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# CHEMICAL DISCRIMINATION OF FOOD, CONSPECIFICS AND PREDATORS BY APPARENTLY VISUALLY-ORIENTED DIURNAL GECKOS, *NAULTINUS MANUKANUS*

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ABSTRACT: Animal life history strategies evolve in response to a range of selective pressures, and often are tightly linked to sensory cues. Squamate reptiles possess well-developed chemosensory systems, which evolved early in their history and remain highly conserved. However, chemosensory abilities are secondarily reduced in primarily visual agamid and chameleonid lizards, which casts doubt on the ubiquity of reliance on chemosensory cues among squamates. Diurnal geckos from New Zealand avoid predators using visual crypsis and are primarily ambush foragers; reliance on visual cues may be a product of strong avian predation pressure and minimal influence from mammals and snakes for the past 80 my. We used New Zealand's diurnal geckos to test the role of local adaptation versus evolutionary conservatism in defining chemosensory systems. Specifically, we tested whether Marlborough green geckos, *Naultinus manukanus*, use chemoreception to detect and behaviorally respond to (1) food, (2) opposite-sex conspecifics, and (3) native reptilian predators (tuatara, *Sphenodon punctatus*). Chemosensory cues mediated gecko interactions with all three stimuli tested: (1) the scent of fruit induced greater exploratory behavior, (2) male geckos responded to scent of female conspecifics by increasing lingual sampling and activity, and (3) tuatara fecal cues (but not skin secretions) elicited characteristic antipredator freeze behavior in geckos. Neither the primarily visual life history strategies nor the reduced range of predators of New Zealand's diurnal geckos appears to have reduced their chemosensory abilities relative to other noniguanid squamate reptiles. Instead, our findings support the notion that chemosensory traits remain highly conserved.

*Key words:* Chemoreception; Evolutionary conservatism; Local adaptation; Sensory mode; Squamate

MANY species display suites of morphological and behavioral characteristics influenced by the primary sensory mechanism that they use. Most squamate reptiles have highly developed chemosensory systems, which mediate a range of intra- and inter-specific interactions (Burghardt, 1970; Gabe and Saint Girons, 1976; Halpern, 1992; Schwenk, 1995). The evolution of chemosensory systems is considered conservative, and largely reflects suprafamilial attributes as opposed to local adaptation (Schwenk, 1993). However, agamid and chameleonid lizards are ambush foragers that rely on visual cues (Cooper et al., 2001; Schwenk, 1993). As a consequence, these families have secondarily reduced chemosensory abilities (Gabe and Saint Girons, 1976; Parsons, 1959, 1970). Secondary loss of chemosensory abilities in some squamate families prompts the question of which criteria are necessary to precipitate an evolutionary switch from primarily chemosensory to primarily visual antipredator and foraging strategies. We investigate the chemosensory abilities of gekkotans that appear to display primarily visual antipredator and prey detection strategies, perhaps as a result of their evolutionary isolation from many ground-dwelling predators and diurnal activity. Using this system, we explore the roles of local adaptation versus evolutionary conservatism in shaping chemoreception.

The highly developed nasal chemosensory systems of most squamate reptiles enable their discrimination of many chemicals (reviewed by Schwenk, 1995). Chemoreception in reptiles is known to be mediated by both the olfactory and vomeronasal systems, but other nasal chemical senses also may be involved (Halpern, 1992). Tongue flicking allows lingual sampling of both substrates and the air via the vomeronasal organ, which enables discrimination between chemical signals and mediates behavioral responses ('vomerolfaction'; sensu Cooper, 1996; Halpern, 1992). Reptiles frequently rely on chemical cues to detect and avoid predators (Dial et al., 1989; Downes, 2002; Downes and Shine, 1998).

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Olfaction and vomerolfaction also can mediate interactions with conspecifics (Bull et al., 2000; Cooper and Pèrez-Mellado, 2002; Cooper and Steele, 1997) and be used to locate prey and other food (Cooper and Habegger, 2000; Cooper and Pèrez-Mellado, 2001).

Reptiles often use chemoreception in combination with other sensory cues, such as vision (Head et al., 2005). Under certain local conditions, use of visual cues may assume greater importance relative to chemosensory cues (e.g., in agamid and chameleonid lizards; Schwenk, 1993). Although gekkotans have highly developed chemosensory abilities (Cooper, 1995; Dial et al., 1989; Downes and Shine, 1999; Schwenk, 1993), some have evolved secondary diurnality, which may be associated with a switch to using primarily visual strategies. For example, diurnal green geckos, *Naultinus* spp., from New Zealand display visual crypsis and secretive behavior as antipredator strategies and appear to ambush their mostly invertebrate prey (Hare et al., in press; Hitchmough, 1978; Whitaker and Gaze, 1999).

The reliance of New Zealand diurnal geckos on visual cues to avoid predators may be a consequence of evolution in isolation from major predatory groups. On a global scale, major lizard predators are birds, reptiles (especially snakes) and mammals. New Zealand had few terrestrial mammalian predators for ca. 80 my prior to the introduction of Polynesian rats, *Rattus exulans*, by Polynesian voyagers ca. 1800 ya (Holdaway, 1999; Worthy et al., 2006), and today mammalian predators remain absent from many offshore islands. Furthermore, there are no confirmed reports of terrestrial snakes in the New Zealand fossil record. Birds are the primary native predators on New Zealand lizards, and tuatara (*Sphenodon* spp.) also prey upon lizards (Walls, 1981). Because birds usually detect their prey from a distance using visual cues, crypsis may assume a greater role in predator avoidance than the ability of prey to detect their predators using chemical cues. Similarly, tuatara appear to use primarily visual foraging cues to detect their prey (Meyer-Rochow, 1988; Meyer-Rochow and Teh, 1991; Walls, 1981). In contrast, other reptiles (especially snakes) and mammals often use chemical cues to detect prey at close range, thus chemoreception may play a key role in predator detection and avoidance by prey (Downes and Shine, 1998). The visual antipredator strategy used by New Zealand's diurnal geckos may reflect an avian dominated predatory fauna, in contrast with the range of predators that tend to elicit chemosensory responses among reptiles on a global scale.

The apparent lack of selection pressure to detect and avoid predators using chemoreception in New Zealand lizards may be countered to some degree by use of chemosensory cues in foraging and in mediating intraspecific interactions. New Zealand lizards (Diplodactylidae and Scincidae) consume fruits and nectar (Lawrence, 1997; Whitaker, 1987; Wotton, 2002), which indicates likely use of chemoreception to find food sources. However, records of frugivory by the diurnal gecko genus *Naultinus* are sparse (Whitaker, 1987), which leaves both the importance of fruit as a food source and the mechanism involved in finding it unresolved. Chemosensory conspecific recognition and predator detection have not been examined in New Zealand geckos, but many possess distinctive femoral pores (e.g., Gill and Whitaker, 1996; Hitchmough, 1982), which may indicate the use of chemical signals to mediate conspecific interactions.

Adaptation to a reduced suite of predators and associated use of a visually-oriented strategy by New Zealand's diurnal geckos provides an opportunity to test the role of local adaptation versus evolutionary conservatism in squamate chemosensory systems. We specifically address whether chemosensory capabilities are reduced in lizards that use primarily visual antipredator and foraging strategies by investigating chemosensory-mediated responses of diurnal, Marlborough green geckos, *Naultinus manukanus*, to fruit, conspecifics and predators.

## MATERIALS AND METHODS

### Study Animals

*Naultinus manukanus* are small (up to 81 mm snout–vent length; Hare et al., in press) green, diurnal geckos which are restricted to the Marlborough region of New

Zealand and occur in forest and scrub habitat (Gill and Whitaker, 1996). These arboreal geckos exhibit limited movement patterns and appear to rely primarily on visual crypsis and secretive behavior to avoid predators (Hare et al., in press; Hitchmough, 1978; Whitaker and Gaze, 1999).

Eighteen adult geckos (snout–vent length 62–81 mm; mass 5.7–11.9 g) captured from Takapourewa (Stephens Island), Cook Strait, New Zealand were held at Victoria University of Wellington between March and October 2003. Because Takapourewa has no introduced mammals or snakes (Brown, 2000), lizards experienced a natural predation regime including only birds and reptiles (other than snakes) prior to being taken into captivity. All 18 adult geckos (nine of each sex, all females pregnant) were tested for behavioral responses to scent stimuli (fruit, conspecifics and native predators) over a 3 wk period in October 2003 during the normal mating season (Gill and Whitaker, 1996). Additionally, 10 predator-naïve juvenile geckos (SVL 43–49 mm; mass 1.8–2.6 g), born to captive-held mothers, were tested for behavioral responses to the scent of their native tuatara predators.

Adult geckos were kept individually in transparent plastic containers (330 × 215 × 110 mm, L × W × H) with 1 × 1 mm wire mesh (165 × 120 mm) in the lids. Food and water were provided *ad libitum*; all other husbandry details are outlined by Hare et al. (2004). Juveniles were held under the same conditions as adults, but were housed in their birth groups (usually two individuals; three individuals in one case when one juvenile had no siblings).

## Experimental Design

We tested behavioral responses of geckos to chemical cues from fruit, conspecific geckos and native reptilian predators to gauge the extent to which chemoreception mediated interactions. Because lizards use tongue flicks to sample substrates and airborne volatile compounds (vomerolfaction), the rate of tongue flicks provides an objective index of chemosensory investigation (Cooper, 1998; Cooper and Pèrez-Mellado, 2002). We also recorded a range of other behaviors to provide context for any changes observed in the rate of tongue flicks (Downes and Shine, 1998), including maintenance behavior (eye-licking), activity and exploratory behaviors (walking, running, climbing, moving limbs and nudging the wall of the arena) and 'freeze' behavior.

The experimental arena was a clear plastic enclosure (280 × 250 × 210 mm, L × W × H) containing a plain cotton cloth of the same dimensions on the base of the enclosure and covered with the scent to be tested. For juvenile geckos, the basal area of the experimental arena was reduced (to 250 × 130 mm) using a divider of the same material as the enclosure walls.

*Scent treatments and controls.*—The cotton scent cloth was washed between trials to remove any scent residue by soaking the cloth in the disinfectant Napisan™ (active ingredient Sodium Percarbonate) for 2 h, rinsing thoroughly, air-drying and steam ironing. Behaviors of geckos presented with a washed cloth previously covered in each scent stimulus did not differ from a negative control (washed cloth which had not been in contact with any of the scents tested; $F_{(21, 51.1)}$ = 0.510, $P$ = 0.954), confirming that the washing methodology was effective at removing all scents.

Scent treatments and controls were: (1) negative control: unscented cloth; (2) positive control: cloth sprayed with commercial cologne ('Smiley' Second Edition No. 42; Liberty Cosmetics Ltd, England); (3) pear: cloth sprayed with a 1:1 solution of natural pear juice and distilled water; (4) conspecific: cloth placed in an enclosure with a conspecific adult gecko of the opposite sex for 4–7 d; (5) native predator skin secretions: cloth placed in an enclosure with an adult tuatara, *Sphenodon punctatus*, for a period of 16 to 24 h; (6) native predator feces: cloth covered in a slurry of tuatara faeces and distilled water.

*Experimental procedure.*—To avoid handling immediately prior to the experiment, geckos were placed into a plastic jar ca. 2 min prior to the experiment. The top one-third of the inner surface of the plastic jar was coated with Fluon® (Tetrafluoroethylene co-polymer), a paint with low surface tension to which geckos cannot adhere (Losos et al., 2001). Geckos were gently tipped into the enclosure at the start of the experiment.

Observations of behavior commenced ca. 10 s after transfer of the gecko to the experimental enclosure. Behavior of each gecko was observed continuously for 12 min from behind a cardboard blind by a single observer. The observational data-logging programme ODLog™ (Macropod Software) was used to directly record behavior onto the computer.

*Behaviors recorded.*—Either the frequency (behaviors 1 and 2 below) or the duration (3 to 8) of the following behavioral acts and locomotor patterns was recorded: (1) tongue flick: tongue is extruded and either waved in the air or lowered to touch the substrate; (2) eye lick: tongue is slowly extruded and passed over an eye; (3) slow walk: gecko proceeds by very slow, stalking or continuous directional movement; (4) run: very fast horizontal locomotion on base of enclosure; (5) climb: directional movement on a wall; (6) non-locomotory movement: gecko moves body parts but does not alter its location; (7) nudge wall: gecko presses its snout against a wall; (8) freeze: gecko remains motionless.

Relative to a negative control, we predicted that scent from fruit and conspecifics would elicit elevated tongue flicking rates and greater exploratory behaviors by geckos, including either climbing or slow, deliberate walking. In contrast, because visual crypsis is the usual mechanism by which these geckos avoid native predators, we predicted that tuatara scent would elicit a higher incidence of freeze behavior and decreased movements.

*Experimental conditioning and scent tests.*— All geckos were conditioned to the experiment by undergoing three practice tests with a negative control prior to scent trials to minimize the influence of the novel experimental procedure on observed behaviors (Hare et al., 2004). The role of conditioning in minimizing behavioral variation was tested using data from the three successive conditioning trials recorded for nine adults and eight juveniles.

We constructed a Wilks Lambda multivariate test to investigate whether the novel environment of the test arena influenced the behavior of geckos and, if so, whether successive conditioning trials reduced behavioral variation associated with the novel test environment. Individual and trial numbers were included as factors in the MANOVA. We compared a complete model (three levels of trial number) with reduced models (merged trial effects) using Wilks Lambda and approximate $F$ tests, based on appropriate sums of squares and cross-products matrices. Significant behavioral variation was observed between the first conditioning trial and subsequent trials ($F_{21,63.72} = 3.615$, $P < 0.001$), but not between the second and third conditioning trials ($F_{21,63.72} = 1.454$, $P = 0.128$), suggesting that the novel test environment influenced behavior during the first conditioning trial only. Our methodology involving three conditioning trials prior to experimental trials therefore was sufficient to minimize the influence of a novel environment on gecko behavior, and this result is consistent with findings from conditioning prior to physiological experiments in this species (Hare et al., 2004).

All 18 adult *N. manukanus* were tested for behavioral responses to the negative control and to conspecific scent. From these, 10 adults were randomly selected to perform all other scent tests. All 10 juvenile geckos were tested for behavioral responses to tuatara fecal cues against a negative control. Geckos were tested a maximum of one time on any day, and the order of scent tests was randomly allocated. All tests were conducted within an ambient temperature range (18.0–20.3 C) at which geckos are active in nature (Werner and Whitaker, 1978) and during the normal activity phase of this species (0900 to 2000 h NZDT; Hare et al., in press).

## Statistical Analyses

Data were analyzed using the statistical programme 'R' (version 1.9.1; R Development Core Team, 2004). Count data were transformed using square roots to normalize data for analyses. Statistical significance was assigned at $\alpha = 0.05$. All data are presented as mean ± SE, unless stated otherwise. All data satisfied the assumptions of the statistical tests used.

The abilities of adult geckos to detect chemical cues of fruit, conspecifics, predator skin secretions and predator feces were assessed based on behavioral responses to these in relation to negative and positive

controls. Additionally, any ontogenetic change in chemosensory-mediated antipredator response was investigated by comparing adult and juvenile *N. manukanus* responses to tuatara fecal cues relative to a negative control.

Multivariate analyses of variance (MANOVAs), using the *F*-approximation to the Wilks test, enabled us to assess the overall importance of the scent stimulus (as an independent variable), in explaining variation in behavioral activities (the correlated dependent variables) and to provide protection against multiple testing of several response variables. Temperature, time of trial (early: 0900–1200 h; mid: 1200–1600 h; late: 1600–2000 h), sex, ontogenetic stage (adult or juvenile) and individual were added as independent variables in the relevant MANOVAs, and interactions between these variables and scent stimuli were assessed. We assessed correlations between behavioral activities using a Bonferroni-adjusted Spearman's correlation analysis.

Significant MANOVA effects were explored via detailed testing using linear mixed effects models (Hair et al., 2006). One univariate ANOVA was performed for each behavioral activity (as separate dependent variables) to assess the relative importance of significant variables (from MANOVA) in determining behavior. Individual was included as a random factor in these analyses to account for it as a source of variation (Sih et al., 2004; Stapley and Keogh, 2004), as is necessary with the repeated measures experimental design.

## RESULTS

### Behavioral Responses to Scent Stimuli

The positive control (cologne) induced geckos to elevate their rate of tongue flicks ($t_{48} = 2.27$, $P = 0.03$) and increase overall activity ($t_{48} = 2.08$, $P = 0.04$), but other behavioral activities were not affected ($P > 0.05$ for all). Encountering a novel scent stimulus, therefore, resulted in greater vomerolfactory response and exploratory behavior, but did not alter other components of behavior. The observed response to the positive control demonstrates that our experimental protocol is valid for *N. manukanus*, and sets a standard from which to explore recognition of fruit, conspecific and predator scents.

Average tongue flick rate for all scent stimuli pooled was 2.75 flicks/min (SE = 0.13, range 0.08–6.42), whereas average eye lick rate was only 0.33 licks/min (SE = 0.04, range 0–1.75). Geckos spent almost one-half (45.8%) of their time during trials motionless, although this varied according to the scent stimuli presented (Fig. 1). The most common activity (34.1% of time) was climbing, followed by movements of head, limbs or tail (8.2%), nudging the wall (7.2%) and slow walking (4.7%; Fig. 1). Not surprisingly, climbing was negatively associated with slow walking, movements of head, limbs or tail, and freeze behavior (Table 1). Exploratory slow walking was positively correlated with tongue flicking rate and movements of head, limbs or tail (Table 1). Running (flight response) accounted for less than 0.1% of time (Fig. 1).

Adult geckos responded to the chemical cues of fruit, conspecifics and native predators (Table 2). Individual variation in behavior was highly significant (Table 2). The only intersexual difference in behavioral patterns (Table 2) was that females spent more time in slow, deliberate walking than males ($t_{16} = 2.93$, $P = 0.01$). Because pregnancy is expected to decrease mobility in female geckos (Downes and Bauwens, 2002), increased walking suggests that reproductive condition did not influence female behavior. We observed an interactive effect between sex and scent, whereas there were no effects of temperature or time of trial (Table 2).

*Fruit scent*.—Geckos did not show an elevated tongue flicking rate in response to fruit scent (Fig. 2a). However, fruit scent elicited more climbing behavior ($t_{48} = 2.57$, $P = 0.01$; Fig. 2b) and a decrease in two correlated behaviours (Table 2): slow, deliberate walking ($t_{48} = -3.33$, $P < 0.01$) and time spent motionless ($t_{48} = -2.17$, $P = 0.04$). Males spent more time in slow, deliberate walking in response to the scent of fruit than females ($t_{48} = 3.02$, $P < 0.01$).

*Conspecific scent*.—Male geckos showed a higher tongue flicking response to conspecific scent than did females ($t_{48} = 2.83$, $P < 0.01$; Fig. 2c). Males also increased time spent in slow, deliberate walking in response to the scent of conspecific females, relative to a negative control ($t_{48} = 2.33$, $P = 0.02$; Fig. 2d).
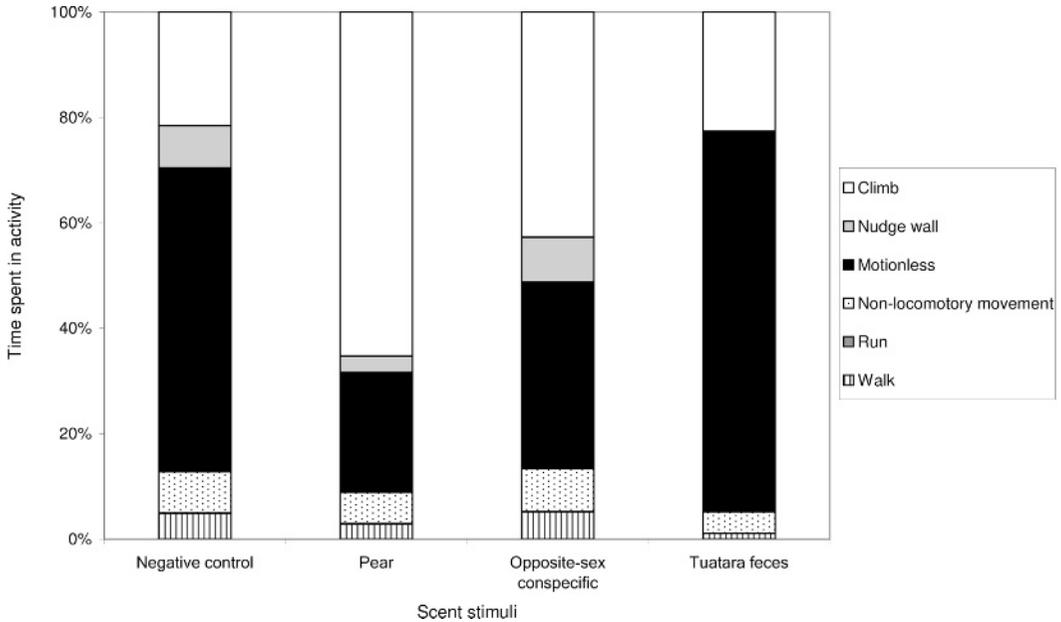
Fig. 1.—Percent time spent in alternate behavior patterns when adult *Naultinus manukanus* were presented with different scent treatments. Time spent running was negligible and thus does not show on the graph.

*Predator scent.*—The response of adult geckos to native predator (tuatara) scent was dependent upon the cue provided. Tuatara skin secretions elicited only a higher rate of eye licking ($t_{48} = 2.89$, $P < 0.01$), but their feces reduced both tongue flicks ($t_{48} = -2.21$, $P = 0.03$; Fig. 2e) and slow, deliberate walking ($t_{48} = -3.43$, $P < 0.01$) which are correlated behaviors (Table 1). Tuatara fecal cues also induced geckos to spend more time motionless ($t_{48} = 2.11$, $P = 0.04$; Fig. 2f). There was a trend for a disproportionate reduction in tongue flicks in response to tuatara scent by females relative to males (Fig. 2), but there was

no statistically significant difference ($t_{48} = 1.86$, $P = 0.07$). We detected no interaction between ontogenetic stage and reaction to tuatara fecal scent ($F_{(7, 11)} = 1.44$, $P = 0.28$). However, adults showed reduced activity ($t_{17} = -2.22$, $P = 0.04$) and exploratory behavior (nudging walls; $t_{17} = -3.39$, $P < 0.01$) relative to juveniles, suggesting overall ontogenetic differences in behavior.

## Discussion

Behavioral responses of *N. manukanus* to the scents of fruit, conspecifics and native predators demonstrate chemosensory recog-

Table 1.—Correlations between activities of Marlborough green geckos and their significance based on Bonferroni-adjusted Spearman's correlation analysis. Significant Spearman's coefficients (bold) indicate one behavior increasing or decreasing (as indicated by the sign) the likelihood of another. See Methods and Materials for definitions of behaviors.

|  | Activity | | | | | | |
|---|---|---|---|---|---|---|---|
|  | Slow walk | Run | Move | Freeze | Nudge wall | Climb | Tongue flick |
| Run | −0.08 | | | | | | |
| Move | **0.40** | 0.03 | | | | | |
| Freeze | 0.11 | 0.01 | 0.15 | | | | |
| Nudge wall | 0.15 | −0.08 | −0.21 | −0.05 | | | |
| Climb | **−0.37** | 0.01 | **−0.38** | **−0.90** | −0.25 | | |
| Tongue flick | **0.44** | −0.18 | 0.33 | 0.24 | 0.12 | −0.39 | |
| Eye lick | −0.14 | −0.04 | 0.14 | 0.34 | −0.27 | −0.22 | 0.09 |

TABLE 2.—Factors influencing behavior of *Naultinus manukanus*. 'F' is the F-approximation to the Wilks test.

| Factor(s) | F | Numerator df | Denominator df | P |
|---|---|---|---|---|
| scent | 2.42 | 35 | 166.49 | <0.01 |
| time of day | 1.21 | 14 | 78 | 0.28 |
| sex | 3.42 | 7 | 39 | <0.01 |
| individual | 2.81 | 112 | 261.8 | <0.01 |
| temperature | 0.78 | 7 | 39 | 0.61 |
| scent:sex | 1.59 | 35 | 166.49 | 0.03 |

nition of a variety of chemical cues, and the ability to respond accordingly. Diurnal geckos from New Zealand are under strong selection from native predators to adopt visual anti-predator strategies and, as a consequence,

limited ability to use chemical cues was expected. However, *N. manukanus* do not appear to have greatly reduced chemosensory abilities or exhibit the visual-chemosensory trade off seen in agamid and chameleonid lizards.

Increased activity in response to fruit scent implies recognition and use of chemical cues to locate fruit. Because observed behavioral changes were not accompanied by a change in frequency of lingual sampling, it is possible that the behaviours were elicited primarily by olfactory cues rather than vomerolfactory cues (Cooper and Pèrez-Mellado, 2001; Whitaker, 1987; Wotton, 2002). Although New Zealand lizards are primarily insectivorous, frequent
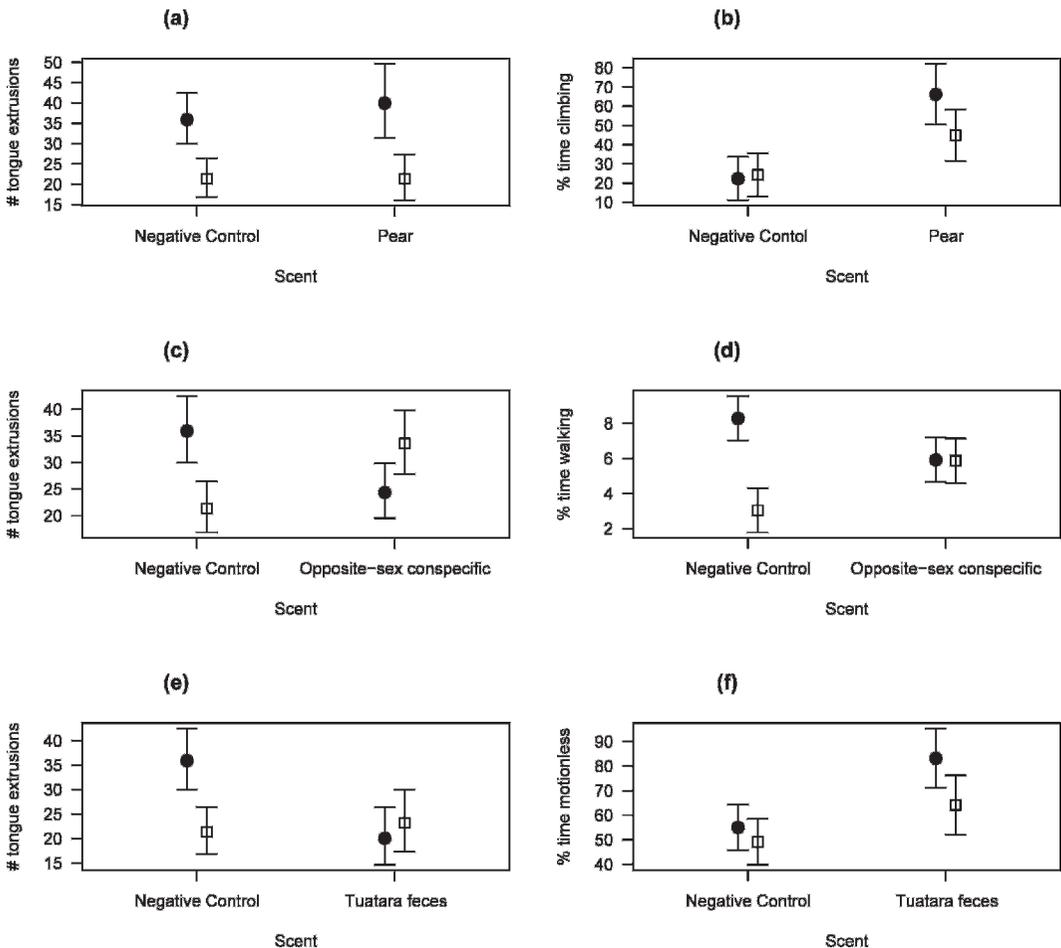


FIG. 2.—Behavioral responses of *Naultinus manukanus* to the scent of pear (a and b), opposite-sex conspecific scent (c and d) and tuatara feces (e and f) during a 12-min trial. Females are represented by filled circles; males are represented by open squares. Data are mean values corrected for individual variation (±1.0 SE).

natural observations of lizards consuming fruit (Whitaker, 1987; Wotton, 2002) together with high capture rates of lizards using traps baited with fruit (Whitaker, 1967) both imply that these lizards use chemical cues to locate fruit. Diurnal New Zealand congeners (*N. grayi*) are known to feed on fruit and nectar, whereas reports of frugivory and nectivory in nocturnal geckos are numerous (Whitaker, 1987; Wotton, 2002). Our observations on the use of chemoreception to recognize fruit in *N. manukanus* support the recent hypothesis that location of fruit using chemical cues is widespread among omnivorous and herbivorous reptiles (Cooper et al., 2001).

Sex-specific vomerolfactory and behavioral responses to conspecific scent in *N. manukanus* suggests that chemoreception mediates intraspecific interactions, which is consistent with findings in other species. For example, the lingual response by male *Podarcis hispanica* was greater to nongravid than gravid females, and conspecific than heterospecific females (Cooper and Pèrez-Mellado, 2002). Increased response of males to female scent may indicate that males use chemical cues to take an active role in searching for mates. However, investigating whether these geckos produce chemical secretions in different seasons and use scent marks on the substrate is necessary for a complete interpretation of the use of chemosensory cues in mediating conspecific interactions.

*Naultinus manukanus* displayed antipredator responses to fecal cues (but not skin secretions) produced by their native predators (tuatara). Tuatara are generalist, medium-sized predators that include geckos in their diet (Walls, 1981) and share both vine and ground habitats with *N. manukanus* on Takapourewa. The decreased activity and tongue flick rate by both adult and juvenile geckos in response to tuatara fecal cues may reflect an antipredator freeze response appropriate to this primarily visual, sit-and-wait predator (Meyer-Rochow and Teh, 1991). Such chemosensory-mediated antipredator freeze responses are common among reptilian prey (Greene, 1988) and can function to increase survival of lizards (Downes, 2002).

Evolution under a reduced suite of selection pressures in isolation from major predators seems not to have decreased chemosensory capabilities of New Zealand's apparently visually-oriented, diurnal geckos. Instead, use of chemosensory cues by *N. manukanus* appears to play a functional role in their biotic interactions and are consistent with other squamates. Our findings support the hypothesis that chemosensory traits remain highly conserved among squamates, reflecting suprafamilial attributes rather than local adaptation.

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