoles ( $\mu_{\beta[\text{use} \times \text{length} \times \text{treefrog}]} = -3.08 [-7.15 - \{-0.97\}]$ ), bullheads ( $\mu_{\beta[\text{use} \times \text{length} \times \text{bullhead}]} = -2.04 [-6.69 - 0.26]$ ), and Centrarchid fishes ( $\mu_{\beta[\text{use} \times \text{length} \times \text{Centrarchid}]} = -0.99 [-2.80 - \{-0.03\}]$ ) less than smaller snakes (Fig. 2). Selection for different prey types also varied across the active season: selection for bullfrog tadpoles and cyprinids was greatest early in the active season, selection for treefrog tadpoles peaked in the middle of the year, and selection for adult bullfrogs and bullheads peaked late in the active season (Fig. 3).

## DISCUSSION

Despite the low abundance of native prey, Giant Gartersnakes exhibited selection for native Sierran Treefrog tadpoles over the seven nonnative prey types. Selection for native prey is not necessarily surprising and supports a similar finding for Giant Gartersnake neonate prey preference (Ersan 2015); however, nonnative prey were consumed more often than Sierran Treefrogs, which is also somewhat common within the genus *Thamnophis* (Emmons et al. 2016; Virgin and King 2019). Predator–prey dynamics are often complex, and whether consumption of nonnative prey is beneficial to a native predator is context-specific (Pintor and Byers 2015). In one instance, consumption of nonnative prey dramatically benefited a native snake predator in terms of fecundity and growth (King et al. 2006). In these cases where

TABLE 2.—Average prey mass (g) of regurgitated prey consumed by Giant Gartersnakes in the Sacramento Valley, California, USA, 2013–2014. Dashes indicate no prey of this type were regurgitated.

	Average	Standard deviation	n
American Bullfrog adult	15.0100	12.0000	50
American Bullfrog tadpole	6.8889	3.2126	18
Centrarchid	4.3000	3.8324	9
Cyprinid	5.0000	3.8612	11
Mosquitofish	1.6000	0.8113	14
Treefrog tadpole	1.6000	0.4899	10
Silverside	4.0000	1.0000	2
Ictalurid	—	—	—

TABLE 3.—Model selection results for Poisson regression models of diet selection by Giant Gartersnakes (*Thamnophis gigas*) in the Sacramento Valley, California, 2013–2014. Models are listed in order of decreasing support. Values in the table are estimate (SE). ELPD = expected log pointwise predictive density, P = model complexity, WAIC = widely applicable information criterion,  $\Delta$ WAIC = difference in WAIC between best-fit model and given model. Models where  $\Delta$ WAIC <  $2 \times$  SE ( $\Delta$ WAIC) are considered competitive. Competitive models are indicated in bold.

Model	ELPD	P	WAIC	$\Delta$ WAIC
<b>Selection <math>\times</math> Length</b>	–2386 (120)	602 (53)	4771 (240)	0 (0)
<b>Selection <math>\times</math> Date</b>	–2391 (115)	597 (51)	4782 (230)	11 (30)
<b>Selection <math>\times</math> Year</b>	–2397 (119)	615 (53)	4793 (237)	22 (28)
Selection $\times$ Sex	–2403 (118)	618 (52)	4806 (237)	35 (29)
Selection $\times$ Habitat	–2410 (120)	622 (53)	4820 (240)	49 (35)
Constant selection	–2417 (119)	619 (53)	4835 (238)	64 (31)
Null	–2613 (121)	625 (51)	5225 (242)	254 (53)

native predators consume introduced prey, whether predation by natives helps limit nonnative prey is usually unknown. Furthermore, nonnative prey might also augment populations of predators, which might in turn diminish native prey populations (Noonburg and Byers 2005). Moreover, it is difficult to assess whether these snakes are showing plasticity or adaptation (Carlsson et al. 2009) and if the ultimate result is a cost or benefit.

In general, selection for frogs was higher than fish, although all tested fish were nonnative. Giant Gartersnakes therefore might have historically preferred consuming frogs, perhaps ranid frogs such as the California Red-legged Frog, *Rana draytonii*, to fish, rather than preferring native prey to invasive prey. Because native fishes were rare in our study system, identifying whether selection is stronger for frogs or for native species is confounded. Large adults of some other aquatic snake species also predominantly consume frogs over fish (Mushinsky et al. 1982; Santos et al. 2000). For example, *Nerodia erythrogaster* prey selection shifts from fish to frogs as snakes increase in size (Mushinsky et al. 1982).

The fish identified in this study were assigned into functional groups (by family) because of similar life histories and difficulty identifying species in the field. Thus, fish preferences based on their status as native or introduced cannot be resolved. Cyprinids were more likely to be selected than other fish groups, particularly in the second year of the study. The effect of year on selection of cyprinids might not be biologically significant because of the low number of cyprinids consumed in general. The overall selection of cyprinids relative to other fish groups might be caused, in part, by the historical presence of several native cyprinids in the Sacramento Valley. In addition to the verified introduced cyprinid species captured in traps, including Common Carp (*Cyprinus carpio*), Fathead Minnow (*Pimephales promelas*), Red Shiner (*Cyprinella lutrensis*), and Golden Shiner (*Notemigonus crysoleucas*), native Cyprinid species that could occur within the range of Giant Gartersnakes include, but are not limited to, hitch (*Lavinia exilicauda*), California Roach (*Hesperoleucus symmetricus*), Speckled Dace (*Rhinichthys osculus*), hardhead (*Mylopharodon conocephalus*), Sacramento Splittail (*Pogonichthys*

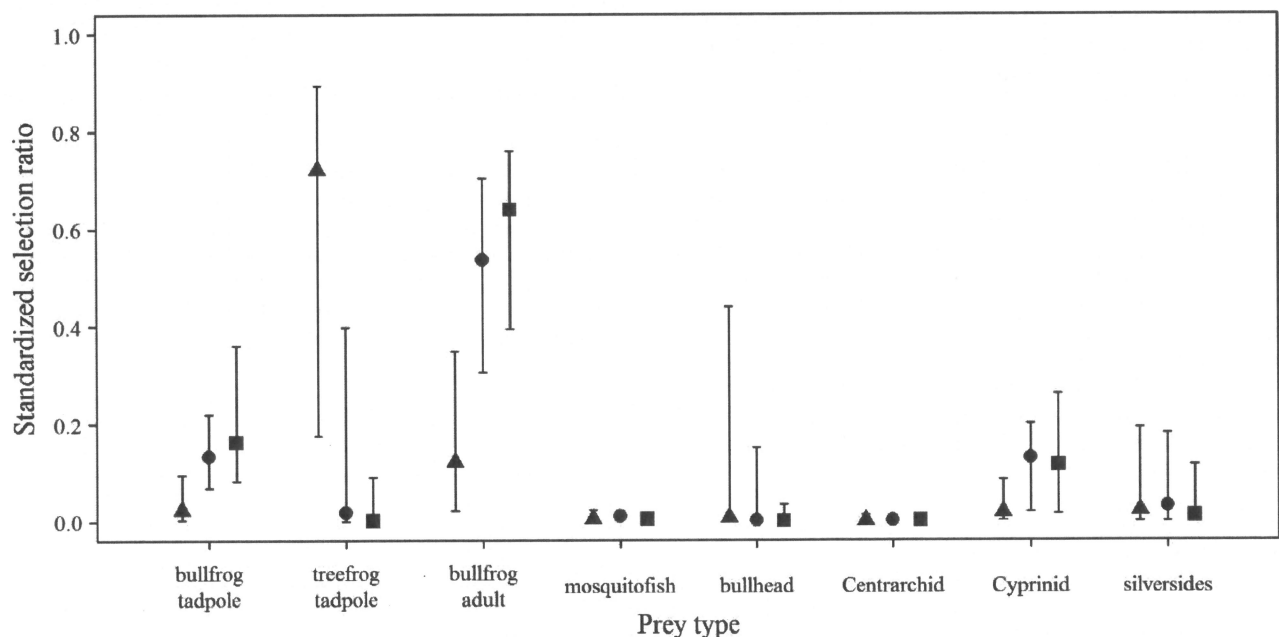


FIG. 2.—Giant Gartersnake (*Thamnophis gigas*) standardized prey selection ratios for 382-mm SVL (snout–vent length) snakes (triangles), 536-mm SVL snakes (circles), and 690-mm SVL snakes (squares). Symbols represent posterior modes; error bars represent 95% highest posterior density intervals.



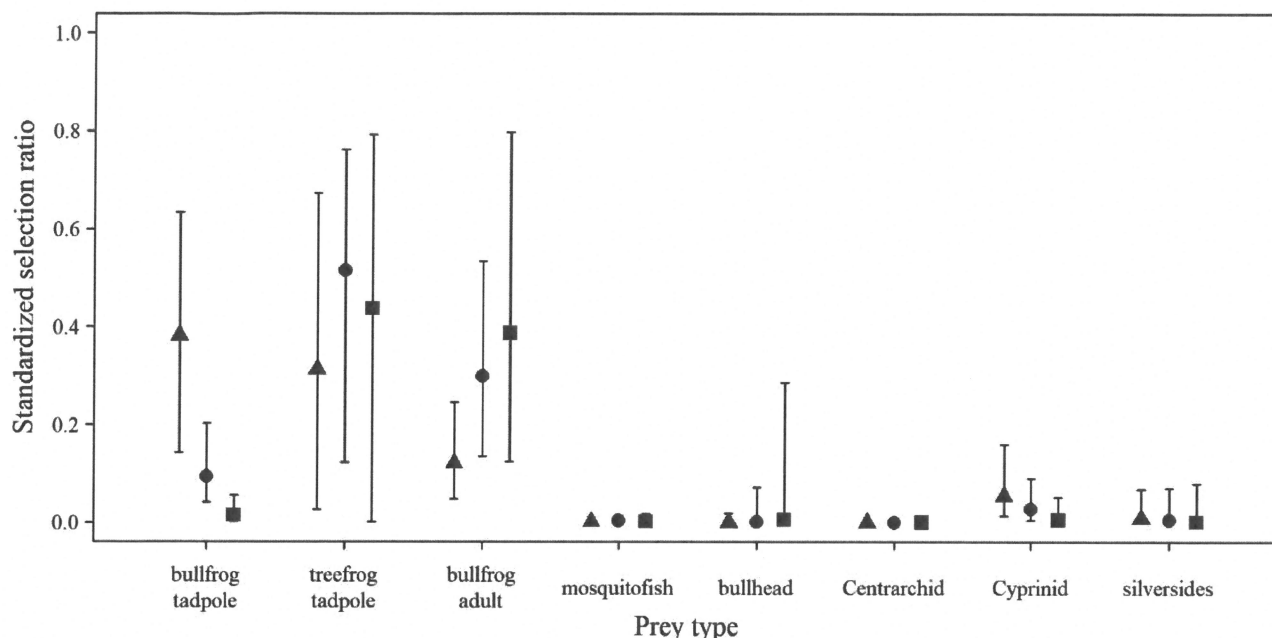


FIG. 3.—Standardized prey selection ratios for Giant Gartersnakes (*Thamnophis gigas*) on 12 May (triangles), 19 June (circles), and 29 July (squares). Symbols represent posterior modes; error bars represent 95% highest posterior density intervals.

*macrolepidotus*), and Sacramento Blackfish (*Orthodon microlepidotus*; McGinnis 2006; University of California, Division of Agriculture and Natural Resources [UC ANR] 2015). Further investigation to identify native and nonnative cyprinids within the Giant Gartersnake range would be valuable because cyprinids appear to be a potentially important component of Giant Gartersnake diet.

Centrarchids, mosquitofish, and Bullhead Catfish were least likely to be selected. There currently exists one native centrarchid, Sacramento Perch (*Archoglytes interruptus*; UC ANR 2015) that historically ranged throughout the Sacramento Valley, but is now restricted to Clear Lake and the Sacramento–San Joaquin River Delta (McGinnis 2006) and has never been identified in U.S. Geological Survey (USGS) traps in over 20 yr of sampling for Giant Gartersnakes. Another native, Tule Perch (*Hysterocarpus traski*) has been confirmed in some locations sampled in this study; however, they were rarely observed and categorized as a centrarchid in our analysis because they have a similar body style and life history and are often associated with centrarchids (UC ANR 2015). In an experiment analyzing prey choice in laboratory trials, neonate Giant Gartersnakes selected mosquitofish and centrarchids significantly less often than treefrog or bullfrog tadpoles when given the choice of both fish and anuran prey (Ersan 2015). Additionally, when given a fish-only prey choice, although neonates selected for centrarchids over mosquitofish, several neonates did not consume any prey within the 45-min trial (Ersan 2015). Here we provide additional evidence that centrarchids and mosquitofish are likely not as important as frogs or cyprinids in the Giant Gartersnake diet. This contrasts with historical management practices for Giant Gartersnakes that focus on fish availability. The practice of stocking fish, usually centrarchids for fishing or mosquitofish for mosquito abatement, is concerning because introduced fish and frogs can degrade native

amphibian communities (Goodsell and Kats 1999; Adams 2000; Adams et al. 2003) and centrarchids can be potentially dangerous to snakes (Hodgson and Hansen 2005; Alarcos et al. 2009).

Date influenced prey selection, though the effects of date were stronger for some species than for others. In particular, bullfrog tadpoles and cyprinids were selected more strongly early in the active season; Sierran Treefrogs were selected more strongly in the middle of the active season; and adult bullfrogs were selected more strongly later in the active season. Seasonally varying selection could indicate frequency-dependent selection whereby abundant prey are selected more than expected because of efficiency (search image, handling) gained by targeting abundant prey (Allen 1988). For example, selection of bullfrog tadpoles during the early spring could be because they overwinter and are available early in the spring when snakes emerge from brumation. Similarly, selection of bullfrog adults, which included all postmetamorphic bullfrogs in our study, could represent exploitation of an abundant food source later in the season as bullfrogs undergo metamorphosis. Recent metamorphs might also be particularly easy for snakes to capture. Seasonal variation in selection of Sierran Treefrogs and centrarchid fishes is more enigmatic.

In addition to seasonal variation, Giant Gartersnake prey selection also varied with snake size. Ontogenetic shifts or telescopes in snake diets are common given the gape limitation of snakes (King 2002; Hamilton et al. 2012). The stronger selection of smaller Sierran Treefrogs by smaller snakes, and the stronger selection of larger American Bullfrogs by larger snakes, are likely related to gape limitation of snakes. In contrast, weaker selection of bullheads by larger snakes might represent learning by snakes to avoid these potentially dangerous prey. Ontogenetic shifts and seasonal variation in prey selection are also

evidenced in *Thamnophis eques* (Macias Garcia and Drummond 1988).

In contrast to the effects of snake length and date, we found that neither sex nor habitat influenced prey selection. Similar studies on other natricine snakes found that both sex and size were factors that influence diet selection. Santos et al. (2000) found sex- and size-dependent prey partitioning in which male viperine snakes (*Natrix maura*) selected carp, females selected adult frogs, and juveniles selected tadpoles. The covariate of sex might not have been as apparent in the estimates of prey selection in this study because of potential limitations in the sampling techniques. In addition to the aforementioned sampling of only nongravid snakes, sampling of adult anurans might have been biased towards the more aquatic American Bullfrog over the more terrestrial Sierran Treefrog. Additionally, snakes captured in traps might have eaten prey items that were bycatch in the trap; thus, diet information from snakes in traps might not be fully representative of the Giant Gartersnake diet in general. More specifically, it might be that the Giant Gartersnakes sampled for this study had a higher prevalence of fish in stomach contents because of abundant fish bycatch in snake traps and possible increase of capture success of trapped prey. Regurgitation of hand-caught snakes would have been a useful comparison, but this species is very wary (Fitch 1940; Wright and Wright 1957) and obtaining sufficient sample sizes by hand capture would have been difficult. Whether basing inference on trapped individuals results in any bias in estimates of prey selection is unknown. Despite these potential limitations, apparent selection for anurans in the current study is consistent with neonate prey preference in this species (Ersan 2015).

To conserve wildlife, the natural history of species of concern must be understood. This includes developing a comprehensive knowledge of the ecological roles these species occupy in their environment. Current management practices for Giant Gartersnakes focus on addressing elements of their habitat, specifically the availability of water and vegetation. To date, little consideration has been given to prey communities, despite evidence that some prey species can be detrimental to Giant Gartersnakes (J.S.M. Ersan, personal observation). Though Giant Gartersnakes primarily prey on American Bullfrogs, large American Bullfrogs prey on Giant Gartersnake neonates (Wylie et al. 2003) and the significance of this trade-off is unknown. Potential management actions to support Sierran Treefrog populations include reduction of pesticide use, management to remove and limit invasive fish, and providing ephemeral shallow waters to support successful reproduction (Sparling and Fellers 2009; Preston et al. 2012; Halstead et al. 2018).

In summary, we found that Giant Gartersnakes selected native frogs more strongly than any other prey type, and selected all frogs, native and introduced, more strongly than introduced fishes. Despite the dominance of invasive prey in their environment, given a choice, Giant Gartersnakes prefer to eat less abundant native treefrogs. Therefore, management for native prey communities that also limits the abundance and distribution of invasive prey will preserve historical trophic dynamics and will likely benefit Giant Gartersnakes and other native predators of the Central Valley.

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