

Social behaviour of the dwarf gecko *Sphaerodactylus vincenti vincenti* on St. Vincent, Lesser Antilles

MARTHA A. MARCUM, MICHAEL A. POWELL, ALEXANDER J. MUENSCH,
HELEN F. ARNOLD & ROBERT POWELL

Abstract. In June 2006, we staged male/male (m/m), male/female (m/f), and female/female (f/f) (seven each) interactions between pairs of *Sphaerodactylus vincenti vincenti* (Sphaerodactylidae) from St. Vincent, West Indies, and evaluated 23 types of behaviours. Behavioural repertoires differed significantly between types of interactions. Six individual behaviours occurred significantly more frequently in at least one type of interaction: crouch, gular-inflation, and antiparallel-positioning more in m/m than in m/f, tongue-flick and rooting more in f/f than either m/m or m/f, and head-turn more in f/f than in m/f encounters. Female/female interactions consistently included the greatest number of behaviours that could be construed as being aggressive, although attack, the most egregious agonistic behaviour documented, occurred at almost equal frequencies in both types of consensual interactions. The most consistently observed pattern (found in all three combinations of interactions) began with stare, followed by signaling from a distance, approach or attack, contact, and finally withdrawal. Some display/approach sequences were performed with a "limp". In intersexual encounters, males would initiate an approach from behind or alongside a female, moving toward her tail, and lick-sniffing her there. The female would then allow the male to mount or, more frequently, violently tail-wave and withdraw.

Key words. Squamata, Sphaerodactylidae, *Sphaerodactylus vincenti vincenti*, St. Vincent, social behaviour.

Introduction

Dwarf geckos in the genus *Sphaerodactylus* are small, voiceless lizards that may be active by day, night, or during crepuscular periods (LEUCK et al. 1988, STEINBERG et al. 2007). The systematic literature on West Indian species of *Sphaerodactylus* is abundant, but that concerned with behaviour of Caribbean (LEUCK et al. 1988, REGALADO 1997, 2003) and specifically Lesser Antillean (WISSMANN et al. 2005) dwarf geckos lags far behind, with only five of the over 80 species known to occur in the region (POWELL et al. 1996) having received more than cursory examination. According to the few detailed studies, visual signals are a primary means of sex recognition, although geckos in general appear to rely heavily on olfactory cues (e.g., DIAL & SCHWENK 1996).

Sphaerodactylus vincenti vincenti (Fig. 1) is the only species of dwarf gecko on St. Vincent and is an island endemic. Other subspecies of *S. vincenti* occur on the Martinique, St. Lucia, and Dominica island banks (STEINBERG et al. 2008). *Sphaerodactylus v. vincenti* is a relatively large sphaerodactyl, with a maximum snout-vent length (SVL) of 40 mm, and is found in leaf litter, bromeliads, and under rocks and rotten logs (SCHWARTZ & HENDERSON 1991), particularly in mesic areas (STEINBERG et al. 2007).

Materials and methods

In June 2006, we collected four groups of 6-10 geckos in a densely shaded area with thick (> 5 cm) mango (*Mangifera* sp.) leaf litter in the Botanical Garden in Kingstown,

St. Vincent. We observed and videotaped 21 intraspecific interactions: seven male/male, seven female/female, and seven male/female encounters. All animals were released at the site of capture after a maximum of three days in captivity.

We sexed geckos and measured SVL to the nearest 0.1 mm. Individuals were housed in 16 x 9 x 10-cm plastic cages and circular plastic containers with screened lids. In order to calm and acclimate geckos prior to each interaction, we isolated them by placing paper between neighbouring cages for a period of at least 20 minutes. We provided each gecko

with a paper towel substrate, and misted containers twice a day for the duration of captivity. Containers were kept outside on a covered porch at ambient temperatures and humidity, and were washed thoroughly with soap and warm water for each new inhabitant to eliminate the possibility of chemical distractions.

After the settling period, we placed two selected geckos into a washed and dried 21 x 14 x 13-cm plastic cage with a fresh, white paper substrate cut to fit the bottom of the cage. Each individual participated in a maximum of three encounters. No animals were used more than once per day and no pairs



Fig. 1. Adult male (top) and female *Sphaerodactylus vincenti vincenti* from the Botanical Garden, Kingstown, St. Vincent, showing some of the colour and pattern variation observed in these geckos. Despite the differences evident in these two individuals, *S. v. vincenti* is not sexually dimorphic, with variation in dorsal and ventral ground colours, colour of the iris, and distinctiveness of pattern elements found in both males and females. Sexes of all lizards used in this study were determined by the presence (males) or absence of enlarged escutcheons. These lizards reach estimated population densities to 5625/ha in moist, shaded leaf-litter (STEINBERG et al. 2007).

were repeated. Every interaction was taped on a video-recorder that simultaneously recorded our audio observations, which were supplemented with notes by at least two observers. We later reviewed the video recordings to obtain a more detailed analysis and more descriptive data set. As in WISSMANN et al. (2005), we began recording each individual's behavioural repertoire, which included notations of behavioural sequences, from the time that one lizard initiated a behaviour or assumed a position directed toward the other. We ceased recording after 15 minutes of inactivity following any interactions or after 20 minutes of total inactivity had passed since the introduction.

Behaviours were characterised as in REGALADO (1997, 2003) and WISSMANN et al. (2005) and included: approach (individual moved toward the other animal at a normal pace), withdrawal (individual moved away from the other animal), stiff (legs extended posteriorly, sometimes with body tilted toward the opponent, almost always accompanied by arched back and head pointed down), crouch (individual rested its legs alongside the body while keeping its trunk close to the substrate and head held above the substrate), head-turn (stationary individual assumes a 45-90° angle between head and long axis of the body, often alternating the direction of flexion to the opposite side of the body), tongue-flick (rapid extension and retraction of tongue), head-bob (up and down movement of the head, noted from the beginning to the end of a series), and stand (individual lifted body partially away from substrate while stationary).

Additional behaviours drawn from WISSMANN et al. (2005) included: stare (individual looked intently at the other animal), walk (individual moved around without appearing to interact with the other animal), tail-wave (tail waved or wagged quickly and rhythmically from side to side, noted from beginning to the end of a series), touch (part of one individual's body touched the other animal), mount (individual climbed on top of the

other animal), on wall (individual climbed the wall of the cage), and rooting (individual touched nose to the substrate).

We noted other behaviours observed by D.S. STEINBERG (pers. comm.) that included: gular-pumping (a series of throat inflations and deflations), gular-inflation (individual maintains an engorged throat sac for a period of time), and antiparallel-positioning (individuals are parallel to one another but facing opposite directions). We modified the latter to include variations of head positioning at the neck or side of the other animal. We believe that redefining this behaviour is appropriate because each head placement was accompanied by licking and/or sniffing and therefore seemed to serve the same purposes of attaining information and sexual identification (REGALADO 2003).

We combined two behaviours that were identified separately by WISSMANN et al. (2005), as it was difficult to distinguish between lick (individual tongue flicks at the other animal) and sniff (individual touches the other animal with its snout without licking), labeling the combined behaviour lick-sniff. We divided raised-tail (WISSMANN et al. 2005) into three behaviours distinguished by duration and extent: raised-tail A (elevated tail curved upward), raised-tail B (tail elevated at the base and center making an arc with the tip pointed down), raised-tail C (tail is flat on the substrate with only the tip curved upward).

We observed and added one behaviour (attack: rapid charge followed by a bite) that was not noted in any of the previous studies.

We analysed our data using Statview 5.0 (SAS Inst., Cary, North Carolina); for all tests, $\alpha = 0.05$.

Results

Repertoires of behaviours (Table 1) differed significantly between types of interaction (contingency test, $df = 23$, $\chi^2 = 144.82$, $P < 0.0001$), but when we compared individual

types of behaviours, the only significant difference was in the occurrence of antiparallel-positioning (ANOVA, $df = 2$, $F = 3.93$, $P = 0.04$). Pairwise comparisons (Fisher's PLSD) revealed the following significant differences: crouch between male/male and male/female interactions ($P = 0.03$), head-turn between female/female and male/female interactions ($P = 0.04$), tongue-flicks between female/female and male/female interactions ($P = 0.005$) and between female/female and male/male interactions ($P = 0.004$), rooting between female/female and male/female interactions ($P = 0.04$) and between female/female and male/male interactions ($P = 0.04$), gular-inflation between male/female and male/male interactions ($P = 0.02$), and antiparallel-positioning between male/female and male/male interactions ($P = 0.01$).

Although differences were not always significant, certain behaviours occurred substantially more frequently than others. Males in same-sex interactions approached and withdrew more frequently than individuals in male-female interactions. Males in same-sex interactions head-turned more than animals in intersexual interactions. Stiff, stare, walk, head-bob, lick-sniff, and gular-pumping occurred least frequently in male/female interactions. Raised-tail A occurred less frequently in male/female interactions than in male/male interactions.

Discussion

Studies of lizards' social behaviours have shown them capable of various behavioural postures, sequences, and degrees of sociality, but reptilian behaviours appear to be specific to the ecological setting (BRATTSTROM 1974). Consequently, comparisons of sphaerodactyl behaviours with those of other lizards, even other geckos, may be inappropriate, particularly because many studies of social behaviours in geckos address those of eublepharids (e.g., GREENBERG 1943, DIAL & SCHWENK 1996, COOPER & STEELE 1997, SAKATA

Tab. 1. Frequencies of behaviours exhibited by *Sphaerodactylus vincenti vincenti* during male/male (MM), male/female (MF), and female/female (FF) interactions. See text for distinctions between "raise-tail A", "raise-tail B", and "raise-tail C".

Behaviour	MM	MF	FF
approach	92	50	79
withdrawal	95	49	77
stiff	61	6	44
stare	106	63	117
walk	74	25	54
crouch	51	14	25
tail-wave	64	53	53
head-turn	142	73	148
tongue-flick	15	16	56
head-bob	115	52	121
lick-sniff	77	29	47
stand	30	30	26
touch	6	9	10
on-wall	2	3	9
rooting	13	14	36
gular-pumping	78	34	70
mount	2	5	0
gular-inflation	57	15	39
antiparallel-positioning	10	0	6
attack	3	2	4
raise-tail A	54	25	38
raise-tail B	7	3	1
raise-tail C	13	5	11
raise-tail total	74	21	50

& CREWS 2004) or gekkonid species that are vocal (e.g., MARCELLINI 1974, 1977a, 1977b). Also, studies of sphaerodactylid geckos in the genus *Gonatodes* often concern species that are more arboreal than litter-dwelling (e.g., ELLINGSON et al. 1995). In addition, many recent studies of behaviours in geckos address foraging rather than social behaviours (e.g., WERNER et al. 2006).

However, DEMETER & MARCELLINI (1981), in a study of courtship and aggressive behaviours of captive *Gonatodes vittatus*, indicated that their observations were similar to those described for other diurnally active

geckos. Also, their results supported observations (e.g., STAMPS 1977) and studies (e.g., GREER 1967, KASTLE 1964) of diurnal species indicating that females exhibit a high degree of aggressive behaviour — as appears to be the case for species of *Sphaerodactylus* (REGALADO 1997, 2003, WISSMANN et al. 2005). As in this study, sample sizes were often small, rendering statistically based distinctions between smaller groups, such as between gravid and non-gravid females, impossible. Also, the available data for *Sphaerodactylus* are incapable of determining the extent to which behavioural repertoires vary between species or to what extent such repertoires are stereotypical of the species studied or of the genus as a whole. However, that very paucity of information provides tantalizing glimpses of interactions that may be every bit as complex as those known to occur in iguanian lizards.

Hereafter, we restrict comparisons to those with other species in the genus *Sphaerodactylus*. Twelve of 23 behaviours occurred primarily in male/male interactions, suggesting that they may be components of agonistic behavioural sequences in *S. vincenti vincenti*. For example, antiparallel-positioning was common in male/male interactions, but was not observed in male/female interactions. D.S. STEINBERG (pers. comm.) observed antiparallel-positioning in two of three male/female encounters in *S. macrolepis*, and surmised that it might serve as a mechanism for gathering information used by females to evaluate males during courtship. In contrast, in our study, males would initiate an approach from behind or alongside the female (and females often positioned themselves facing away from males), always moving toward her tail, and lick-sniffing her there. The female would then allow the male to mount or, more frequently, violently tail-wave and withdraw.

Rigorous tail-waves preceded withdrawals, which REGALADO (1997) also observed in *S. elegans*. Mounting occurred twice during male/male interactions, suggesting that this behaviour is not only for copulation, but also

may be used to establish dominance. Only one mount lasted for more than a few seconds in an intersexual interaction and, in that encounter, we observed no copulation. This probably is attributable to the fact that males mounted only non-gravid females, and four of seven females in inter-sexual encounters were gravid.

Lick-sniffing occurred in conjunction with antiparallel-positioning on 13 occasions. In that position, the presumably dominant individual lick-sniffed up and down the other lizard's back, moving between the neck, trunk, and tail. This would usually provoke the presumptive submissive to withdraw, ending the encounter.

As REGALADO (1997) observed in *S. elegans*, crouch occurred more frequently during male/male interactions than in male-female interactions, and usually was used by submissive animals, suggesting that this behaviour was a component of agonistic encounters. Similarly, according to REGALADO (1997), head-turning was "agonistic ... Such head orientation reveals the inflated throat to the antagonist". Our study found most instances of this behaviour in consensual interactions. Head-turn was the most frequently observed behaviour in our trials.

Tongue-flicks were more abundant in female/female interactions than either male/female or male/male interactions. Licking behaviours may be used in vomerolfaction and pheromone detection/sex identification (REGALADO 1997), although DIAL & SCHWENK (1996), for example, indicated that olfaction, rather than vomerolfaction, may be more important in geckos. Tongue-flicking the substrate (i.e., rooting) to determine the sex of a conspecific would seem less aggressive and intrusive than licking. Rooting may be used for identification, obviating a potentially more hostile and energetically costly behaviour, suggesting that females in same-sex interactions attempted to avoid escalated encounters more than sphaerodactyls in other situations.

Males in same-sex interactions displayed

gular inflation significantly more frequently than animals in male/female encounters. This behaviour appears to be a “modifier” when performed in combination with other displays, and a “low level agonistic behaviour, probably signaling awareness of conspecific proximity” when performed by itself (REGALADO 2003). Females in same-sex interactions also used gular inflation more frequently than either sex in intersexual encounters.

Other presumably agonistic behaviours that occurred substantially less frequently in intersexual encounters were stiff, head-bob, lick-sniff, and gular-pumping. Conversely, presumed submissives often raised their tails (A), an action most commonly seen in male/male interactions, perhaps correlating with the higher frequencies of approaches found in that type of encounter. Head-bobbing was the second most frequently observed behaviour, and both stiff and head-bob have been frequently seen in other *Sphaerodactylus* (REGALADO 1997). Lick-sniff seems to be an agonistic behaviour in the context of same-sex interactions, but may also be a means of appeasement in courtship (REGALADO 2003).

Our observations were similar to those of WISSMANN et al. (2005) and REGALADO (1997, 2003) in that female/female interactions often were aggressive. Attack, the most egregious agonistic behaviour documented, however, occurred almost equally in both types of consensual interactions, with four attacks in female/female encounters and three in male/male interactions. Female/female interactions also generated the greatest frequencies of head-bobs and stare.

The most consistent behavioural pattern (found in all three types of interactions and performed by both sexes) began with stare, followed by signaling from a distance (sometimes animals would skip this element), approach or attack, contact, and finally withdrawal. This sequence varied somewhat among individuals, but followed the same general pattern. Individuals stared while head-turning from one side of the body to the other, and signaled with gular-inflation,

gular-pumping, stiff, raised-tail, and head-bob as singular acts or in various combinations. Signaling or staring sometimes occurred with the two individuals positioned in an antiparallel orientation, bodies curved toward one another in a “c” shape, but with varying degrees of space separating them. Approach often followed along a curved pathway toward the other lizard; REGALADO (2003) noted that stiff often was performed along a “roundabout path toward a conspecific”. At times, approach evolved into attack. Contact occurred by sniff-licking or biting, in the case of an attack, until one of the individuals chose to withdraw, which thus terminated the sequence. Conversely, a withdrawal could also transform into a signaling display or another approach, restarting the pattern. In this way, dominance passed back and forth between individuals until one yielded. For the majority of encounters, however, one animal would dominate interactions by initiating this pattern of behaviour with an approach or display, and remain dominant until the end of the interaction.

A display observed by REGALADO (2003) in *S. nicholsi* and in four instances during our study was a display/approach sequence performed with a “limp”. The dominant animal lifted the front leg closest to the conspecific and folded it against the body. This was first performed with a stationary head-bob and then while approaching, giving the appearance of a limp. The folded leg occurred in combinations of behaviours similar to non-limping approaches.

We noted another recurring combination of behaviours 44 times: approaching individuals synchronised head-bobs with tail-waving. The tip of the tail twitched rapidly in time with each up-and-down movement of the head. Individuals displayed this sequence from a stationary signaling stance, during an approach, or both. The tail-twitch sometimes evolved into a larger tail-wave or whipping movement when the displaying individual closely approached the other lizard or when “provoked” by some sort of agonistic behav-

our. These synchronous head-bobs and tail-waves occurred in sequences of as many as 53 repetitions.

Repertoires of behaviours apparently are shared by both sexes of *S. vincenti vincenti* and the congeners that have been studied. Frequencies of behaviours varied considerably among sexes and types of interactions, but agonistic behaviours were significantly more abundant during consensual interactions. *Sphaerodactyls* can occur in remarkably high densities (RODDA et al. 2001, STEINBERG et al. 2007), possibly resulting in intense competition for resources (e.g., space), which, in turn, may have led to the evolution of territorial and aggressive behaviours. Intersexual encounters, on the other hand, were relatively docile, suggesting that females are not coaxed into receptivity by aggressive males.

We found many differences in frequencies of behaviours in different types of interactions to be substantial but not significant, indicating that larger sample sizes might reveal stronger trends. Certain combinations of behaviours, all of which varied to some degree, also are suggestive of trends that might be confirmed with additional research. However, these data should help establish a foundation upon which further investigations can build: research capable of characterising predictable sequences of behaviours and their corresponding functions so that we may achieve a more thorough understanding of social interactions and idiosyncrasies of this ubiquitous genus of West Indian geckos.

Acknowledgements

DAVID S. STEINBERG helped collect geckos. ROBERT W. HENDERSON and JOHN S. PARMERLEE, JR. reviewed an early draft of this paper. Permits to conduct research on St. Vincent were issued by the Department of Forestry, St. Vincent and the Grenadines. BRIAN JOHNSON, Director, Department of Forestry, CORNELIUS RICHARDS, AMOS GLASGOW, and especially FITZGERALD PROVIDENCE facilitated our efforts. NIGEL WEEKS, Director of National Parks, granted permission to conduct research on

the grounds of the Botanic Garden. Protocols were approved by the Avila University Animal Care and Use Committee. Fieldwork was funded by a grant from the National Science Foundation (U.S.A.) to ROBERT POWELL (DBI-0242589).

References

- BRATTSTROM, B.H. (1974): The evolution of reptilian social behavior. – *American Zoologist*, **14**: 35-49.
- COOPER, W.E., JR. & L.J. STEELE (1997): Pheromonal discrimination of sex by male and female Leopard Geckos (*Eublepharis macularius*). – *Journal of Chemical Ecology*, **23**: 2967-2977.
- DEMETER, B.J. & D.L. MARCELLINI (1981): Courtship and aggressive behavior of the Streak Lizard (*Gonatodes vittatus*) in captivity. – *Herpetologica*, **37**: 250-256.
- DIAL, B.E. & K. SCHWENK (1996): Olfaction and predator detection in *Coleonyx brevis* (Squamata: Eublepharidae), with comments on the functional significance of buccal pulsing in geckos. – *Journal of Experimental Zoology*, **276**: 415-424.
- ELLINGSON, J.M., L.J. FLEISHMAN & E.R. LOEW (1995): Visual pigments and spectral sensitivity of the diurnal gecko *Gonatodes albogularis*. – *Journal of Comparative Physiology*, **177**: 559-567.
- GREENBERG, B. (1943): Social behavior of the Western Banded Gecko, *Coleonyx variegatus*. – *Physiological Zoology*, **15**: 110-122.
- GREER, A.E. (1967): The ecology and behavior of two sympatric *Lygodactylus* geckos. – *Breviora*, **268**: 1-19.
- KASTLE, W. (1964): Verhaltensstudien an Taggeckonen der Gattungen *Lygodactylus* und *Phelsuma*. – *Zeitschrift für Tierpsychologie*, **21**: 486-507.
- LEUCK, B.E., K.W. HUGHES & H.Y. CHENG (1998): Social displays of experimentally paired dwarf geckos (*Sphaerodactylus clenchi*). – *Journal of Herpetology*, **24**: 416-418.
- MARCELLINI, D.L. (1974): Acoustic behavior of the gekkonid lizard, *Hemidactylus frenatus*. – *Herpetologica*, **30**: 44-52.
- MARCELLINI, D.L. (1977a): Acoustic and visual display behavior in gekkonid lizards. – *American Zoologist*, **17**: 251-266.

- MARCELLINI, D.L. (1977b): The function of a vocal display of the lizard *Hemidactylus frenatus* (Sauria: Gekkonidae). – *Animal Behaviour*, **25**: 414-417.
- POWELL, R., R.W. HENDERSON, K. ADLER & H.A. DUNDEE (1996): An annotated checklist of West Indian amphibians and reptiles. – pp. 51-93 + 8 pls. in POWELL, R. & R.W. HENDERSON (eds.): *Contributions to West Indian Herpetology: A Tribute to ALBERT SCHWARTZ*. – Ithaca, New York (Soc. Study Amphib. Rept. Contrib. Herpetol., Vol. 12).
- REGALADO, R. (1997): Social behavior of the Ashy Gecko (*Sphaerodactylus elegans* MACLEAY): Repertoire and sex recognition. – *Herpetological Natural History*, **5**: 41-52.
- REGALADO, R. (2003): Social behavior and sex recognition in the Puerto Rican Dwarf Gecko *Sphaerodactylus nicholsi*. – *Caribbean Journal of Science*, **39**: 77-93.
- RODDA, G.H., G. PERRY, R.J. RONDEAU & J. LAZELL (2001): The densest terrestrial vertebrate. – *Journal of Tropical Ecology*, **17**: 331-338.
- SAKATA, J.T. & D. CREWS (2004): Developmental sculpting of social phenotype and plasticity. – *Neuroscience & Biobehavioral Reviews*, **28**: 95-112.
- SCHWARTZ, A. & R.W. HENDERSON (1991): *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. – Gainesville, Florida (Univ. Florida Press).
- STAMPS, J.A. (1977): Social behavior and spacing patterns in lizards. – pp. 265-334 in GANS, C. & D.W. TINKLE (eds.): *Biology of the Reptilia*, Vol. 7, Ecology and Behavior A. New York, New York (Academic Press).
- STEINBERG, D.S., S.D. POWELL, R. POWELL, J.S. PARMERLEE, JR. & R.W. HENDERSON (2007): Population densities, water-loss rates, and diets of *Sphaerodactylus vincenti* on St. Vincent, West Indies. – *Journal of Herpetology*, **41**: 330-336.
- STEINBERG, D.S., J.L. HITE, R. POWELL & R.W. HENDERSON (2008): *Sphaerodactylus vincenti*. – *Catalogue of American Amphibians and Reptiles*: in press.
- WERNER, Y.L., H. TAKAHASHI, Y. YASUKAWA & H. OTA (2006): Factors affecting foraging behaviour, as seen in a nocturnal ground lizard, *Goniurosaurus kuroiwaie kuroiwaie*. – *Journal of Natural History*, **40**: 439-459.
- WISSMANN, S.M., R.L. HENSLEY, R. POWELL & J.S. PARMERLEE, JR. (2005): Social behaviour in the dwarf geckos *Sphaerodactylus sabanus* and *S. sputator* from St. Eustatius, Netherlands Antilles. – *Salamandra*, **41**: 45-50.

Manuscript received: 22 January 2007

Authors' addresses: MARTHA A. MARCUM, Department of Biology, University of North Florida, Jacksonville, Florida 32224, USA; MICHAEL A. POWELL, Department of Political Science, Truman State University, Kirksville, Missouri 63501, USA; ALEXANDER J. MUENSCH, Department of Biology, Avila University, Kansas City, Missouri 64145, USA; HELEN F. ARNOLD, Department of Biology, Arkansas State University-Beebe, Beebe, Arkansas 72012, USA; ROBERT POWELL, Department of Biology, Avila University, Kansas City, Missouri 64145, USA.