Zoological
Studies

Agonistic Behavior of the Mediterranean Gecko *Hemidactylus turcicus*

Venetia S. Briggs[1,2]

[1]*Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, MS 39406, USA*
[2]*Department of Wildlife Ecology and Conservation, IFAS-FLREC, University of Florida, Fort Lauderdale, FL 33314, USA*

Venetia S. Briggs (2012) Agonistic behavior of the Mediterranean gecko *Hemidactylus turcicus*. *Zoological Studies* **51**(7): 956-965. Agonistic behavior may influence the dispersal of species and spatial distribution of individuals within a population. The Mediterranean gecko *Hemidactylus turcicus* was used to test 2 hypotheses: 1) adult behavior differs in responses to conspecifics and resource limitations; and 2) juvenile behavior is affected by visual, chemical, and tactile adult male cues. I quantified behavioral responses of males to different levels of food quality, availability of retreat sites, and the presence of a resident male. Aggression was significantly more prevalent in the presence of a conspecific male regardless of resource availability. To test the 2nd hypothesis, I observed juvenile responses to chemosensory cues of either a confined or non-confined adult male. Both visual and chemosensory cues combined, rather than chemical cues alone influenced juvenile responses. Juveniles also exhibited sensory behavior (tongue-flicking) upon entering a novel environment, indicating that chemical mediation may be sufficient to impact behavior. Results of these contests illustrate the importance of chemical communication in providing information which influences behavioral responses and suggests a role for self and mutual assessments during intraspecific encounters. The outcome of competitive encounters may heavily rely on information collected via chemical cues and may ultimately regulate aggression by informing individuals about whether or not to fight and thus adhere to the confines of social dominance within the species. http://zoolstud.sinica.edu.tw/Journals/51.7/956.pdf

Key words: Aggression, Chemical communication, Gekkonid, Intraspecific competition, Invasive species.

Studies of competition often examine lizard species because many of their communication signals, such as chemical cues and threat displays, allow them to avoid physical combat and risks of injury (Martins 1994, McMann 2000); however, factors affecting behavior once chemical information has been transferred are not always delineated. Though chemical cues are known to play an important role in the intraspecific communication of lizards (Halpern 1992, Mason 1992, Cooper 1994), and several studies have shown pheromonal detection of conspecifics in different species (Mason 1992, Gomez et al. 1993, López and Martín 2001), there is no large body of work pinpointing the factors that affect the intensity of agonistic encounters. In general, individuals of many species can use chemical-borne information about familiarity to alter behaviors, such as aggression (Aragón et al. 2000, Font and Desfils 2002), when associating with other individuals (López and Martín 2001), in how they tolerate the presence of conspecifics (Brown et al. 1998, Aragón et al. 2000), in dividing up space (Schall 1974, Stamps and Krishnan 2001), and when selecting a mate (Walls et al. 1989). Such chemical-borne information presumably saves energy when encounters occur again (Jaeger 1981). This study presents potential factors that may influence how conspecifics respond to each other during dyadic encounters.

Within populations, there is usually aggression among adult males, but adult males tolerate

and are able to coexist with juveniles to varying degrees. Research shows that juvenile habitat segregation in lizards is an outcome of aggressive exclusion by adults living in optimal habitats (Schall 1974, Civantos 2000). Yet, other studies have illustrated that juveniles often defer to adults and avoid living near them (Stamps 1977, Stamps and Krishnan 1994) and certainly use information about familiarity to govern behavior (Hanley et al. 1999, Font and Desfils 2002). Because of the variability of aggression, behavior between adults and juveniles is dependent upon the aggression or tolerance of males and the deference and/or avoidance by juveniles. Juveniles, then, ought to employ effective behaviors that will inform them of how to proceed during encounters with each other and with adult members. Herein, I presented a suite of cues to juveniles to determine what combination was most effective in affecting behavior during adult/juvenile interactions.

The Mediterranean gecko *Hemidactylus turcicus* is a small Old World species with one of the largest range extensions of any squamate reptile (Carranza and Arnold 2006). *Hemidactylus turcicus* is native to the Mediterranean basin, is currently found in the New World, and is considered a widespread species (Carranza and Arnold 2006). Dispersal events readily occur by accidental transport of gravid females or a communal egg cache, and breeding populations have radiated out from major highways (Davis 1974). The 1st recorded individual in North America was in Key West, FL in 1910 (Fowler 1915) and then in Brownsville, TX in 1950 (Davis 1974). This gecko is commonly found throughout the southern US and is moving further north (Meshaka 1995). The species was introduced into Cuba (Schwartz and Henderson 1991), Panama, and Mexico (Collins and Irwin 2001), is found in Belize (pers. observ.) and as far south as the island of Trinidad (pers. observ.). The Mediterranean gecko is now referred to as the "house gecko" and is established in most tropical areas (Carranza and Arnold 2006).

Populations exist as a male-dominated social system, where vocalization is observed in males, females, and juveniles, but dominant males produce a series of clicks not found elsewhere in the hierarchy (Marcellini 1977, Werner et al. 1978, Frankenberg 1982). Anecdotal reports document that males of *H. turcicus* are aggressive during the breeding season, fight over insects, often have scars on their bodies, and are frequently missing toes and tails (Frankenberg 1982 1984, Selcer 1986, Saenz 1996). There is little known about

the social hierarchy of *H. turcicus*, and less on its behavioral repertoire of displays employed during the breeding season when territory establishment and defense may be important (Stamps and Krishnan 1997 2001).

I conducted a laboratory study to analyze social relationships between adult males and between adult males and juveniles of the Mediterranean gecko *H. turcicus* to 1) quantify agonistic behavior in males and 2) determine the factors that influence agonistic behaviors in adult males during dyadic encounters. Juvenile/adult habitat segregation in lizards sometimes results from aggressive exclusion by adults living in optimal habitats (Bradshaw 1971, Schall 1974) but also occurs because juveniles defer to adults and avoid living near them (Stamps 1983). Thus, in the 2nd part of this study, I examined interactions between juveniles and adult males to test 2 hypotheses: 1) adult males aggressively exclude juveniles from optimal habitats and 2) juveniles use chemosensory cues to respond to adult males.

MATERIALS AND METHODS

Pilot study

During May and June 2000, I observed geckos in their natural habitat for 60-min periods from the onset of dusk to 02:00 to acquire base-line behavioral data on adults and between juveniles and adults. Behavioral postures relevant to aggression and/or submission previously observed in other species (Jaeger 1984, Stamps 1992, Schwenk 1993, Jennings and Thompson 1999) were supplemented by those observed during this pilot period and were grouped for analyses (Table 1). Behavioral postures, such as "tongue-flicks" and "nose-taps" were observed during encounters and were used more for chemoreception and information acquisition than toward agonistic behavior of an individual; these I categorized as sensory behaviors (Schwenk 1993), and they were not included in agonistic behavioral displays (Table 1).

Collection and maintenance

I collected 100 adult males and 20 juveniles by hand from concrete walls of buildings between 20:00 and 02:00 (the period of peak activity). Females were gravid, lacked noticeable femoral pores, and were released upon capture. All

animals were collected under a Department of Wildlife, Fisheries, and Parks collection permit in Hattiesburg, Forrest County, MS during June and Sept. 2000. Individuals were measured for snout-vent-length (SVL: tip of snout to posterior margin of vent) and total body length to the nearest 0.01 mm with calipers and labeled according to the site of capture. Individuals were separately housed in glass jars (10 × 18 cm) covered with fiberglass mesh and containing suitable refugia. Room temperature was subject to ambient fluctuations, and a 12:12-h light: dark photoperiod was implemented using full-spectrum lighting hung 0.5 m above the housing units. I fed geckos on alternate days with 2-wk old crickets (Gryllidae), worker termites (Rhinotermitidae: *Reticulitermes flavipes*), and worker ants (Formicidae: *Solenopsis molesta*) that were all dusted with calcium and vitamins. I provided water by misting the sides of the housing chambers. All individuals were numbered and released at the point of capture at the end of the study.

Experimental procedures: adult male agonistic interactions

I conducted experiments with adult males from 30 June to 22 July 2000 from 20:00 to 02:00 when animals were most active (Selcer 1986) using a 15-W red incandescent light for observation. Plastic experimental chambers (41 × 29 × 25 cm) were divided into 2 sections using a cardboard divider and covered with fiberglass mesh to increase ventilation and ease of observation. A single individual was placed in 1 section of the chamber 5 d prior to testing and labeled as a "resident" male (for territory establishment see Stamps and Krishnan 1994, McMann 2000). Residents were provided shelter and food in the test chamber and allowed to deposit fecal pellets and femoral secretions on the substrate. Thirty minutes prior to an observation, a conspecific (an "intruder") was placed into the other section of the chamber. The resident male was handled for the same time duration but placed

Table 1. Behavioral displays observed during dyadic encounters between male conspecifics and between males and juveniles of *Hemidactylus turcicus*

Behavioral category	Agonistic behavior	Definition	Authors
Avoidance	Retreating	A gecko turns in the opposite direction of the other individual and proceeds forward.	Pers. observ.
	Freezing	A gecko ceases all action and remains motionless.	Jennings and Thompson 1999
Warning	Facing-off	Two individuals turn to face each other, orienting their bodies in a head-to-head manner without further movement.	Jennings and Thompson 1999
	Tail wagging	A gecko raises its tail above its body and waves it repeatedly without advancing.	Selcer 1986
	Squeaking	A gecko produces vocal sounds in a series of low-pitched squeaks or chirps.	Pers. observ.
	Push-ups	A gecko raises its body off of the substrate by extending its legs.	Stamps 1992
	Arching the back	A gecko raises its back producing an arched/bowed effect, higher in the center along the longitudinal axis.	Jennings and Thompson 1999
Overt aggression	Snapping	A gecko opens and snaps its jaws shut without making contact.	Jaeger 1984
	Chasing	One individual rapidly pursues another individual.	Jennings and Thompson 1999
	Fighting	One individual lunges at and makes contact using its mouth with the body of another individual.	Pers. observ.
Sensory behavior[a]	Nose tapping	An individual repeatedly touches its snout to the substrate.	Brillet 1990, Schwenk 1993
	Tongue flicking	An individual extends its tongue into the air and onto the substrate, then retracts it into its mouth.	Schwenk 1993

[a]Not included in the agonistic analyses.

back on his side of the chamber. The divider was removed, and subsequent agonistic behaviors were observed between both males for 30 min. There were 20 replicates for each treatment of the 3 experiments described below. I tested 20 different focal males against 20 different residents per treatment. Individuals were reused, and both focal and resident individuals were independently assigned to trials to ensure that there were no carryover effects. There was a 5-day interval between testing for each individual. Males were matched for size (within 2 mm) in each experiment, and no 2 animals were tested against each other more than once.

Experiment 1a: the effect of male presence on male behavior

To test the hypothesis that adult male geckos exhibit agonistic behavior, I observed behavioral responses of the same focal gecko to both a surrogate and a live male gecko in a randomized order. Surrogate geckos, a plastic straw cut to the mean SVL of male geckos (47 mm), were used to control for space occupied by live males in the chamber. I recorded the frequency of focal male behaviors listed in table 1 and recorded which animal initiated displays. I tested the same focal gecko against both a surrogate resident and a live resident in a randomized order for a total of 20 focal males and 20 resident males.

Experiment 1b: the effect of resource quality on male behavior

To test the hypothesis that resource quality influences agonistic behavior in male geckos, I observed the behavioral frequencies of a resident male paired with an intruder (and documented which animal began the behavioral displays) in the presence of either low- (worker ants) or high-quality prey (worker termites) items that formed a subset of the prey base on which Mediterranean geckos forage (Carey 1988). Chitinous contents of these 2 prey items present extremes of a soft-bodied prey, the termite, to an armored-bodied prey, the ant, and these choices may reflect a difference in food quality (Gabor and Jaeger 1995) and are a large component of tropical lizard diets (Huang 2010 2011). Once the divider was lifted, prey items were placed (by hand using a pair of forceps) in the center of the experimental chamber 5 min prior to the start of observations. There were 20 replicates for each treatment (presence of low- vs. high-quality food) for which 21 focal males were tested against 20 resident males for a total of 81 males in this experiment. An extra focal male was tested in these food quality trials, and thus $n = 41$ (not 40).

Experiment 1c: the effect of refugia availability on male behavior

To test the influence of the availability of retreat sites on agonistic behavior, I presented a resident male with a conspecific in the absence and presence of refugia and recorded the frequencies of subsequent behaviors and the animal which exhibited each behavior. The extra focal male that was used in the food-quality treatments was not available for use in the refugia trials; thus, there were 19 replicates with 19 focal males tested in the presence of 19 resident males, and $n = 39$. Small sections of cardboard egg carton were used as shelter, similar to those used by males in individual housing units where they had been kept leading up to the experiments. Shelter was provided once the divider was lifted and placed in the center of the chamber.

Statistical analyses

I grouped the 10 agonistic postures into 3 categories (avoidance, warning, and aggression; Table 1) to reduce the number of response variables (Hokit et al. 1996, Wiltenmuth and Nishikawa 1998). Tongue-flicks and nose-taps were kept separate, because they were not used in aggressive encounters (Table 1). All data were analyzed using the SPSS statistical program vers. 16.0 (George and Mallery 1999). I assessed the effects of resident type on the frequency data using a (2-tailed) nonparametric Wilcoxon matched-pairs signed-ranks test. I used separate (2-tailed) nonparametric Mann-Whitney U-tests to test if behavioral frequencies differed in response to the quality of food and the availability of shelter. According to Bonferroni's inequality, I reduced alpha from 0.05 to 0.017 (2-tailed) to accommodate testing of 3 simultaneous response variables (Zar 1996; Table 1). A 2-tailed Chi-squared analysis was conducted to determine whether residents or intruders initiated encounters. I used a Spearman's rank correlation coefficient to investigate whether the behavior of 1 individual affected conspecific behavior.

Experimental procedure: juvenile response to adult male cues

I conducted experiments on 4-22 Oct. 2000 to investigate behavioral responses of juveniles to manipulated visual and olfactory cues of adult males. All observations were done at 20:00-02:00 using a 15-W red incandescent light. Each experimental chamber (41 × 29 × 25 cm) contained a sealed glass jar. The 5 experimental treatments consisted of: 1) a live adult male gecko that was allowed to freely roam the experimental chamber for 5 d to establish residency (and remained present during the experimental trials) and provided visual and chemical cues via fecal pellets and femoral secretions; 2) an adult male that was placed inside a sealed glass jar to provide visual cues only; 3) fecal pellets and femoral secretions of an adult male that were present as olfactory cues only; 4) an adult male that was confined to a sealed glass jar with fecal pellets and femoral secretions present in the experimental chamber (visual and olfactory cues); and 5) a control which held no adult cues. A glass jar was present in all 5 treatments to control for the effect of its presence on the behavior of geckos. I used 20 adult males for all treatments (n = 100) and exposed juveniles to each treatment in a random order with a 5-d interval between testing. No 2 animals were exposed to each other more than once. One side of the experimental chamber housed a retreat site, water, food, and the prescribed treatment. I introduced a juvenile to the empty side of the chamber 30 min prior to testing. The adult male conspecific was similarly handled. I then recorded adult/juvenile behaviors during a subsequent 30-min period.

Several of the behaviors in this adult/juvenile experiment were the same as those observed during adult/adult interactions and previously observed in other species, except for "push-up" and "chase" which were not observed in juvenile/adult interactions. Juveniles exhibited more tongue-flicks (Schwenk 1993) and nose-taps (Brillet 1990, Schwenk 1993) than observed in adult/adult interactions. These behaviors were categorized as chemosensory behaviors (Table 1).

Statistical analyses

To investigate whether juveniles could discriminate among the different adult male cues, I compared the frequency of behavioral displays (avoidance, warning, overt aggression, and sensory; Table 1) per observation period using the (2-tailed) nonparametric repeated-measures Friedman's test and reduced alpha from 0.05 to 0.0125 (2-tailed), to accommodate the simultaneous testing of 4 response variables (Zar 1996). I used a Chi-squared test to determine whether males or juveniles more frequently initiated encounters.

RESULTS

Experiment 1a: the effect of male presence on male behavior

Adult males of *H. turcicus* exhibited agonistic behavior during encounters with conspecifics. Twenty of the 40 trials used to investigate the effect of a male's presence on male behavior involved surrogate residents; thus, there were no encounters. In 9 trials between a live resident and a focal male, individuals did not engage in encounter behavior, but instead remained motionless. Therefore, 11 trials contained encounters between resident and intruder males. Of these encounters, resident males initiated 64% of the encounters, but this did not significantly differ from the number of encounters initiated by intruders (Chi-squared; χ^2 = 0.81, n = 11, p = 0.366). Intruder males engaged in more display behaviors when a live conspecific was present (Table 2). Intruder males also engaged in more avoidance and warning behaviors when paired with a live resident male than with a surrogate male (Table 2) but displayed very little overtly aggressive behavior toward live residents (Table 2). Tongue-flicking behavior by the intruder occurred with nearly equal frequency between the 2 treatments (live and surrogate males), and these did not significantly differ (Table 2).

Experiment 1b: the effect of food quality on male behavior

Behavioral display frequencies of agonistic behavior did not differ between resident and intruder males when food was present (p > 0.05). During food trials, an extra focal male was tested; thus, n = 41. Food quality also did not affect agonistic behavior of either the intruder or resident male. Intruding males, initiated 73.2% (30 of 41) of the encounters (Chi-squared; χ^2 = 4.545, n = 41, p = 0.033). Intruders also exhibited significantly more tongue-flicking (mean ± 1 S.E.: 0.98 ±

0.377) than residents (0.05 ± 0.049) despite the quality of prey items present (Z = -2.232, n = 41, p = 0.026). In only three of the 41 trials was prey consumed, twice by the resident and once by the intruder. When investigating behavioral displays between the resident and intruder within each food-quality treatment, I found that intruding males displayed significantly more warning behaviors than did resident males when only low-quality prey items were present (Z = -2.156, n = 20, p = 0.031). There was no evidence of differences in display frequencies of behavior between resident and intruder males when high-quality prey items were in the test chamber (p > 0.05).

Individual agonistic behavior between male geckos was most highly affected by the behavior of the other individual in the test chamber. When a resident displayed warning behavior, it was correlated with a similar warning display by the intruder (Spearman's rho r = 0.669, n = 41, p < 0.001), but most highly correlated with a display of overt aggression by the intruding male (r = 0.735, n = 41, p < 0.001) and was less correlated with an intruder's display of avoidance (r = 0.586, n = 41, p < 0.001). An intruder's display of aggression was positively correlated with a resident's aggressive display (r = 0.733, n = 41, p < 0.001). In contrast, when an intruder male exhibited aggressive behaviors, the highest correlation existed when the resident male responded by displaying avoidance behavior ($r_{aggression}$ = 0.666, n = 41, p < 0.001).

Experiment 1c: the effect of refugia availability on male behavior

The availability of refugia did not affect the frequencies or durations of agonistic behavior between paired intruder and resident males. Encounters occurred in 36 of 39 trials. The extra focal male that was tested in the food quality

trials was not available for testing in the refugia trials, hence n = 39. Of the recorded encounters, resident males initiated behavior 47.2% (n = 17) of the time, which did not differ from the frequency of intruder-initiated encounters at 52.8% (n = 19; χ^2 = 0.059, n = 36; p = 0.808). Neither agonistic behavioral frequencies nor durations differed between residents and intruders when both treatments were combined, but intruders exhibited significantly more tongue-flicking (2.46 ± 0.872) than did residents (0.08 ± 0.077; Z = -2.677, n = 39, p = 0.007). When shelter was absent, intruders displayed more tongue-flicking than resident males (Z = -2.232, n = 19, p = 0.026), but there was no evidence of a difference in tongue-flicking behaviors between intruder and resident males when shelter was present. Behavioral postures were often in response to a previous posture and/or display, and positive correlations were detected between encounters of residents and intruders for some of the behavioral categories. A resident's aggressive display was most highly correlated with an intruder's avoidance response (Spearman's rho; $r_{aggression}$ = 0.795, n = 39, p < 0.001) than a counter-response of warning and/or aggressive behavior on behalf of the intruder. Similarly, an intruder's display of aggression was most highly correlated with a resident's avoidance response ($r_{aggression}$ = 0.610, n = 39, p < 0.001). There was a strong positive correlation between the warning behaviors displayed by a resident and the avoidance behavior of intruding males ($r_{warning}$ = 0.666, n = 39, p < 0.001), but not with aggressive displays (p > 0.05) or warning displays by the intruder (p > 0.05). However, when intruder males displayed warning behavior, it was most highly correlated with a resident displaying similar warning behaviors (r = 0.618, n = 39, p < 0.001) and not a response of avoidance (p > 0.05) or aggression (p > 0.05).

Table 2. Mean (± 1 S.E.) behavioral displays per observation period of an intruder male *H. turcicus* in response to the presence of a surrogate or live conspecific resident. Means were compared using Wilcoxon's matched-pairs signed-ranks test (n = 40, *Bonferroni correction significant difference at ∝ = 0.017)

Behavior	Surrogate	Live	Z	p
Avoidance	0.00 ± 0.00	41.58 ± 32.429	-3.007	0.003*
Warning	0.01 ± 0.095	12.05 ± 6.261	-2.889	0.004*
Overt aggression	0.00 ± 0.00	0.79 ± 0.544	-1.868	0.064
Tongue flicks	3.05 ± 1.534	2.74 ± 1.531	-0.245	0.806
Total	1.57 ± 0.764	5.89 ± 2.080	-2.379	0.017*

Juvenile responses to adult male cues

Results from these analyses revealed that juveniles displayed only avoidance and sensory behaviors across all treatments and very few warning behaviors. There were no displays of aggression by juveniles (Table 3). When a juvenile was presented with a non-confined male and an encounter ensued, adult males initiated agonistic behavior 90% of the time (χ^2 = 6.4, n = 20, p = 0.011). Juveniles exhibited significantly more avoidance behaviors in the presence of male cues and especially when approached by an adult male (Friedman's repeated-measures test; χ^2 = 70.567, n = 100, p < 0.001; Table 3). In the single instance in which a juvenile approached an adult male, it was consequently bit on its side. Juveniles displayed warning behaviors when both a confined and non-confined adult male were accompanied by its own visual and chemical cues, and there were no warning displays by juveniles in treatments with only 1 manipulated cue (χ^2 = 44.480, n = 100, p < 0.001; Table 3). Juveniles engaged equally in sensory behaviors (nose-taps and/or tongue-flicks) in all treatments (Table 3).

DISCUSSION

Adult male responses to manipulated resources and conspecifics

The results of this study provide experimental evidence of aggression among males and between males and juveniles of *Hemidactylus turcicus* and the factors prompting such behavior. Symmetrical contests between size-matched males illustrate that contests can be multidimensional, such that the resource-holding potential that comes

with residence time may negate the influence of body size and alter behaviors during encounters (Maynard Smith 1976, McMann 2000). In this study, residents were more aggressive toward intruding males who did not defer to them upon entering the chamber. Instances of warning behavior were met by increasingly escalated warning behaviors by residents, but in no cases did overt aggression begin immediately upon an encounter. Rather, resident males engaged in warning behaviors that usually began with an undulation of the tail and moved into tail-wagging, which was then followed by vocalization such as squeaking/chirping.

Results of a previous study show that geckos react to sound and have a repertoire of vocal behaviors during social interactions that are good indicators of subsequent behavior (Tang-Martinez 2001). In the current study, when vocalizations were produced, behavior then escalated into push-up displays and back-arching, presumably to inflate one's body size as an added threat. Only after this progression of behaviors did some form of overt aggression occur, such as lunging or biting. Intruders, when threatened, fled encounters, and no other aggressive displays were noted; but if a resident exhibited some warning behavior and the intruder responded similarly, then escalated aggression occurred. If an intruder met the threat of the resident and did not "back down" then a contest ensued. This behavior reflects self-recognition of one's fighting ability or at best, an honest signal of motivation (Enquist and Leimar 1987, Arnott and Elwood 2009).

In determining what factors influenced agonistic behaviors during 1st encounters, neither a difference in prey items as a measure of caloric quality nor the availability of shelter produced variance in behavioral displays between male

Table 3. Mean (± 1 S.E.) behavioral displays per observation period of a focal juvenile *Hemidactylus turcicus* to the cues of an adult male. Data are reported as the frequency of a behavioral act per observation period. χ^2 = test statistic for Friedman's test; p = level of significance, two-tailed (n = 100, * Bonferroni correction significant difference at α = 0.0125)

| | Adult male cues | | | | | | |
Behavior	Control	Visual	Chemical	Visual and chemical (confined)	Visual and chemical (non-confined)	χ^2	p
Avoidance	0.00 ± 0.0	0.05 ± 0.02	0.00 ± 0.00	0.00　± 0.00	0.83 ± 0.12	70.567	< 0.001*
Sensory	6.13 ± 0.5	5.83 ± 0.59	6.50 ± 0.72	5.00　± 0.51	3.83 ± 0.45	9.855	0.043
Warning	0.00 ± 0.0	0.00 ± 0.00	0.00 ± 0.00	0.0125 ± 0.01	0.23 ± 0.06	44.480	< 0.001*
Overt aggression	0.00 ± 0.0	0.00 ± 0.00	0.00 ± 0.00	0.00　± 0.00	0.00 ± 0.00	0.00	> 0.001

geckos in this study. Rather, focal male behavior was related to the presence of a conspecific male, and each responded to the mutual actions of the other.

Despite comprising a large component of the lizard diet, prey items in this study did not influence male behaviors (Klawinski et al. 1994, Meshaka 1995, Huang 2010 2011), and while it is possible that *H. turcicus* might not have been assessing these prey items based on caloric quality, both prey items were consumed during feeding bouts outside of the experimental trials. Thus, male geckos were accustomed to the prey items presented in the trials. Prey items were simply not sufficiently important to affect behavior when an intruder was forced to share the same space with a resident male for the 1st time. There was, however, a high frequency of tongue-flicking by intruding males that was observed. This is best explained by the highly developed olfaction and vomerolfaction system combined with lingual specialization in gekkonids (Schwenk 1993, Cooper 1999) which presents the opportunity to use different chemosensory behaviors during foraging and in encounters with conspecifics. Olfactory cues collected in this manner may be sufficient to inform an intruder of its surroundings and serve to minimize the intensity and costs of fighting within the social systems of lizards (Cooper 1994, López and Martín 2002).

Similarly, when presented with the availability of shelter, intruding males of *H. turcicus* displayed equal frequencies of agonistic behavior across all treatments involving a conspecific, but their behavior was relative to the behavior of the resident male. Again, intruders spent more time engaged in chemoreception via tongue-flicking the substrate, whereby agonistic behaviors could be altered via chemical mediation by providing information regarding competitors and predators (Schwenk 1993, Downes 2001, López and Martín 2002). Intruders, being less familiar with the novel space, might not have been as highly motivated as residents to compete for the space (Stamps and Krishnan 1997). Consequently, intruders that are at a competitive disadvantage may defer to the resident regardless of whether shelter is present or not because of the greater risks involved in a challenge and therefore, exhibit only low levels of agonistic behavior. However, it is up to the resident to display his 'willingness' to defend a site, and an intruder male may then decide to defer or fight in response. In this study, aggressive displays were met with submissive behavior by some males but aggressive behavior by others. This suggests that self-assessment of one's fighting ability determines whether or not an individual ought to engage in a fight (Briffa and Elwood 2008).

Juvenile responses to adult male cues

The 2nd component of this study investigated the recognition abilities of juvenile geckos at an age at which individuals seemingly share space rather than exclusively defend territories. The results revealed that in no case did juveniles aggressively approach adult males when entering a novel space, but generally engaged in submissive behaviors that did not elicit aggression. There were no fights, and very little tactile contact was observed in this experiment. Size differences between juveniles and males probably made it cost-ineffective for adult males to expend energy during an encounter, and therefore adults engaged in display behaviors as opposed to escalated aggression (Maynard Smith and Parker 1976). However, during the observed interactions, males initiated most of the encounters with juveniles, which supports the hypothesis that adult males aggressively exclude juveniles from optimal habitats (Stamps and Krishnan 1997) and may even attack and drive away juvenile offspring to maintain social dominance (Fraňková et al. 2012).

Juvenile response behaviors significantly differed across the presented suite of male cues; however, juveniles were much more behaviorally active when visual and chemical cues of an adult male were provided. Clearly, a non-tethered adult male with accompanying cues elicited the most behaviors in juveniles, perhaps because this allows for an interaction, and although juveniles may spend time in sensory behavior-collecting information, the presence of a live male is sufficient to prompt more-submissive behavior (Mason 1992). Without the opportunity to interact with a male, juveniles may use sensory behaviors to acquire vital information about a novel area that can then influence their response behavior (Stamps and Krishnan 1994 2001). Indeed, juvenile lizards were shown to have higher tongue-flick rates than adults when introduced to a novel environment (Downes 2001). Here, juveniles potentially avoided escalated fights with adults and predominantly exhibited avoidance behavior largely due to the chemical cues collected during tongue-flicking. The damage that a juvenile would sustain from an attacking adult male may alter the response of the juvenile and prompt more-submissive behavior. While juveniles may be more

aggressive with each other, these results are also consistent with the hypotheses that asymmetrical contests are unlikely to occur, and that juveniles defer to adults, particularly adult males (Hanley et al. 1999, Font and Desfils 2002). As a result, there was a combination of behavioral repertoires that was used between adults and juveniles where males both tolerated juveniles to varying degrees and juveniles were submissive to varying degrees.

To conclude, studies on signaling behaviors illustrate the importance of chemical communication in mediating behavioral encounters between conspecifics, particularly in avoiding highly energetic and costly escalated fights. Previous anecdotal reports demonstrated that agonistic behaviors occur in adults of *H. turcicus* (Frankenberg 1982 1984, Selcer 1986, Saenz 1996), but until this study, behavioral displays were not quantified nor was it known what factors were directly involved in eliciting such behaviors. Resources considered vital, such as food quality and shelter, did not affect the outcome of the 1st dyadic encounter between unfamiliar male geckos in this study. However, it is likely that if presented with the same suite of resources, conspecifics that are familiar with each other may behave differently in subsequent bouts (López and Martín 2002). The initial interaction between potential competitors often provides information for follow-up encounters (Stamps and Krishnan 1994 1997). These findings suggest that *H. turcicus* uses some measure of mutual and self-assessment that goes beyond perceived body size to regulate agonistic behavior. This research also provides observational and empirical information needed to understand the social structure within *Hemidactylus* and highlights a dependence on olfactory cues for behavioral responses during interactions. The suite of behaviors presented here demonstrates that *H. turcicus* is aggressive with conspecifics and may provide the foundation for understanding behavioral differences between *H. turcicus*, as an invasive species, and native species that are forced to share the same niche or be excluded during competitive encounters.

REFERENCES

Aragón P, P López, J Martín. 2000. Size-dependent chemosensory responses to familiar and unfamiliar conspecific faecal pellets by the Iberian rock-lizard, *Lacerta monticola*. Ethology **106:** 1115-1128.

Arnott G, RW Elwood. 2009. Assessment of fighting ability in animal contests. Anim. Behav. **77:** 991-1004.

Bradshaw SD. 1971. Growth and mortality in a field population of amphibolurus lizards exposed to seasonal cold and aridity. J. Zool. **165:** 1-25.

Briffa M, RW Elwood. 2008. Difficulties remain in distinguishing between mutual and self-assessment in animal contests. Anim. Behav. **77:** 759-762.

Brillet C. 1990. Rôle des informations olfactives et visuelles dans la discrimination du sexe chez deux espéces de geckos nocturnes: *Eublephairs macularius* et *Paroedura pictus*. Biol. Behav. **15:** 1-22.

Brown SG, F Gomes, FL Miles. 1998. Feces avoidance behavior in unisexual and bisexual geckos. Herpetologica **8:** 169-172.

Carey SD. 1988. Food habits of gulf coast Mediterranean geckos (*Hemidactylus turcicus*). J. Alabama Acad. Sci. **59:** 103.

Carranza S, EN Arnold. 2006. Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. Mol. Phylogen. Evol. **38:** 531-545.

Civantos E. 2000. Home-range ecology, aggressive behavior, and survival in juvenile lizards, *Psammodromus algirus*. Can. J. Zool. **78:** 1681-1685.

Collins JT, KJ Irwin. 2001. Geographic distribution: *Hemidactylus turcicus* (Mediterranean gecko). Herp. Rev. **32:** 276.

Cooper WE Jr. 1994. Chemical discrimination by tongue-flicking in lizards: a review with hypothesis on its origin and its ecological and phylogenetic relationships. J. Chem. Ecol. **20:** 439-487.

Cooper WE Jr. 1999. Prey chemical discrimination in ambush foragers: absence in representatives of two additional iguanian lizard families and probable olfactory mediation in a gekkonine gecko. Chemoecology **9:** 155-159.

Davis WK. 1974. The Mediterranean gecko, *Hemidactylus turcicus*, in Texas. J. Herp. **8:** 77-80.

Downes S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. Ecology **82:** 2870-2881.

Enquist M, O Leimar. 1987. Evolution of fighting behavior: the effect of variation in resource value. J. Theor. Biol. **127:** 187-205.

Fowler HW. 1915. Cold-blooded vertebrates from Florida, the

West Indies, Costa Rica, and eastern Brazil. Proc. Acad. Nat. Sci. Phil. **67:** 244-269.

Font E, E Desfils. 2002. Chemosensory recognition of familiar and unfamiliar conspecifics by juveniles of the Iberian wall lizard, *Podarcis hispanica*. Ethology **108:** 319-330.

Frankenberg E. 1982. Vocal behavior of the Mediterranean house gecko *Hemidactylus turcicus*. Copeia **1978:** 770-775.

Frankenberg E. 1984. Interactions between two species of colonizing house geckos, *Hemidactylus turcicus* and *Hemidactylus garnotii*. J. Herp. **18:** 1-7.

Fraňková M, R Palme, D Frynta. 2012. Family affairs and experimental male replacement affect fecal glucocorticoid metabolites levels in the Egyptian spiny mouse *Acomys cahirinus*. Zool. Stud. **51:** 277-287.

Gabor CR, RG Jaeger. 1995. Resource quality affects the agonistic behavior of territorial salamanders. Anim. Behav. **49:** 71-79.

George D, P Mallery. 1999. SPSS for Windows step by step: a simple guide and reference. Boston, MA: Viacom.

Gomez A, E Font, E Desfils. 1993. Chemoreception in the Lacertidae: exploration and conspecific discrimination in the Spanish wall lizard, *Podarcis hispanica*. *In* ED Valakos, W Boehme, V Perez-Mellado, P Maragoua, eds. Lacertids of the Mediterranean region. Athens, Greece: Helenic Zoological Society, pp. 213-230.

Halpern M. 1992. Nasal chemical senses in reptiles: structure and function. *In* C Gans, D Crews, eds. Biology of the Reptilia, Vol. 18. Chicago, IL: Univ. of Chicago Press, pp. 423-523.

Hanley KA, ML Elliott, JA Stamps. 1999. Chemical recognition of familiar vs. unfamiliar conspecifics by juvenile iguanid lizards *Ctenosaura similis*. Ethology **94:** 530-549.

Hokit DG, SC Walls, AR Blaustein. 1996. Context-dependent kin discrimination in larvae of the marbled salamander, *Ambystoma opacum*. Anim. Behav. **52:** 17-31.

Huang WS. 2010. Ecology and reproductive characteristics of the skink *Sphenomorphus incognitus* on an East Asian island, with comments on variations in clutch size with reproductive modes in *Sphenomorphus*. Zool. Stud. **49:** 779-788.

Huang WS. 2011. Ecology and reproductive patterns of the littoral skink *Emoia atrocostata* on an East Asian tropical rainforest island. Zool. Stud. **50:** 506-512.

Jaeger RG. 1981. Dear enemy recognition and the costs of aggression between salamanders. Am. Nat. **117:** 962-974.

Jaeger RG. 1984. Agonistic behavior of the red-backed salamander. Copeia **1984:** 309-314.

Jennings WB, GG Thompson. 1999. Territorial behavior in the Australian scincid lizard *Ctenotus fallens*. Herpetologica **55:** 352-361.

Klawinski PD, RK Vaughan, D Sanez, W Godwin. 1994. Comparison of dietary overlap between allopatric and sympatric geckos. J. Herp. **28:** 225-230.

López P, J Martín. 2001. Pheromonal recognition of females takes precedence over the chromatic cue in male Iberian wall lizards *Podarcis hispanica*. Ethology **107:** 901-912.

López P, J Martín. 2002. Chemical rival recognition decreases aggression levels in male Iberian wall lizards, *Podarcis hispanica*. Behav. Ecol. Sociobiol. **51:** 461-465.

Marcellini E. 1977. Acoustic and visual display behavior of gekkonid lizards. Am. Zool. **17:** 251-260.

Martins EP. 1994. Structural complexity in a lizard communication system: the *Sceloporus graciosus* "push-up" display. Copeia **1994:** 944-955.

Mason RT. 1992. Reptilian pheromones. *In* C Gans, D Crews, eds. Biology of the Reptilia, Vol. 18. Chicago, IL: Univ. of Chicago Press, pp. 114-228.

Maynard Smith J. 1976. Evolution and the theory of games. Am. Sci. **64:** 41-45.

Maynard Smith J, GA Parker. 1976. The logic of asymmetric contests. Anim. Behav. **24:** 159-179.

McMann S. 2000. Effects of residence time on displays during territory establishment in a lizard. Anim. Behav. **59:** 513-522.

Meshaka WE. 1995. Reproductive cycle and colonization ability of the Mediterranean gecko (*Hemidactylus turcicus*) in south-central Florida. Fla. Sci. **58:** 10-15.

Saenz D. 1996. Dietary overview of *Hemidactylus turcicus* with possible implications of food partitioning. J. Herp. **30:** 461-466.

Schall JJ. 1974. Population structure of the Aruban whiptail lizard *Cnemidophorus arubensis* in varied habitats. Herpetologica **30:** 38-44.

Schwartz A, RW Henderson. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. Gainesville, FL: Univ. of Florida Press.

Schwenk K. 1993. The evolution of chemoreception in squamate reptiles: a phylogenetic approach. Brain Behav. Evol. **41:** 124-137.

Selcer KW. 1986. Life history of a successful colonizer: the Mediterranean gecko, *Hemidactylus turcicus*, in southern Texas. Copeia **1986:** 956-962.

Stamps JA. 1977. The relationship between resource competition, risk and aggression in a tropical territorial lizard. Ecology **58:** 349-358.

Stamps JA. 1983. Sexual selection, sexual dimorphism, and territoriality. *In* RB Huey, ER Pianka, TW Schoener, eds. Lizard ecology: studies of a model organism. Cambridge, MA: Harvard Univ. Press, pp. 169-204.

Stamps JA. 1992. Simultaneous versus sequential settlement in territorial species. Am. Nat. **139:** 1070-1088.

Stamps JA, VW Krishnan. 1994. Territory acquisition in lizards I. First encounters. Anim. Behav. **47:** 1375-1385.

Stamps JA, VW Krishnan. 1997. Functions of fights in territory establishment. Am. Nat. **150:** 393-405.

Stamps JA, VW Krishnan. 2001. How territorial animals compete for divisible space: a learning-based model with unequal competitors. Am. Nat. **157:** 154-169.

Tang-Martinez Z. 2001. The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. Behav. Proc. **53:** 21-40.

Walls SC, A Mathis, RG Jaeger, WF Gergits. 1989. Male salamanders with high quality diets have faeces attractive to females. Anim. Behav. **38:** 546-548.

Werner YL, E Frankenberg, O Adar. 1978. Further observations on the distinctive vocal repertoire of *Ptyodactylus hasselquistii* cf. *hasselquistii* (Reptilia: Gekkonidae). Israeli J. Zool. **27:** 176-188.

Wiltenmuth EB, KS Nishikawa. 1998. Geographical variation in agonistic behavior in a ring species of salamander, *Ensatina eschscholtzii*. Anim. Behav. **55:** 595-606.

Zar JH. 1996. Biostatistical analysis 3rd ed. Upper Saddle River, NJ: Prentice Hall.