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SNAKE (COLUBRIDAE: *THAMNOPHIS*) PREDATORY RESPONSES TO CHEMICAL CUES FROM NATIVE AND INTRODUCED PREY SPECIES

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ABSTRACT—Several aquatic vertebrates have been introduced into freshwater systems in California over the past 100 years. Some populations of the two-striped garter snake (*Thamnophis hammondi*) have lived in sympatry with these species since their introduction; other populations have never encountered them. To assess the possible adaptation to a novel prey, we tested the predatory responses of *T. hammondi* from different populations to different chemosensory cues from native and introduced prey species. We presented chemical extracts from potential prey types and 2 control odors to individual snakes on cotton swabs and recorded the number of tongue flicks and attacks directed at each swab. Subject response was higher for prey odors than control substances. Odors from introduced centrarchid fish (*Lepomis*) elicited higher response levels than other prey types, including native anuran larvae (*Pseudacris regilla*). The pattern of response was similar for both populations of snakes (experienced and naïve, with respect to the introduced prey). We suggest that the generalist aquatic lifestyle of *T. hammondi* has allowed it to take advantage of increasing populations of introduced prey. Decisions on the management strategies for some of these introduced prey species should include consideration of how *T. hammondi* populations might respond in areas of sympatry.

RESUMEN—Algunos vertebrados acuáticos han sido introducidos en sistemas de agua dulce en California durante los últimos 100 años. Algunas poblaciones de la culebra de agua nómada de dos rayas (*Thamnophis hammondi*) han cohabitado con estas especies exóticas desde su introducción; otras poblaciones nunca las han encontrado. Para evaluar la posible adaptación a una presa exótica, probamos las respuestas predatorias de *T. hammondi* de distintas poblaciones a señales químicosensoriales de especies de presas nativas e introducidas. Presentamos extractos químicos de presas verdaderas y dos olores de control a cada culebra por medio de cotonetes y registramos el número de sacadas de lengua y ataques al cotonete. La respuesta de los sujetos fue más intensa a olores de presas que a olores de control. Las culebras respondieron más intensamente a olores del pez exótico (*Lepomis*) que a otras presas, incluyendo el anuro nativo *Pseudacris regilla*. El patrón de respuesta fue similar para culebras de ambas poblaciones (con y sin experiencia con presas introducidas). Sugerimos que el comportamiento acuático generalista de *T. hammondi* le ha permitido aprovecharse del aumento de poblaciones introducidas. Decisiones en cuanto a las estrategias de manejo de algunas de las especies de presas introducidas deben considerar cómo las poblaciones de *T. hammondi* pueden responder en áreas de simpatria.

Whether accidental or intentional, introductions of exotic species often have unexpected ecological consequences, ranging from minor trophic web alteration (Hasegawa, 1990) to competitive displacement (Losos et al., 1993), to native species extirpation (Savidge, 1987).

Species introduced on islands and in freshwater aquatic ecosystems seem to be especially detrimental, because native taxa have lost certain defenses or immunity (Savidge, 1987; Quammen, 1996), or the habitat available to escape the effects of the introduced species is

limited (Schwalbe and Rosen, 1988; Henne-man and Memmott, 2001). However, native taxa occasionally can be indifferent to an introduced species (Rissler et al., 2000) or benefit from its presence because it represents an additional food resource.

The ecological integrity of many aquatic habitats in California has suffered over the past century, in part due to various species introductions (Bury and Luckenbach, 1976; Cooper et al., 1986; Dill and Cordone, 1997). Notable among these taxa are several species of sunfish (*Lepomis*) introduced to lakes in the 1890s (Swift et al., 1993; Dill and Cordone, 1997); bullfrogs (*Rana catesbeiana*) and other ranid frogs established in the state for approximately 100 years (Bury and Luckenbach, 1976); and breeding populations of the African clawed-frog (*Xenopus laevis*) established within the past 40 years (McCoid and Fritts, 1993). Subsequent to their introductions, these taxa are thought to be responsible for population declines of native aquatic vertebrate and invertebrate species due to predation, competition for resources, or both, especially at the sub-adult stages (Bury and Luckenbach, 1976; Fisher and Shaffer, 1996). However, nonnative anurans and juvenile sunfish also represent possible additional food resources for native species of semi-aquatic predators, such as natricine snakes.

Toxic granular gland secretions from *X. laevis* have been shown to elicit avoidance responses in some North American natricine snakes (Barthalmus and Zielinski, 1988) or, if ingested, cause injury to them (Zielinski and Barthalmus, 1989). However, the two-striped garter snake (*Thamnophis hammondi*) has recently been observed eating *X. laevis* in the wild (Ervin and Fisher, 2001), suggesting that this snake species has a tolerance for this exotic prey. Among the most aquatic of garter snakes (Rossman et al., 1996), *T. hammondi* typically preys on anurans (both larvae and adults) and fish. In southern California, some populations of *T. hammondi* are sympatric with introduced populations of *X. laevis*, *R. catesbeiana*, and sunfish (and they all have been recorded in the diet; Ervin and Fisher, 2001; L. Pardy, pers. comm.), whereas others have never been exposed to these prey types. As with other studies examining generalist predators (Drummond, 1983; Drummond and Macías

Garcia, 1989), *T. hammondi* might take advantage of preying on available exotic species in times of low native prey populations or if the former is of equal energetic value.

The purpose of this study was to compare the predatory responses of *T. hammondi* collected from different populations to chemosensory cues from both native and introduced prey species. We addressed the following null hypotheses: 1) predatory interest by *T. hammondi* is similar regardless of the source of chemosensory cue, and 2) predatory interest by *T. hammondi* is similar regardless of the population of origin of the subject (i.e., whether or not it has previously been exposed to chemosensory cues from exotic prey).

METHODS—In June 2001 and May 2002, we collected *T. hammondi* from 2 localities: isolated ponds in Jamul Valley (JV), Jamul, and adjoining ponds at Laguna Meadows (LM) within the Cleveland National Forest, Laguna, both of which are in San Diego County, California. The JV ponds (269 m elevation) are used as breeding sites by *Rana catesbeiana* and *Pseudacris regilla*, and are inhabited by *X. laevis* and *Lepomis macrochirus*. Only *P. regilla* is found in the LM ponds due to their semi-permanent hydroperiod, higher elevation (1,635 m), relative isolation from other aquatic habitat, and the fact that exotic species have not been introduced there.

We caught snakes by hand in or near (<5 m) aquatic habitat and determined their size (mass \pm 1 g, snout-vent length [SVL] \pm 1 mm) and sex on the day of capture. Upon their return to the lab, snakes were housed individually in either plastic containers with dimensions of 38 \times 26 \times 16 cm or glass aquaria with dimensions of 51 \times 31 \times 28 cm. Within each container, we placed vermiculite or newspaper substrate, water in a plastic dish ad libitum, a plastic shelter, and a rock for shedding substrate. Paper was affixed along the outside walls of each container to prevent subjects in adjacent cages from observing activity in the cage occupied by another. All containers were maintained at 21 to 27°C and a photoperiod of 13.5L:10.5D.

We collected post-metamorphic *X. laevis* and larval *P. regilla* from aquatic habitats in San Diego County using dip nets and returned them to the lab where they were sacrificed and stored in a freezer for future use. We collected *R. catesbeiana*, *Lepomis macrochirus*, and *L. cyanellus*, all of which have been introduced in aquatic habitats in San Diego County (Swift et al., 1993; Fisher and Shaffer, 1996; Dill and Cordone, 1997), and adult *Lumbricus* (earthworm) in Coles County, Illinois, as needed for extract preparation in the experimental trials. We prepared all

odor extracts following the methods of Cooper et al. (2001) immediately prior to a trial. Extracts were comprised of the following prey types: post-metamorphic *X. laevis*, larval *R. catesbeiana*, adult *R. catesbeiana*, larval *P. regilla*, *Lumbricus*, and juvenile sunfish (*Lepomis*). We rubbed a 15-cm cotton swab along the moistened dorso-lateral surface of a prey specimen (thawed, if necessary) prior to presentation. Distilled water and English Leather (Dana, Inc., Toledo, Ohio) cologne (mixed to a 1:3 dilution, cologne:distilled water) were used as negative and positive controls, respectively, the latter being a novel, pungent scent. A new swab was prepared every 15 min or if any subject bit the swab during a trial.

We conducted experimental trials during June and July of 2001 and 2002. Trials were not performed on any subjects during periods of ecdysis; we restricted the diet of all subjects to water alone for at least 3 d prior to any trial. Due to limited availability of either subjects or prey types during portions of the study period, not all subjects were exposed to all prey odors. Each experimental trial consisted of a presentation of 5 or 6 different odor types (both control odors were always included in each trial), with each presentation separated by a minimum of 15 min. If a subject attacked a swab during presentation, it was offered *R. catesbeiana* tadpoles after the trial to minimize the possibility that predatory interest would be extinguished without reinforcement (Burghardt, 1992). We tested subjects in their home cages over a minimum of 4 trials (each separated by the 3-d restricted diet period) and randomized the order of odor presentation within and between trials such that the order of presentation for each subject was never the same to control for differential habituation to the various stimuli over repeated swab presentations (Ford, 1995).

During any 1 odor presentation, the swab was moved slowly to approximately 2 cm from the snout of the subject (Cooper et al., 2001), but moved closer to touch the labial scales if no response to the swab was recorded within 30 s. We acknowledge that movement of the swab provided a visual cue that, by itself, might elicit tongue flicks (Burghardt and Denny, 1983); however, the response levels for swabs prepared with prey odors were higher than those for swabs bearing control odors (see below) suggesting that chemical cues supersede the swab movement. For a period of 60 s, we recorded the number of tongue flicks directed at the swab. In the event that the subject bit the swab, we also recorded the latency (± 1 s) to attack (Burghardt, 1993). These parameters were converted into a tongue flick-attack score appropriate for repeated presentations of odor stimuli (TFAS[R]; Cooper and Burghardt, 1990). This index adjusts the value of response variable upwards when the snake bites the swab to reflect an increased level of predatory interest:

$$\text{TFAS(R)} = \text{TF}_{\text{max}} + (\text{TL} - \text{latency})$$

where TF_{max} is the maximum number of tongue flicks for that odor type over all presentations, TL is the duration of swab presentation (60 s), and latency is the time taken to attack the swab. Thus, if a swab is not attacked, TFAS(R) simply equals the number of tongue flicks directed at the swab over the presentation period.

Because our data violated certain assumptions associated with parametric analyses, we rank transformed the TFAS(R) values (Conover and Iman, 1976). We then analyzed these data with a univariate repeated-measures analysis of variance ($\alpha = 0.05$) including collection locality as a between-subjects independent variable. Following Dunn (1964), we calculated the mean rank value for each treatment level (odor type) over all trials and detected any differences between treatments with Dunn's test for multiple pair-wise comparisons (Zar, 1999). This procedure protects against Type I errors that might occur due to uneven sample sizes. We compared morphometric parameters of all subjects by sex and collection site using a 2-way analysis of variance. In all cases, untransformed data are reported below.

RESULTS—We used 28 *T. hammondi* in this study, with 24 coming from the higher elevation (LM) site. Subjects collected at this locality were smaller in SVL ($F_{1,26} = 36.57$, $P < 0.001$) and mass ($F_{1,26} = 26.26$, $P < 0.001$) than subjects from the JV site (Table 1). There were no differences in tail length as a function of collection site ($F_{1,26} = 0.23$, $P = 0.64$), or in any body size parameter as a function of subject gender ($F_{1,26} \leq 2.85$, $P \geq 0.10$). Of the snakes collected from JV, 2 had recently eaten; the gut contents of both were small (<5 cm SVL) adult *X. laevis*.

Snakes used in this study responded to the presence of a swab introduced to their container with an elevated rate of tongue flicking. We needed to elicit tongue flicks by touching the swab to the labial scales of subjects during only 2.6% of the presentations. Subjects bit swabs containing odors from prey species on 12.0% of the presentations, but never struck at swabs containing control odors. Prey odors elicited strikes more often than expected ($\chi^2_{(df=7)} = 339.0$, $P < 0.001$). Mean TFAS(R) values did not differ as a function of collection locality ($F_{1,24} = 0.02$, $P = 0.89$). Responses were also similar between years in which the study was conducted ($F_{1,24} = 0.10$, $P = 0.76$), and there were no changes in response values to the

TABLE 1—Locality, gender, and morphometrics (mean \pm 1 SE) of two-striped garter snakes (*Thamnophis hammondi*) collected in San Diego County, California, and used in odor presentation trials in June 2001 and June 2002. Snakes from Laguna Meadows (LM) had smaller masses and snout-vent lengths (SVL) than snakes from Jamul Valley (JV) (analyses of variance; $F_{1,26} \geq 26.26$, $P < 0.001$).

Locality	Sex	Sample size	SVL (mm)	Tail length (mm)	Mass (g)
JV	M	2	636.0 \pm 6.0	121.5 \pm 21.5	91.1 \pm 0.1
	F	2	703.0 \pm 242.0	115.0 \pm 20.0	155.0 \pm 113.0
LM	M	14	395.4 \pm 13.6	107.5 \pm 8.8	28.4 \pm 2.8
	F	10	386.6 \pm 16.1	111.1 \pm 11.0	27.2 \pm 3.9

same odor source over repeated presentations ($F \leq 0.19$, $P \geq 0.90$).

Mean TFAS(R) values varied by odor source ($F_{7,114} = 26.92$, $P < 0.001$) with higher responses recorded when subjects were presented with odors from all prey species except *Lumbricus* (Fig. 1). The mean (\pm SE) response to this prey type (17.3 \pm 2.1) was similar to that for both of the control odors (Dunn's $Q \leq 0.62$), the latter of which also were similar to each other ($Q = 0.71$). The mean TFAS(R) response to odors from *Lepomis* was higher than for other prey types ($Q \geq 3.18$). Mean TFAS(R) values in response to odors from *Rana* adults and larvae, *Xenopus*, and *Pseudacris* larvae were higher than the control and *Lumbricus* odors ($Q \geq 3.84$), but not different from each other ($Q \leq 2.58$).

DISCUSSION—There is little doubt that *T. hammondi* has added to its diet at least 3 non-

native prey types since the introduction of these species (pers. observ.; Ervin and Fisher, 2001). Quantifying the impact of *T. hammondi* as a predator on populations of *R. catesbeiana*, *X. laevis*, and *Lepomis*, however, is more difficult because of the relatively secretive nature of both predator and prey species. These 3 prey species not only elicited predatory responses that were comparable to native prey, but have also been ingested by *T. hammondi* in laboratory settings simulating natural conditions (Mullin, pers. observ.). Even if introduced prey have depressed the population densities of native prey species, *T. hammondi* that are sympatric with introduced prey might have more opportunities to successfully capture prey occupying similar aquatic habitats.

Snakes collected from lowland areas inhabited by *X. laevis* and *R. catesbeiana* are larger in both mass and SVL than snakes from the LM site (Table 1; Mullin and Ervin, pers. observ.),

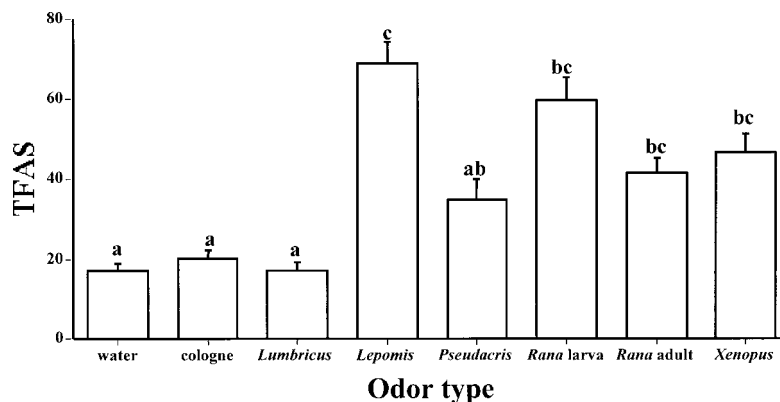


FIG. 1—Mean (\pm 1 SE) tongue-flick attack score (TFAS) of two-striped garter snakes (*Thamnophis hammondi*) presented with different chemosensory cues in June 2001 and June 2002. See text for a description of the source of different odor types. Letters above bars denote differences between responses to different odor types (as detected by an analysis of variance on rank-transformed TFAS values).

a morphological difference having several possible explanations: 1) higher absolute prey density at the JV site (sensu Lindell, 1997); 2) a shift to nonnative prey at JV ponds when native species are less abundant (Drummond, 1983; Drummond and Macías Garcia, 1989); 3) small snakes are rare at JV because they are preyed upon by adult *R. catesbeiana* (Rosen and Schwalbe, 1995); 4) large snakes are rare at LM because that population experiences high predation pressure that depresses snake growth rates (Reinhardt and Healey, 1997); 5) lower elevations having longer activity seasons and higher temperatures that might promote growth rate; and 6) JV ponds having longer site permanency, meaning that aquatic prey are available for a longer portion of the activity season. As we did not specifically test any of these ideas here, further research should attempt to identify a specific cause, or the synergistic effects of more than 1 cause, for this size disparity.

Using methods similar to this study, other researchers have shown that snakes feeding on annelids, anurans, and fish respond to different prey types with different levels of predatory interest (Arnold, 1981, 1992; Burghardt, 1992). Some snake species can even learn to avoid certain prey types because they are unpalatable (Mori, 1989) or potentially dangerous if ingested (Drummond and Macías Garcia, 1995). As a highly aquatic representative of its genus, *T. hammondi* is known to eat fish and larvae of several anuran species (Cunningham, 1959; Rossman et al., 1996), including some possessing relatively toxic integumentary secretions (e.g., *Bufo*). Our data indicated that *T. hammondi* responded to the chemosensory cues of several prey types with equal vigor (admittedly, prey having close phylogenetic relatedness might not be distinguishable by snakes solely on the basis of tongue-flicking; Burghardt, 1993). Because there is some overlap between the components of integumentary toxins found in *Xenopus* and *Bufo* (Daly et al., 1987), *T. hammondi* might have a tolerance for *Xenopus* skin toxins. Resistance to the effects of highly-toxic integumentary secretions of amphibian prey (Salamandridae: *Taricha*) has been documented in another member of this genus, *Thamnophis sirtalis* (Brodie and Brodie, 1990).

Despite LM snakes not having previous ex-

posure to any of the nonnative prey used in this study, levels of predatory interest to all chemosensory cues were similar in snakes collected from both the LM and JV sites. Given the significance levels associated with TFAS values for the collection sites ($P = 0.98$) and the site-x-odor interaction ($P = 0.46$), we consider it unlikely that additional individuals from JV would reveal any differences in response level. De Queiroz and Lawson (1994) recognized *T. hammondi* as closely related to *T. couchii* (Sierra garter snake), another species commonly associated with aquatic habitat and a predator on a variety of prey types (Cunningham, 1959; Rossman et al., 1996). We suggest that the generalist nature of *T. hammondi* is such that it readily accepts many aquatic prey species. The distribution of *T. hammondi* might be limited less by the presence of a particular prey species, and more by the availability of habitat that supports populations of aquatic and semi-aquatic vertebrates.

Predatory response to integumentary odors of *Lepomis* was higher than for other prey types, including native species. Conversely, responses to *Lumbricus* odors were low and not distinguishable from control odors (Fig. 1). We find the latter result of greater interest because *T. hammondi* from LM ponds have recently been observed eating other annelid species (*Erypobdella*; Ervin et al., 2003). Although leeches and other annelids are eaten by several garter snake species (Arnold, 1992; Drummond and Macías Garcia, 1995), *T. hammondi* might not recognize *Lumbricus* odors as suitable prey because of the low incidence of encountering terrestrial oligochaetes in aquatic habitats. Taken together, these results are of additional interest for 2 reasons. First, *T. hammondi* has a consistently strong response to chemical cues from aquatic and semi-aquatic vertebrates, even if recently introduced. Second, *T. hammondi* did not respond strongly to worm odors in spite of the facts that worms: 1) have long been in sympatry with *T. hammondi*; 2) might be encountered in areas immediately adjacent to aquatic habitat; and 3) are readily accepted as prey by other members of the genus (Burghardt et al., 1988; Arnold, 1992). In other words, whereas *T. hammondi* has adapted to accept exotic vertebrates, this species refuses a native palatable prey. The pattern of response to prey odors illustrated here provides a notable contrast to

other studies on learning and prey preference in *Thamnophis* (Burghardt, 1992; Drummond and Macías García, 1995).

Two-striped garter snakes in our study responded to chemosensory cues from native and nonnative prey with equal vigor, a result with 2 possible explanations. Similar to patterns observed in other squamate reptiles (Malhotra and Thorpe, 1991; Madsen and Shine, 1992), a rapid evolutionary change might have led to *T. hammondi* adapting to the presence of nonnative prey within the time of the introductions of these species (40 to ca. 100 years; Bury and Luckenbach, 1976; Dill and Cordone, 1997). Although molecular genetics studies might bear this out, a more likely possibility is that the generalist nature (sensu Drummond, 1983) of *T. hammondi* has allowed it to utilize these nonnative prey opportunistically, as they become established within the distribution of the snake. Further support for this latter possibility is obtainable by examining *T. hammondi* populations near the expanding ranges of the nonnative prey species both before and after the occurrence of sympatry.

Jennings and Hayes (1994) described *T. hammondi* as a species of conservation concern in California. We suggest that any management strategy designed to reduce or eradicate the nonnative aquatic vertebrates in southern California consider the effects of this strategy on sympatric *T. hammondi* populations. Nonnative anurans and fish are now predominant components of the diet of other garter snake species (Hansen and Tremper, unpubl. data, cited in Rossman et al., 1996). Although the presence of *R. catesbeiana* and *X. laevis* is often associated with depressed populations of native amphibians in California (Hayes and Jennings, 1986; Stebbins and Cohen, 1995), they are now regularly included in the *T. hammondi* diet. Thus, management plans advocating the removal of these prey species (at best, a difficult task in lotic habitats) should be linked to restoration of native amphibians and fish to avoid any negative impacts on natricine snakes.

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