DISCRIMINATION OF PREY, BUT NOT PLANT, CHEMICALS BY ACTIVELY FORAGING, INSECTIVOROUS LIZARDS, THE LACERTID *Takydromus sexlineatus* AND THE TEIID *Cnemidophorus gularis*

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Abstract—Sampling environmental chemicals to reveal prey and predators and to provide information about conspecifics is highly developed in lizards. Actively foraging lizards can discriminate between prey chemicals and control stimuli, but ambush foragers do not exhibit prey chemical discrimination. Recent experiments on a few species of herbivorous lizards have also demonstrated an ability to identify plant food chemicals. We studied chemosensory responses to chemicals from prey and palatable plants in two species of actively foraging, insectivorous lizards. Both the lacertid *Takydromus sexlineatus* and the teiid *Cnemidophorus gularis* exhibited strong responses to prey chemicals, but not to plant chemicals. These findings increase confidence in the relationship between prey chemical discrimination and foraging mode, which is based on data for very few species per family. They also provide data showing that actively foraging insectivores in two families do not respond strongly to plant cues. Such information is essential for eventual comparative studies of the relationship between plant diet and responses to food chemicals. The traditional method of presenting stimuli by using hand-held cotton swabs worked well for *T. sexlineatus* but could not be used for *C. gularis* due to repeated escape attempts. When stimuli were presented to *C. gularis* on ceramic tiles and no experimenter was visible, the lizards responded readily. Presentation of stimuli on tiles in the absence of a visible experimenter may be a valuable approach to study of food chemical discrimination by active foragers in which antipredatory behavior interferes with responses to swabs.

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1623

INTRODUCTION

Chemical cues are important to many animals for location, identification, and assessment of food. Many lizards are capable of identifying food chemicals, as indicated by greater tongue-flicking rates and higher frequencies of biting when tested with chemical cues from food than from control chemical stimuli (Cooper, 1994a, 1995, 1997). Lizards use the tongue–vomeronasal system to detect chemical cues from prey, predators, and conspecifics (reviewed by Burghardt, 1970; Halpern, 1992; Mason; 1992; Cooper, 1994a). Chemicals are sampled from the environment lingually and pass from the mouth through the vomeronasal ducts to the sensory epithelia of the vomeronasal organs for chemosensory analysis (Halpern, 1992). In the only lizard species tested, individuals in which access of chemicals to the vomeronasal organs was blocked by sealing the vomeronasal ducts lost the ability of discriminate between food chemical stimuli and control substances, despite having intact olfactory and gustatory senses (Cooper and Alberts, 1991).

Comparative studies have revealed correlated evolution between foraging mode and prey chemical discrimination in lizards (Cooper, 1994b, 1995, 1997, 1999a). The major foraging modes of insectivorous lizards are active foraging and ambush foraging. Active foragers move through the habitat while searching for prey, tongue-flick frequently while searching, and are capable of prey chemical discrimination (Cooper, 1995, 1997). Ambush foragers wait immobile for prey to approach, tongue-flick at much lower rates, and do not discriminate between prey chemicals and control substances (Cooper, 1995, 1997, 1999a).

In most lizard families, all species studied exhibit only one of the two modes, so that a given family typically consists entirely of ambush foragers or entirely of active foragers (Cooper, 1994a; Perry, 1995). There are exceptions, primarily in Gekkonidae, Scincidae, and Lacertidae (Cooper, 1994a; Perry, 1995), but the stability of foraging mode is sufficient to permit comparative analyses that use familial traits (Cooper, 1995, 1997, 1999a). The data indicate that prey chemical discrimination is acquired upon evolutionary adoption of active foraging and is absent in ambush foragers through retention of the ancestral condition or through loss of active foraging (Cooper, 1995, 1997). However, data on prey chemical discrimination are available for, at most, a few species per family. More information is needed to determine the generality of the relationship.

Herbivorous and omnivorous lizards appear to use tongue-flicking to identify plant food (Cooper and Alberts, 1990, 1991; Cooper unpublished data). A large majority are insectivores, but omnivory and herbivory have originated indepen-

dently in several lineages (Pough, 1973; Iverson, 1982). In herbivores and omnivores derived from active foragers, an ability to identify prey from chemical cues is already present when plant consumption appears. Chemosensory assessment of plant foods could be accomplished by adding responsiveness to plant food chemicals to the existing discriminatory repertoire. This presumes that strictly or nearly exclusively insectivorous active foragers do not respond strongly to chemical stimuli from plants palatable to herbivorous lizards, but there is little empirical evidence on this point. The only species of insectivorous actively foraging lizard yet tested, the skink *Scincella lateralis*, responded strongly to prey chemicals but not to plant chemicals (Cooper and Hartdegen, 1999). Comparative study of the evolutionary relationship between diet and food chemical discrimination in active foragers requires data on responses to plant and animal food chemicals in diverse taxa of insectivores, as well as herbivores and omnivores.

Here, we report the findings of experiments on lingual and biting responses to prey chemicals and plant chemicals in two species of actively foraging, insectivorous lizards, the lacertid *Takydromus sexlineatus* (Cooper, 1994a; Rogner, 1997) and the teiid *Cnemidophorus gularis* (Smith, 1946). Previous studies have detected prey chemical discrimination in the lacertids *Acanthodactylus boskianus* (Cooper, 1999a), *Podarcis hispanica* (Cooper, 1990), and *P. muralis* (Cooper, 1991) and in the teiids *Tupinambis rufescens* (Cooper, 1990), *T. nigropunctatus* (Cooper, 1993), and *T. teguixin* (Yanosky et al., 1993). The only one of these species for which responses to plant chemicals were tested is *T. teguixin*, an omnivorous species that responded strongly to plant food stimuli. Our goals are: (1) to increase the number of genera and species for which the presence or absence of prey chemical discrimination is known in Lacertidae and Teiidae, thereby increasing knowledge of the relationship between foraging mode and prey chemical discrimination in insectivores; and (2) to provide the first tests for both families of responsiveness to plant chemical stimuli by insectivores, providing baseline information for a future comparative analysis.

METHODS AND MATERIALS

Subjects and Maintenance. Adult *T. sexlineatus* were obtained from a commercial dealer (Bronx Reptiles, New York), and adult *C. gularis* were collected in Hidalgo and Brooks counties, Texas. All were housed in an accredited (AAALAC) animal care facility at Indiana University-Purdue University at Fort Wayne. Each was kept singly, *T. sexlineatrus* ($N = 18$) in $41 \times 28 \times 23$-cm translucent plastic cages and *C. gularis* ($N = 20$) in $50 \times 31 \times 27$-cm glass terraria, each of which contained a substrate of indoor–outdoor carpet and a water bowl. Each cage for *C. gularis* also contained a plastic shelter. Ambient temperature was 28°C for both species, but heat lamps produced a thermal gradient

that permitted *C. gularis* to thermoregulate. Both species were active and fed readily under the conditions of housing and testing. Room light was provided by fluorescent bulbs on a 13L:11D cycle. Lizards were maintained on a diet of domestic crickets (*Acheta domesticus*) dusted with commercial vitamins and calcium carbonate. Food was withheld from *C. gularis* for three days and from *T. sexlineatus* for two days before the experiments to ensure adequate motivation. Water was available ad libitum.

Experimental Procedures. We evaluated the hypotheses that these lizards use chemical cues sampled by tongue-flicking to discriminate between prey and control stimuli, but not between plant chemicals and control stimuli, by observing their responses to chemical stimuli from prey and control substances. Responses of both species to prey chemicals, chemicals from a plant palatable to herbivorous lizards, and deionized water were recorded. We also studied responses of *C. gularis* to cologne. The prey stimuli were integumentary chemicals from domestic crickets, and the plant chemical stimuli were surface chemicals from romaine lettuce. Deionized water served as an odorless control to permit assessment of response levels attributable to the experimental milieu in the absence of chemical stimuli. Cologne (Mennen Skin Bracer, Spice Scent) was used as a pungency control to assess responses to a highly volatile, odorous stimulus unrelated to food sources. Because cologne may be aversive at full strength (Dial and Schwenk, 1996; Cooper, 1998a,b), it was diluted 3:1 (deionized water–cologne by volume). Diluted cologne is detectable, but does not induce avoidance or other signs of aversion.

We presented stimuli to *T. sexlineatus* on cotton tips of wooden applicators. The first step in stimulus preparation was to immerse the tip of an applicator in deionized water. Excess fluid was removed by a flick of the wrist. To add other stimuli, the wetted swab was rolled firmly over the surface of a living cricket or a leaf of romaine lettuce. Because *C. gularis* would not respond consistently in swab tests with the experimenter present, we presented the stimuli to that species on ceramic tiles (15×15 cm) in the absence of an experimenter. Each clean tile was prepared by moistening with deionized water and then rubbing its surface with a cricket or a leaf of romaine lettuce. Diluted cologne was applied to tiles directly without prior moistening. Tests were conducted when visible moisture was no longer detectable. Each stimulus swab or tile was used only once.

To conduct a trial for *T. sexlineatus*, the experimenter slowly approached a lizard's cage, removed its lid, and placed a swab 1–2 cm anterior to a lizard's snout. He recorded number of tongue-flicks directed to the swab for 60 sec, starting with the first tongue-flick, unless the lizards bit the swab, in which case the trial was terminated and the latency to bite in seconds was recorded. If a lizard did not tongue-flick within 30 sec after the swab was placed before it, the experimenter gently touched the lizard's anterior labial scales with the swab, which induced tongue-flicking.

In the study of *C. gularis*, a lizard was transferred from its home cage to a test chamber in an adjacent room. The lizard was placed on a ceramic tile that formed the floor of the transparent plastic test chamber. The experimenter placed a lid on the cage, withdrew to a position out of the lizard's view, observed the lizard through one-way glass, and recorded the number of tongue-flicks that touched the tile in the 2-min interval beginning with the first tongue-flick that touched the tile. If a lizard did not tongue-flick after 15 min, zero tongue-flicks were recorded.

Randomized block designs were used for both species, each lizard responding to all stimuli. For the 18 *T. sexlineatus* tested, the sequence of stimulus presentation was counterbalanced with three complete replications of all possible sequences. Because it bit repeatedly before tongue-flicking, one individual was discarded, giving a final sample size of 17. All trials were conducted on a single day with a minimum intertrial interval of 60 min. For the 20 *C. gularis*, the testing sequence was partially counterbalanced by randomly eliminating one sequence beginning with each stimulus. Each individual participated in only one tile test per day.

Although we recorded numbers of tongue-flicks in both studies, the primary response variable in the study of *T. sexlineatus* was the tongue-flick attack score for experiments that used repeated measure designs, TFAS(R) (Cooper and Burghardt, 1990). TFAS(R) is the number of tongue-flicks in 60 sec if the lizard does not bite the swab. If the lizard bites, TFAS(R) is the maximum number of tongue-flicks performed by that individual under any of the stimulus conditions plus [60 minus the latency to bite in seconds]. Biting is given heavier weighting than any number of tongue-flicks (unless the bite occurs at exactly 60 sec) because it is a predation attempt.

Statistical Analysis. The tongue-flick and TFAS(R) data were examined for heterogenity of variance by using Hartley's F_{max} test (Winer, 1962). When significant heterogenity of variance was detected, the data were logarithmically transformed to reduce heterogeneity. One was added to the number of tongue-flicks for *C. gularis* prior to transformation due to the presence of zero tongue-flicks in a few trials. For raw or transformed data having homogeneous variances, the data were tested for significance of differences among stimuli by using analysis of variance for a single-factor experiment having a randomized block design (Winer, 1962). When the main effect was significant, Newman-Keuls tests were used to assess significance of differences between pairs of stimulus means. If variances were heterogeneous for both the raw and transformed data, the significance of the main stimulus effect was tested nonparametrically by Friedman two-way analysis of variance (Zar, 1996). This test was also used for differences among stimuli in latency to bite. Nonparametric paired comparisons between conditions were performed as in Zar (1996). Differences among conditions in proportion of lizards biting were examined by a Cochran's Q test fol-

lowed by sign tests of the significance of difference among sets of conditions
(Siegel, 1956). Although unadjusted probabilities are reported for the sign tests,
the pattern of significance is the same after sequential Bonferroni adjustment for
the number of tests (Wright, 1992). Tests of significance were two-tailed with
$\alpha = 0.05$. Data are reported as mean $\pm$ 1.0 SE. Statistical power was determined
as in Zar (1996) for *T. sexlineatus* by using TFAS(R) for swab data on *Scincella
lateralis* (Cooper and Hartdegen, 1999). Because no comparable estimate could
be made for tile data on *C. gularis*, power was estimated from the *C. gularis*
data themselves (Zar, 1996).

In addition to the primary tests described above, we tested responses of
each species to internal chemical cues from banana fruit and of *C. gularis* to
external chemical cues from strawberry fruit. Neither species ate romaine lettuce
or banana placed in their home cages.

RESULTS

Takydromus sexlineatus. The lizards readily investigated the swabs by
tongue-flicking. All 17 individuals tongue-flicked at least once under all three
conditions, and all individuals bit swabs under one or more conditions (Tables
1 and 2). Tongue-flick variances were homogeneous ($F_{max} = 1.55$; $df = 3, 16$;
$P > 0.10$). Mean numbers of tongue-flicks were low (Table 1) and did not differ
among conditions ($F = 0.225$; $df = 2, 32$; $P > 0.10$).

TFAS(R) variances differed among conditions ($F_{max} = 43.79$; $df = 3, 16$;
$P < 0.01$) and were not made homogeneous by logarithmic transformation. Non-
parametric analysis of variance indicated strong differences among conditions
(Table 1; $\chi^2 = 18.56$, $df = 2$, $P < 0.001$), with stronger responses to cricket

TABLE 1. TONGUE-FLICKS AND TONGUE-FLICK ATTACK SCORES [TFAS(R)] OF
Takydromus sexlineatus ($N = 17$) IN RESPONSE TO SWABS BEARING CHEMICAL STIMULI
OR WATER IN 60-SECOND TRIALS

	Cricket	Romaine lettuce	Deionized water
Tongue-flicks			
Mean	4.4	4.1	3.7
SE	0.8	0.8	0.7
Range	1–13	1–14	1–10
TFAS(R)			
Mean	58.1	16.8	16.1
SE	0.9	5.7	5.7
Range	48–61	1–61	1–60

TABLE 2. INDIVIDUALS THAT BIT AND LATENCY TO BITE FOR *Takydromus sexlineatus* ($N = 17$) RESPONDING TO SWABS BEARING CHEMICAL STIMULI

	Cricket	Romaine lettuce	Deionized water
Number that bit	17	5	4
Latency to bite			
Mean	6.3	46.7	47.8
SE	1.4	5.7	5.6
Range	1–21	1–60	1–60

stimuli than to romaine lettuce or deionized water ($P < 0.001$ each), but no difference between the romaine lettuce and deionized water conditions ($P > 0.10$). An approximate ANOVA gave an identical pattern of significance. The phi coefficient was 4.31, corresponding to a power of > 0.99 to reject the hypothesis of no difference between control and experimental stimuli by using parametric AVOVA.

All lizards bit swabs bearing cricket stimuli, and several bit swabs bearing each of the other stimuli (Table 2). The number of individuals that bit differed among conditions ($Q = 20.93$; $df = 2$; $P < 0.001$). More individuals bit in the cricket condition than in the romaine lettuce condition ($P < 0.0005$) and the deionized water condition ($P < 0.00025$). Numbers of individuals that bit did not differ between the romaine lettuce and deionized water conditions ($P > 0.10$).

Latency to bite also varied greatly among conditions (Table 2). Data for all individuals were analyzed nonparametrically due to extreme nonnormality. Latency to bite differed among stimuli ($\chi^2 = 18.62$, $df = 2$, $P < 0.001$). Lizards bit at shorter latency in the cricket condition than in the romaine lettuce ($P < 0.001$) and the deionized water condition ($P < 0.01$). Differences among conditions in latency to bite were smaller when only individuals that bit in a given condition are included: 6.3 ± 1.4 sec in the cricket, 14.8 ± 8.8 sec in the romaine lettuce, and 8.0 ± 3.6 sec in the deionized water condition. Four of five individuals that bit swabs bearing romaine lettuce stimuli and three of four that bit swabs in the deionized water condition did so before being tested with cricket stimuli.

In the trials with banana stimuli for 10 individuals, rate of tongue-flicking was similar to that for all stimuli in the experiment (5.4 ± 1.5), but no lizard bit a swab.

Cnemidophorus gularis. All individuals tongue-flicked tiles in the cricket and cologne conditions (Figure 1), and all but two did so in the romaine lettuce and deionized water conditions. Variances differed among conditions ($F_{max} = 43.56$; $df = 4$, $P < 0.01$) for the raw data, but were homogeneous for the logarithmically transformed data ($F_{max} = 2.54$; $df = 4$, 19; $P > 0.05$). The main
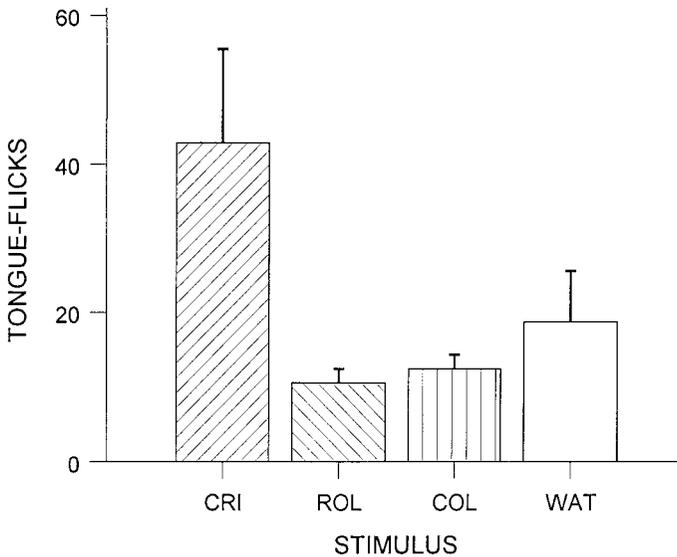
FIG. 1. Mean number of tongue-flicks by *Cnemidophorus gularis* (*N* = 20) responding to ceramic tiles labeled with chemical stimuli from domestic crickets (CRI), romaine lettuce (ROL), cologne (COL), and deionized water (WAT) for 2 min. Error bars represent 1.0 SE.

stimulus effect was significant (F = 7.29; df = 3, 57; P < 0.0004; Figure 1). Number of tongue-flicks was greater in the cricket than in the romaine lettuce (P < 0.006), cologne (P < 0.002), and deionized water (P < 0.004) conditions. Differences among pairs of romaine lettuce, cologne, and deionized water stimuli were not significant (P > 0.10). The phi coefficient was 4.60, giving a statistical power > 0.99.

DISCUSSION

Prey Chemical Discrimination. In *T. sexlineatus*, prey chemical discrimination was indicated by the greater tongue-flick attack scores and proportion of individuals that bit swabs in response to prey chemicals than to any of the other stimuli. Tongue-flicks alone did not reveal differential response rates among conditions because all individuals bit swabs in the cricket condition. The shorter latency to bite in the cricket condition than in the other conditions left less time for tongue-flicking, especially for the majority of individuals that did not bite in the other conditions. The rapid biting shows that few tongue-flicks were required to identify the prey chemicals.

Biting by all individuals in the cricket condition is unusual in studies of lizards. Although a majority of individuals have bitten swabs in a few species (e.g., Cooper and Vitt, 1989), in none of the more than 60 other species tested by Cooper has the proportion of individuals that bit closely approached 1.0. The lizards may have been unusually hungry because they were tested shortly after arrival and their prior feeding history is unknown. Another possibility is that visual properties of the swabs resemble key features of natural prey of *T. sexlineatus.* In scincid lizards, chemical cues permit location and identification of prey and sometimes release of attack on the stimulus source (e.g., Burghardt, 1973; Nicoletto, 1985; Cooper and Vitt, 1989; Cooper and Hartdegen, 1999), but visual cues such as movement are also important for releasing attack (e.g., Cooper, 1981; Nicoletto, 1985). Similarity in size, color, and/or shape of cotton swabs to natural prey of *T. sexlineatus* might explain biting of swabs by several individuals in the absence of prey chemicals, but relevant dietary data are lacking.

In *C. gularis*, the greater number of tongue-flicks in response to cricket stimuli than to the other stimuli demonstrates prey chemical discrimination. Although no lizards attempted to bite the tile surface, a few individuals oriented to tiles after tongue-flicking, arching the neck and peering at the tile as if searching for prey. Some individuals performed rapid bursts of tongue-flicks, but only in the cricket condition, indicating intensive investigation of the cricket chemicals. Such rapid tongue-flicking may help *Cnemidophorus* lizards locate prey by using chemical cues. Cooper observed a *C. uniparens* that stopped after tongue-flicking an apparently bare patch of ground and dug into the sand for over 10 min before extracting a large insect larva. Auditory or seismic cues cannot be ruled out, but it seems likely that *Cnemidophorus* lizards tongue-flick to locate hidden prey. Similar behavior has been reported in the varanoid lizards *Heloderma suspectum* (Bogert and Martin del Campo, 1956) and *Varanus bengalensis* (Auffenberg, 1983).

Both species exhibited lingually mediated prey chemical discrimination. All species of actively foraging lacertids and teiids tested with adequate sample sizes show similar ability in the absence of visual prey cues. The present data extend previous findings (Cooper, 1994a,b, 1995, 1997) that prey chemical discrimination occurs in all lizard families of active foragers. In Lacertidae, the only ambush forager that has been studied exhibits prey chemical discrimination, but the discrimination is weaker than in a congener that forages actively (Cooper, 1999a), suggesting that the importance of chemical cues for detecting prey has decreased as the degree of foraging activity has decreased.

Tiles vs. Swabs. Previous work with teiids that used the swab method suffered from inconsistency of response due to escape behavior [*Ameiva undulata* (Cooper, 1990), *Tupinambis rufescens*, *T. nigropunctata* (Cooper, 1990, 1993), *Cnemidophorus tigris* (Cooper, unpublished observations] or attacks on the experimenter [*T. nigropunctatus*, *T. rufescens* (Cooper, 1990, 1993)]. Prey

chemical discrimination was detected in both species of *Tupinambis*, but the swab method was difficult to use, and variability of response among stimuli and individuals was high. For *A. undulata* the swab method was not feasible due to high variability and small sample size.

Tile tests have been used as a method of testing for possible prey chemical discrimination by ambush foragers that do not exhibit it in swab tests (e.g., Cooper, 1999b, unpublished data). The findings for *C. gularis* suggest that chemosensory responses of teiid lizards can be more efficiently assessed when no experimenter is visible to the lizards. Use of tiles to present stimuli in the absence of an experimenter may be a valuable method for studying responses to chemical stimuli by lizards that are too defensive to respond normally in the presence of human beings.

Responses to Plant Chemicals. Neither species gave an indication of elevated response to chemical cues from palatable plants. This confirms the predicted lack of response to plant food chemicals for these insectivores. If the lizards detected chemical cues from the plants tested, their tongue-flicking and biting responses were not affected, as indicated by the lack of differences between responses to plant food chemicals and control stimuli. In contrast, herbivorous lizards that consume leafy vegetables respond strongly to chemical cues from romaine lettuce [e.g., *Corucia zebrata* (Cooper, unpublished data); *Tiliqua rugosa* and *T. scincoides* (Cooper, unpublished data)].

Given the relatively large sample sizes used for both species and the consequent high statistical power, we conclude that the absence of difference is real: plant chemicals from romaine lettuce do not alter tongue-flick rates and tongue-flick attack scores in *T. sexlineatus* and *C. gularis.* Although not as well documented as for romaine lettuce cues, the lack of heightened response to banana stimuli by *T. sexlineatus* and *C. gularis* also appears to be reliable. Other lizard species that eat leaves or fruits respond strongly to chemical cues from them (Cooper, unpublished data).

The present data show that strong responses to chemical stimuli from palatable plants are absent in two species of actively foraging insectivores representing two closely related families. A similar finding was made for the scincid lizard *S. lateralis* (Cooper and Hartdegen, 1999). These results are consistent with the hypothesis that lingually mediated discrimination of plant chemicals is absent in insectivores. Combined with the presence of plant food chemical discrimination in the few tested herbivores and omnivores (Cooper and Alberts, 1990; Cooper, unpublished data), the data suggest that response to plant chemicals is absent ancestrally in many insectivorous lizards and is derived in herbivores and omnivore that consume substantial amounts of plant matter. However, testing for correlated evolution between plant consumption and chemosensory discrimination of plant foods from nonfoods will require data on responses to plant chemicals for a wide range of insectivores and herbivores.

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