

Short Note

Crotalus viridis viridis

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Rattlesnakes use chemical stimuli in ambush site selection and for relocation of envenomated prey through strike-induced chemosensory searching. Shifts in responsiveness to prey chemicals have been documented in many snakes, and often correlate with prey commonly taken as snakes increase in age and size as well as geographical locations of the species. For instance, neonate rattlesnakes that prey primarily on ectotherms responded ~~more strongly to novel prey than to familiar prey~~ ~~more strongly to novel prey than to familiar prey~~. These results suggest that ontogenetic shifts in responsiveness to natural prey chemical cues are innately programmed and are not based on body size or feeding experience. *Crotalus viridis viridis*. This does not imply, however, that growth and experience are without effects, especially with novel prey or rare prey. *Crotalus viridis viridis* have experienced recent population expansion [Current Zoology 59 (2): 175–179, 2013].

Chemical cues, Chemoreception, *Crotalus viridis viridis*, Prey choice, Vomeronasal

It is well established that many squamate reptiles, especially snakes, are excellent at recognizing and discriminating between chemical cues of prey sources (Burghardt, 1970; Cooper et al., 1990, Chiszar et al., 1992; Clark, 2004). Behavioral plasticity has also been documented, as shifts in responsiveness to prey-derived

(see Mackessy, 2008 for a review).

The present sample of *C. v. viridis* were collected as neonates in 2008 from the same population and location

scores in order to account for strikes (Cooper and Burghardt, 1990); four strikes occurred during all trials. So, TFA scores were essentially the same as the number of tongue flicks during the 60 sec tests. We used a log-10 transformation to normalize the data and to achieve homogeneity of variance in the six conditions.

Inferential analyses used Chi-square (χ^2) and repeated-measures analyses of variance (ANOVA) followed by non-orthogonal contrasts. Alpha was set at 0.01 for these contrasts to control type I errors. Use of both nonparametric and parametric tests was predicated on our desire to see different statistical tools converge on the same conclusions. Comparisons of characteristics

for understanding the behavior and ecology of these species. Although the present snakes had eaten only *M. musculus*, the response to *P. maniculatus* had developed more-or-less on the same schedule as that of normally fed adult snakes, while the response to *S. undulatus* extract had not dropped significantly, as is seen in wild-caught snakes (see Saviola et al., 2012a). Further, the only strikes observed during trials were toward these native prey extracts (*P. maniculatus* and *S. undulatus*, two strikes towards each). Hence, these snakes behaved like normal subadults, even though they were closer to the size range of neonates and could not ingest adult mice.

Development of response to chemical cues of natural prey might be innately programmed, or experience with these or similar items might be required. In the present case, the responses to *P. maniculatus* and *S. undulatus* extracts were of normal intensity, even though the snakes probably had never seen or eaten these prey. This is suggestive of and might be taken as evidence for innate ontogenetic programming. It remains possible that feeding on *M. musculus* provided sufficient surrogate cues to promote development of response to *P. maniculatus* extracts. However, if this is true, then why did the snakes not respond strongly to *M. musculus* extracts? We cannot resolve this conundrum on the basis of present data, but we can provide two hypotheses: (1) response to *P. maniculatus* cues developed innately, perhaps even earlier than usual because of hunger and underfeeding, and (2) this sensitivity to rodent cues may have been the reason the snakes accepted *M. musculus* (rather than the other way around). Although captivity may influence chemosensory responses it has been documented that long-term captive rattlesnakes (*C. atrox*, *C. durissus*, *C. horridus*, *C. vegrandis*, *C. unicolor*) demonstrate no significant differences in strike-induced chemosensory searching when compared to wild-caught rattlesnakes (Chiszar et al., 1985). Similarly, long-term captivity did not appear to affect the ability of *C. o. oreganus* to strike, dispatch, or relocate prey normally (Alving and Kardong, 1994).

There is evidence that snakes can acquire responsiveness to new or unusual foods if the snakes are fed such foods but not their usual fare (Burghardt et al., 2000), and our data for *M. musculus* extracts agree with this finding. It is also known that naïve neonatal snakes respond to chemical extracts of natural foods (Cooper et al., 1990), and our data for *S. undulatus* extracts agree with those of Burghardt (working with garter snakes). The data for *P. maniculatus* extracts suggest that onto-

genetic appearance of response to prey normally taken later in life does not require experience with that prey. Similarly, adult *C. horridus* born and raised in captivity showed significant responses to chemical cues of preferred natural prey, even though these snakes were fed entirely *M. musculus*, never encountering natural prey items (Clark, 2004).

Being gape-limited forces snakes to consume prey that are small enough for them to swallow, and chemo-genetsensor relate with the most commonly consum

the foraging ecology of the snake (see Cooper, 1996, genet2008 v. *viridis* prey primarily on small ectotherms such as the lesser earless lizard *Holbrookia maculata*, prairie lizard *S. undulatus* and plains spadefoot toad *Spea bombifrons*; however, shifts to endotherm prey such as the western

- Chiszar D, Lee RKK, Radcliffe CW, Smith HM, 1992. Searching behaviors by rattlesnakes following predatory strikes. In: Campbell JA, Brodie ED Jr ed. *Biology of the Pitvipers*. Tyler, Texas: Selva, 369-382.
- Clark RW, 2004. Timber rattlesnakes *Crotalus horridus* use chemical cues to select ambush sites. *J. Chem. Ecol.* 30: 607–617.
- Cooper WE Jr, 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* 50: 973–985.
- Cooper WE Jr, 2008. Tandem evolution of diet and chemosensory responses in snakes. *Amphibia-Reptilia* 29: 393–398.
- Cooper WE Jr, Burghardt GM, 1990. A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. *J. Chem. Ecol.* 16: 45–65.
- Cooper WE Jr, Buth DG, Vitt LJ, 1990. Prey odor discrimination by ingestively naïve coachwhip snakes *Masticophis flagellum*. *Chemoecology* 1: 86–91.
- Duvall D, Chiszar D, Hayes WK, Leonhardt JK, Goode MJ, 1990. Chemical and behavioral ecology of foraging in prairie rattlesnake *Crotalus viridis viridis*. *J. Chem. Ecol.* 16: 87–101.