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Microhabitat Use by the Invasive Green Anole, *Anolis carolinensis*, and Native Lizards on Zamami-jima Island, Ryukyu Archipelago, Japan

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Abstract: This study aimed to clarify microhabitat use by the invasive green anole, *Anolis carolinensis* and four native lizard species on Zamami-jima Island, Japan. Daytime and nighttime field surveys were conducted at sites with (GAP) and without *A. carolinensis* (GAA). At the GAP sites daytime use of plant species, substrates and perch height by *A. carolinensis* differed from native lizards, whereas the parts of plants used by *A. carolinensis* were similar to those used by native lizards. The perch substrate types (plant parts, ground or artificial substrates) used by native lizards during the daytime differed slightly between the GAP and GAA areas. During the night, the resting plant species used by *A. carolinensis* differed from those used by the native lizards at the GAP area, although the plant parts and height above ground were similar to those used by the native lizards at the GAP area. In particular, *Takydromus smaragdinus* used *Pennisetum purpureum* leaves at a high frequency as a resting place in the GAA area. In contrast in the GAP area *T. smaragdinus* was never found resting on *P. purpureum* leaves while 77% of *A. carolinensis* were found resting on *P. purpureum*. These findings suggest that the overlap of microhabitats between *A. carolinensis* and native lizards is small during the daytime, but that this invasive lizard species influences the selection of resting sites by *T. smaragdinus*. Further studies are required to understand how *A. carolinensis* may exclude *T. smaragdinus* from resting sites.

Key words: *Anolis carolinensis*; Continental island; Habitat use; Invasive lizard; Ryukyu Archipelago

Introduction

Alien species may directly and indirectly affect native species and ecosystems through predation, interspecific competition, acting as vectors for pathogens, genetic pollution, and disturbing pollination (Kupferberg, 1997; Holway, 1999; Huxel, 1999; Rushton et al., 2006; Pintor et al., 2009; Spatz et al., 2017). Some alien reptiles have significant impacts on ecosystems. For example, the brown tree snake, *Boiga irregularis* invaded Guam via cargo shipping and subsequently caused the extinction of many vertebrate species that had

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evolved in an environment without natural predators (Savidge, 1987; Rodda and Fritts, 1992; Rodda et al., 1999; Wiles et al., 2003). Following the extinction of endemic birds, the seeds of certain plants cannot be properly dispersed, leading to indirect effects on ecosystem (Rogers et al., 2017). The house gecko, *Hemidactylus frenatus* was introduced to many Pacific islands through transportation of materials and competed with the mourning gecko, *Lepidodactylus lugubris*, for food in urban environments, ultimately displacing *L. lugubris* (Case et al., 1984; Petren and Case, 1996). Furthermore, breeding of abandoned pet turtles with native species results in hybrids, leading to concerns regarding genetic pollution (Ota and Hamaguchi, 2003).

The green anole, *Anolis carolinensis* (Iguania: Anolidae), is a diurnal lizard with a snout-vent length ranging from 42 mm to 73 mm (The Herpetological Society of Japan, 2021). Naturally occurring in the southeastern United States, this species has been introduced to Micronesia, Hawaii, Guam, Taiwan, and several islands in Japan (Norval et al., 2012; The Herpetological Society of Japan, 2021). The primary cause of invasion is thought to be the escape of pets (Ota, 2002). The direct and indirect impacts of this species on native ecosystems include predation on native insects (Makihara et al., 2004; Karube, 2005; Takahashi et al., 2014), inter-specific competition with native lizards (Suzuki and Nagoshi, 1999), and disturbance of pollination (Abe et al., 2008). This species is classified as a trunk-crown ecomorph that utilizes both higher trunk and lower crown areas in the vegetation (Jenssen et al., 1995). However, previous researches indicated that introduced populations of this species utilized various plant species and occupied both higher and lower perch sites (Anzai et al., 2017; Mitani et al., 2020). Suzuki and Nagoshi (1999) investigated possible habitat overlap between the introduced *A. carolinensis* population in the Ogasawara Islands and the sole indigenous lizard (*Cryptoblepharus nigropunctatus*), however no similar studies have been conducted on other islands where *A. carolinensis* has been introduced.

The Ryukyu Archipelago is one of the areas where *A. carolinensis* has been introduced. *Anolis carolinensis* is currently found on Okinawa-jima and Zamami-jima Islands. They were first observed on Okinawa-jima Island in 1989 (Chigira, 1991) where they established in the southern part of the island (Ota, 2002). Later, they expanded from the southern and central parts of the island (just outside the natural heritage area, Yambaru) to the present distribution (Ishikawa et al., 2011; Okinawa Prefectural Government, 2023). Although their occurrence is currently limited to urban areas in the south-central part of the island, a niche-modeling analysis suggested that this species had the potential to inhabit almost the entire island (Suzuki-Ohno et al., 2017). *Anolis carolinensis* was first recorded on Zamami-jima Island in 2013 (Iwao, 2015). Although the initial colonization site was surrounded by natural forests, the occurrence of *A. carolinensis* has remained confined to a limited area (NCDDEAO, 2024). Despite their possible negative impacts on the native fauna of Okinawa-jima and Zamami-jima islands, no studies have been conducted on the habitat usage of *A. carolinensis* or their interactions with native lizards on these islands. This study aimed to investigate microhabitat use of *A. carolinensis* and native lizards on Zamami-jima Island.

MATERIALS AND METHODS

Study site

Zamami-jima Island is located 35 km west of Okinawa-jima Island and is 6.7 km^2 in area. Four native diurnal lizards (*Takydromus smaragdinus* [Lacertidae], *Diploderma polygonatum polygonatum* [Agamidae], *Plestiodon marginatus* [Scincidae], and *Ateuchosaurus okinavensis* [Scincidae]) occur on the island (Maenosono and Toda, 2007). In 2020, the occurrence of *A. carolinensis* was limited to the southern part of the island (Furuzamami Area) (NCDDEAO, 2024). This study was

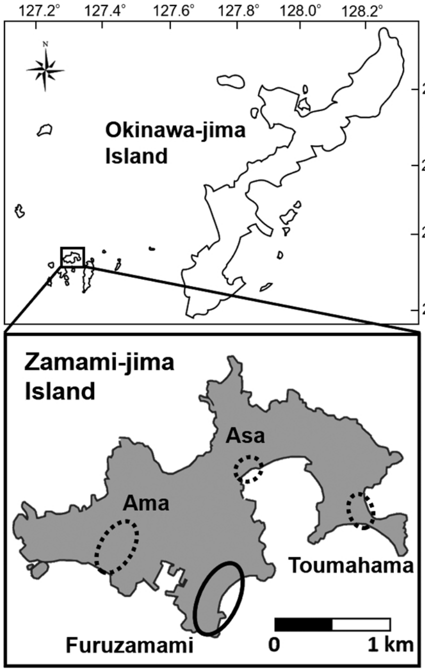

FIG. 1. A map of Zamami-jima Island showing location of the study sites. Circle with unbroken margins indicates *Anolis carolinensis* present site (Furuzamami site) and circles with broken margins indicate *A. carolinensis* absence sites (Ama, Asa, and Toumahama sites).

conducted at two types of sites: areas where the anoles are present (GAP) at the Furuzamami site, and areas where the anoles are absent (GAA) at the Ama, Asa, and Toumahama sites (Fig. 1). The GAP site comprised secondary forests, coastal forests, meadows, and wastelands. Common tree species in secondary forests included *Pinus luchuensis*, *Ficus erecta*, *Macaranga tanarius*, and *Toxicodendron succedaneum*, whereas *Casuarina* sp., *Pandanus odorifer*, *Leucaena leucocephala* and *Hibiscus tiliaceus* were common in coastal forests. Meadows are dominated by the grass *Pennisetum purpureum*. Similar secondary and coastal forest habitats were found in the GAA sites. In addition, the Ama site featured wetlands with *Typha latifolia*, along with human houses surrounded by hedges and gardens, whereas the Asa site contains meadows dominated by *P. purpureum*.

Route census surveys

Census routes were established along paved and unpaved roads at the study sites. The lengths of these routes were 1,300, 480, 230, and 470 m in the Furuzamami, Ama, Asa, and Toumahama sites, respectively (Table 1). Although a few sections of these routes were covered with canopy of tall trees, they mostly passed through areas with shorter trees, grass land, and patches of *Bidens* sp.

Census route surveys were conducted on September 20–22, 2021; September 9–10, 2022; and September 29–30, 2022. Two or three persons (authors) conducted surveys during the daytime (0930–1630 h) and nighttime (1930–0100 h), during which we walked along the routes and searched for the anoles and the four native diurnal lizard species both on tracks and in bordering vegetation. The total census times were 29 h 30 min, 5 h 15 min, 1 h 40 min, and 5 h 10 min in the Furuzamami, Ama, Asa, and Toumahama sites, respectively (Table 1). Whenever lizards of any five species were found we recorded species, perch height above the ground, plant species on which the lizard was perched, and perch substrate types

TABLE 1. Census route length and time in each study route.

Area	Distribution of *Anolis carolinensis*	Census route length (m)	Daytime surveyed time (h)	Nighttime surveyed time (h)
Furuzamami	○	1,300	19.2	10.3
Ama	×	480	3.5	1.8
Asa	×	230	1.0	0.7
Toumahama	×	470	2.9	2.3

(plant parts, ground or artificial substrates, such as glass house stainless frames, plastic buckets, and concrete blocks). Lizards were not captured. The perch height was measured using a digital laser distance meter (Leica DISTOTM X310; Leica, Germany).

Data analysis

Due to small sample sizes in each green anole absent site, data from these sites were combined. Differences in substrate types between GAP and GAA areas for each species were examined using Fisher's exact test. In addition, niche breadth (B) and niche overlap (O_{ab}) of substrate types were calculated following Pianka (1986) and Pianka (1973), respectively. Each formula is shown below:

$$\text{Niche Breadth (B)} = \frac{1}{\sum_{i=1}^{n} Pi^2}$$

$$\text{Niche Overlap } (O_{ab}) = \frac{\sum_{i=1}^{n} Pi_a Pi_b}{\sqrt{\sum_{i=1}^{n} Pi_a^{\,2} \times \sum_{i=1}^{n} Pi_b^{\,2}}}$$

where i indicates i-th substrate type number I, Pi indicates the ratio of substrate type number I to the total, and n indicates the total number of substrate types. These scores are relative indexes, so that the absolute baseline was not determined. Differences between species in perch heights above the ground were tested by Tukey's HSD test. All statistical analyses were performed using R version 4.2.1 (R Core Team, 2022).

RESULTS

Microhabitat uses during daytime

All four native diurnal lizards known from Zamami-jima Island were recorded in this study: *A. carolinensis* (GAP area; day: N=50, night: N=93), *T. smaragdinus* (GAP area; day: N=54, night: N=30, GAA area; day: N=36, night: N=75), *D. p. polygonatum* (GAP area; day: N=20, night: N=4, GAA area; day: N=24, night: N=11), *P. marginatus* (GAP area; day: N=11, GAA area; day: N=4), *A. okinavensis* (GAP area; day: N=3) (Table 2). *Ateuchosaurus okinavensis* was not observed in the GAA areas, and neither *P. marginatus* nor *A. okinavensis* were observed at night.

During the daytime *A. carolinensis* utilized plants and artificial steel frames, which were remnants of old greenhouses. Eight plant species were identified as being used by the anoles, with *P. odorifer* having the highest frequency (Table 2). *Anolis carolinensis* predominantly used leaves (84.0%), followed by branches and veins (12.0%) (Fig. 2a). The recorded height above the ground for the anoles was 1.12±0.70 (mean±SD) m. *Takydromus smaragdinus* was the most frequently recorded native species, most often on *Bidens* sp. in daytime (Table 2). It was frequently observed on leaves (57.4%) and the ground (37.0%) in the GAP area (Fig. 2a), and the niche breadth of the substrate types was 1.386 (Table 3). The plant species (Table 2) and substrate types (Fig. 2a) used by *T. smaragdinus* at the GAP area were not significantly different from those used by conspecifics at the GAA area (Fisher's exact test; P=0.54), and the niche overlap score for substrate types between GAP *T. smaragdinus* and GAA *T. smaragdinus* was high (O_{ab}=0.980). The height above ground for *T. smaragdinus* in the GAP area (0.34±0.63 m) was not significantly different from that in the GAA area (0.26±0.34 m) (Tukey's HSD test; P>0.01, Fig. 3a). *Diploderma polygonatum polygonatum* was frequently observed on tree trunks at both the GAP and GAA areas (GAP area: 60.0%, GAA area: 64.0%, Fisher's exact test; P=0.17, Fig. 2a), and the niche overlap score obtained between the GAP and GAA areas was high (O_{ab}=0.931), with niche breadths of 2.138 and 2.258 in the GAP and GAA areas, respectively (Table 3). *Diploderma p. polygonatum* also used dead branches, herb stems, leaves at the GAA area, but not at the GAP area. No significant difference was observed in height above ground between the GAP area (1.22±1.10 m) and the GAA area in this species (0.79±0.62 m) (Tukey's HSD test; P>0.01, Fig. 3a). *Plestiodon marginatus* and *A. okinavensis* were only observed on the ground in both areas (Fig. 2a).

TABLE 2. Number of observed plant species and parts used by each lizard and skink species during daytime and nighttime. GAP: the green anole present site, GAA: combined data in three green anole absent sites, D: daytime, N: nighttime.

Family	Species	Plant type	*Anolis carolinensis*		*Takydromus smaragdinus*				*Diploderma polygonatum polygonatum*				*Plestiodon marginatus*		*Ateuchosaurus pellopleurus*
			GAP		GAP		GAA		GAP		GAA		GAP	GAA	GAP
			D	N	D	N	D	N	D	N	D	N	D	D	D
Pinaceae	*Pinus luchuensis*	Tree									3				
Chloranthaceae	*Sarcandra glabra*	Tree							1						
Lauraceae	*Machilus thunbergii*	Tree									1				
Pandanaceae	*Pandanus odorifer*	Tree	26	2	3	1	3	6							
Poaceae	*Pennisetum purpureum*	Herb	10	72	3			37		1		3			
Poaceae	*Oplismenus undulatifolius*	Herb			1										
Poaceae	*Miscanthus sinensis*	Herb				1		2							
Poaceae		Herb		1	2	1	4	4		1					
Typhaceae	*Typha latifolia*	Herb						3							
Urticaceae		Herb		1											
Celastraceae	*Gymnosporia diversifolia*	Tree					1								
Clusiaceae	*Calophyllum inophyllum*	Tree							4						
Fabaceae	*Acacia confusa*	Tree		2		1									
Fabaceae	*Canavalia lineata*	Vine			2										
Fabaceae	*Leucaena leucocephala*	Tree		1	1	5					2				
Fabaceae		Herb					1								
Moraceae	*Morus australis*	Tree		1		1		1	8	1	1	2			
Moraceae	*Ficus erecta*	Tree		1											
Euphorbiaceae	*Macaranga tanarius*	Tree					1								
Casuarinaceae	*Casuarina* sp.	Tree	2	3		12		5	3	1	1				
Caricaceae	*Carica papaya*	Tree	1								2				
Malvaceae	*Hibiscus tiliaceus*	Tree									1				
Elaeocarpaceae	*Elaeocarpus zollingeri*	Tree									4				
Vitaceae	*Ampelopsis glandulosa*	Vine	1												
Crassulaceae	*Kalanchoe pinnata*	Herb			1		1								
Nyctaginaceae	*Bougainvillea* sp.	Vine	1		1		1	3			1	2			
Sapotaceae	*Planchonella obovata*	Tree							1		1				
Pittosporaceae	*Pittosporum tobira*	Tree						2							
Goodeniaceae	*Scaevola taccada*	Tree	1												
Asteraceae	*Bidens* sp.	Herb	7	8	18	1	9	4			1	1			
Asteraceae	*Erigeron annuus*	Herb						1							
Gleicheniaceae	*Dicranopteris pedata*	Herb			2										
	Unknown herbs	Herb		1		7		5			1	2			
	Ground	—			20		9		3		3		11	4	3
	Dead branch	—					2				2				
	Dead leaf	—					4	2				1			
	Steel pipe	—	1												
Total			50	93	54	30	36	75	20	4	24	11	11	4	3

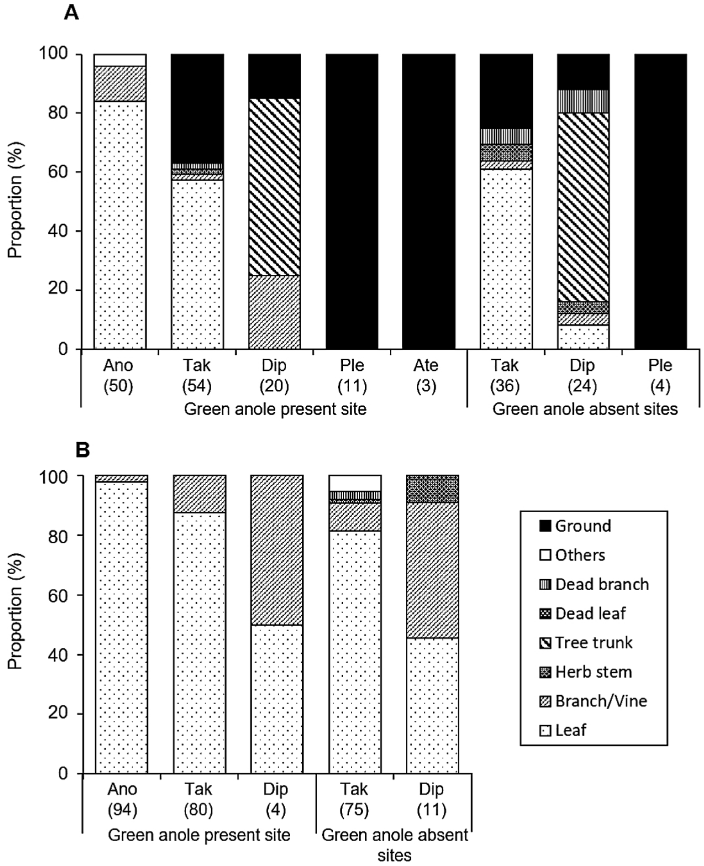

FIG. 2. Recorded substrate types of the lizards. A: daytime, B: nighttime. Ano: *Anolis carolinensis*, Tak: *Takydromus smaragdinus*, Dip: *Diploderma polygonatum polygonatum*, Ple: *Plestiodon marginatus*, At: *Ateuchosaurus pellopleurus*. Numbers in parentheses indicate sample size.

TABLE 3. Niche width of microhabitat in each species at day and night.

	Green Anole Presence Site		Green Anole Absenct Site	
	Day	Night	Day	Night
Anolis carolinensis	1.386	1.043	—	—
Takydromus smaragdinus	2.138	1.280	2.258	1.484
Diploderma polygonatum polygonatum	2.247	2.000	2.361	2.373
Plestiodon marginatus	1.000	—	1.000	—
Ateuchosaurus pellopleurus	1.000	—	—	—

The niche overlap score between *A. carolinensis* and *T. smaragdinus* was the highest for GAP area (O_{ab}=0.834, Table 4), but the frequency of use for substrate types between these two species was significantly different (Fisher's exact test; P<0.01). The observed height of *A. carolinensis* was significantly higher than that of *T. smaragdinus* (Tukey's

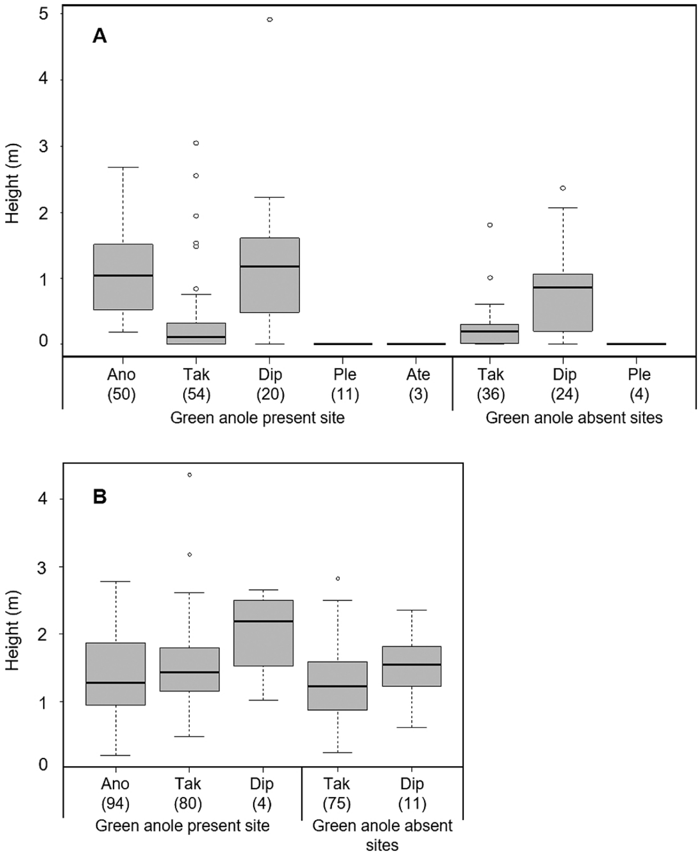

FIG. 3. Perch height above the ground for the five lizard species studied. A: daytime, B: nighttime. Ano: *Anolis carolinensis*, Tak: *Takydromus smaragdinus*, Dip: *Diploderma polygonatum polygonatum*, Ple: *Plestiodon marginatus*, At: *Ateuchosaurus pellopleurus*. Numbers in parentheses indicate sample size.

HSD test; P<0.01), whereas it was not significantly different from that of *D. p. polygonatum* (Tukey's HSD test; P=0.99) (Fig. 3a). Niche overlap scores between *A. carolinensis* and *T. smaragdinus* or *D. p. polygonatum* in GAP (Table 4) were smaller than those in GAA (Table 5).

Resting places at nighttime

Plestiodon marginatus and *A. okinavensis* were not found at night. All lizards found at night did not move when approached. *Anolis carolinensis* was most frequently found on *P. purpureum* (Table 2), and 97.9% of resting substrate types was on leaves (Fig. 2b). The niche breadth of the anole was 1.043. The mean resting height above ground for *A. carolinensis* was 1.38±0.58 m, which was not significantly different from that of *T. smaragdinus* (1.53±0.58 m) and *D. p. polygonatum* (2.01±0.71 m) in the GAP area (Tukey's HSD test; P>0.01, Fig. 3b). *Takydromus smaragdinus* was frequently observed on *P. purpureum* at the GAA area (49.3%), whereas it was frequently observed on *Casuarina* spp. (40.0%) instead of *P. purpureum* (0%) at the GAP area (Table 2). The most common resting substrate types of *T. smaragdinus* were leaves at both sites (GAP area: 87.5%, GAA area: 81.3%, Fig. 2b), and the niche breadths were 1.280 and 1.484 in the GAP and GAA areas, respectively (Table 3). The resting substrate types of

TABLE 4. Niche overlap score of microhabitat in daytime (upper diagonal) and nighttime (lower diagonal) in the green anole present (GAP) area. NA indicates not able to compare due to one or both species were not observed.

Daytime Nightime	*Anolis carolinensis*	*Takydromus smaragdinus*	*Diploderma polygonatum polygonatum*	*Plestiodon marginatus*	*Ateuchosaurus pellopleurus*
Anolis carolinensis		0.834	0.053	0.000	0.000
Takydromus smaragdinus	0.993		0.132	0.542	0.542
Diploderma polygonatum polygonatum	0.722	0.781		0.225	0.225
Plestiodon marginatus	NA	NA	NA		1.000
Ateuchosaurus pellopleurus	NA	NA	NA	NA	

TABLE 5. Niche overlap score of microhabitat in daytime (upper diagonal) and nighttime (lower diagonal) in the green anole absent (GAA) area. NA indicates not able to compare due to one or both species were not observed.

Daytime Nightime	*Anolis carolinensis*	*Takydromus smaragdinus*	*Diploderma polygonatum polygonatum*	*Plestiodon marginatus*
Anolis carolinensis		NA	NA	NA
Takydromus smaragdinus	NA		0.208	0.376
Diploderma polygonatum polygonatum	NA	0.776		0.192
Plestiodon marginatus	NA	NA	NA	

T. smaragdinus did not differ significantly between the GAP and GAA areas (Fisher's exact test; P=0.06), with the niche overlap score of substrate types between those areas was 0.997. The mean resting height above ground for *T. smaragdinus* did not differ between the GAP and GAA areas (1.26±0.53 m) (Tukey's HSD test; P>0.01, Fig. 3b). The most common resting substrate types of *D. p. polygonatum* were branches and veins at both the GAP and GAA areas (Fig. 2b) and the niche breadths were 2.000 and 2.373 at the GAP and GAA areas, respectively (Table 3). The resting substrate types of *D. p. polygonatum* did not differ significantly between the GAP and GAA areas (Fisher's exact test; P=1.00), with the niche overlap score of substrate types between those areas was 0.990. The mean resting height above ground for *D. p. polygonatum* did not differ between the GAP and GAA areas (1.50±0.55 m) (Tukey's HSD test; P>0.01, Fig. 3b).

The niche overlap scores in the GAP area obtained for *A. carolinensis* and *T. smaragdinus* (O_{ab}=0.993) were high compared with that for *A. carolinensis* and *D. p. polygonatum* (O_{ab}=0.722, Table 4), but the frequency of substrate type differ significantly among the three species (Fisher's exact test; P<0.01). Unlike during the daytime, the nighttime niche overlap of the invasive anole and these two native lizards at the GAP area (Table 4) did not differ from that at the GAA area (Table 5). The frequency of use of particular plant species was different among these three species within the GAP area, and also differed across GAP and GAA areas for the native species (Table 2). The resting heights above the ground did not differ significantly among all the observed lizards (Tukey's HSD test; P>0.01, Fig. 3b).

TABLE 6. SVLs based on The Herpetological Society of Japan (2021) and habitat types of lizard species.

Family	Species	SVL (mm)	Habitat type
Anolidae	*Anolis carolinensis*	42–73	Tree
Lacertidae	*Takydromus smaragdinus*	50–72	Herb
Agamidae	*Diploderma polygonatum polygonatum*	51–80	Tree
Scincidae	*Plestiodon marginatus*	60–90	Ground
Scincidae	*Ateuchosaurus pellopleurus*	42–70	Ground

DISCUSSION

Microhabitats use by the lizards during daytime

Habitat selection by a species is determined by its own ecology and by interactions with other species, such as inter-specific competition and resource partitioning (Krebs, 2001). A previous study confirmed that the snout-vent lengths of native *T. smaragdinus*, *D. p. polygonatum*, and *P. marginatus* were similar (Table 6). Although detailed food habits have not been identified, these lizards all primarily consume invertebrates such as insects (The Herpetological Society of Japan, 2021). In the present study, the utilized plant species, parts, and perch heights above ground of native lizards differed in the GAA area (see Table 5). This suggests that these native lizards primarily utilize different microhabitats, allowing them to coexist on the small island, although detailed comparisons of food habits are required.

Anolis carolinensis prefers relatively light and open areas, with its habitat being the trunk-crown (Jenssen et al., 1995). In the present study, this species was frequently observed in places where sunlight penetrated, such as the leaves and branches. This suggests that the introduced green anole utilizes habitats similar to its original habitats in the native region. A possible reason for this is that the anoles are likely to use habitats that native lizards do not fully occupy or as a result of competition with native lizards.

Important factors for coexistence in lizards are segregations in temporal, spatial, trophic, and thermal resources (Pianka, 1986; Watson and Gough, 2012). When segregations in these resources are not enough, alien species may drive away native species (Downes and Bauwens, 2002; Damas-Moreira et al., 2020). In the present study, the plant species used by *A. carolinensis* differed from those frequently used by native lizards, but the niche overlap score of substrate types between *A. carolinensis* and *T. smaragdinus* was relatively high and the scores were near to 1. In addition, the perch height above the ground of *A. carolinensis* was similar to that of *D. p. polygonatum*. These results suggest that parts of the green anole microhabitat overlap with those of the native species. Furthermore, the niche overlap scores between the anole and native lizards (*T. smaragdinus* and *D. p. polygonatum*) at the GAP area were lower than those at the GAA rea. These results suggest that *A. carolinensis* has provided negative effects on these native lizards on Zamami-jima Island through competition. Although the results of Fisher's exact test indicated that there are some differences in substrate types between the invasive anole and the native lizards, it is difficult to evaluate at the moment whether the differences are large enough to allow these species to coexist. Anzai et al. (2017) and Mitani et al. (2020) demonstrated that patterns of microhabitat usage in *A. carolinensis* varied between males and females, and between juveniles and adults in the Ogasawara Islands. Therefore, further studies are required to more precisely evaluate the extent of inter-specific competitions between *A. carolinensis* and native lizards in particular age classes and or different sexes.

Resting place selection

The mean resting height above the ground of

A. carolinensis, *T. smaragdinus*, and *D. p. polygonatum* did not differ between the GAP and GAA areas. With respect to the substrate types of the resting places, the niche overlap pattern between *A. carolinensis* and *T. smaragdinus* differ between the GAP and GAA areas. *Takydromus smaragdinus* seldom utilized the leaves of *P. purpureum* as a resting place in the GAP area, whereas it commonly used that species at the GAA areas (Table 2). This suggests that *A. carolinensis* and *T. smaragdinus* may compete for resting places.

The selection of resting places is crucial for avoiding predation and accessing the habitat utilized during the daytime, as well as for providing benefits for social behaviors (Christian et al., 1984; Clark and Gillingham, 1990; Lima et al., 2005; Singhal et al., 2007). Although studies on the resting places of lizards are limited, several authors have focused on *Anolis* lizards. For instance, three *Anolis* species (*A. lineatopus*, *A. grahami*, and *A. valencienni*) that inhabit different daytime habitats, also exhibit differences in their resting perch characteristics and height above the ground at night (Singhal et al., 2007). Combined together, the putative shift in plant species used as resting sites in GAP *T. smaragdinus* may reduce the accessibility of preferable daytime habitat, increase the predation pressure, and change their social behaviors. Nonetheless, the leaves of *P. purpureum*, the most frequent resting place of *A. carolinensis*, are abundant at the GAP area and appear to be still available for *T. smaragdinus*. Thus, exact cause of the putative effects of *A. carolinensis* on the substrate plant for resting in *T. smaragdinus* should be carefully examined in the future studies.

Although previous studies (e.g., Lima et al., 2005; Singhal et al., 2007; Asato et al., 2021) have primarily focused on resource utilization by native lizards with no comparisons with alien species, the present study suggests resting place competition and displacement between *A. carolinensis* and one species of native lizard. Given the limited research on resting place selection and competition, further studies examining potential changes of predation pressure and social behaviors are needed to understand potential negative effects of *A. carolinensis* on *T. smaragdinus* and *D. p. polygonatum*.

Concerns for the future

Anolis carolinensis was introduced to Zamami-jima Island approximately 10 years ago, in 2013. A control program for this species has been ongoing since its initial establishment (Ministry of the Environment, Government of Japan, 2023; Okinawa Prefectural Government, 2023). These efforts seem helpful in preventing population expansion of the anole, although they may not be sufficient to eradicate it. The intensity of interspecific competition is inversely proportional to the amount of resources allocated between species (Pacala and Roughgarden, 1982). Microhabitat overlap between the green anole and native lizards was observed in this study, and the direct and indirect effects on the native species might increase if the anole expands its range or if the population density rises. Controlling green anoles requires significant effort (Toda et al., 2009; Toda, 2022), but further efforts to monitor and eradicate *A. carolinensis*, as well as to monitor impacts on native species, are necessary.

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Literature Cited

Abe, T., Makino, S. I., and Okochi, I. 2008. Why have endemic pollinators declined on the Ogasawara Islands? *Biodiversity and Conservation* 17: 1465–1473.

Anzai, K., Takahashi, H., Toda, M., and Endo, H. 2017. Difference in the green anole microhabitat usage between the islands and between sexes on Chichijima Is. and Hahajima Is. *Ogasawara Kenkyu Nenpo* 40: 45–52.

Asato, H., Tatetsu, M., Kamizato, H., Tokumine, K., Tokumine, M., Kamiji, S., Ikawa, K., Ishikawa, S., Gima, T., Gonda, M., Saiki, M., and Toda, M. 2021. Sleeping-site selection in the Miyako glass lizard, *Takydromus toyamai*. *AKAMATA* 30: 29–33.

Case, T. J., Bolger, D. T., and Petren, K. 1984. Invasions and competitive displacement among house geckos in the Tropical Pacific. *Ecology* 752: 464–478.

Chigira, Y. 1991. Introduced amphibian and reptiles in Okinawa Island. p. 43–53. *In*: S. Ikehara (ed.), *Influences upon the Wildlife by Introduced Animals in the Nansei Shoto*. WWF Japan Comittee, Tokyo.

Christian, K. A., Tracy, C. R., and Porter, W. P. 1984. Physiological and ecological consequences of sleeping-site selection by the Galapagos land iguana (*Conolopus pallidus*). *Ecology* 65: 752–758.

Clark, D. L. and Gillingham, J. C. 1990. Sleep-site fidelity in two Puerto Rican lizard. *Animal Behaviour* 39: 1138–1148.

Damas-Moreira, I., Riley, J. L., Carretero, M. A., Harris, D. J., and Whiting, M. J. 2020. Getting ahead: exploitative competition by an invasive lizard. *Behavioral Ecology and Sociobiology* 74: 117.

Downes, S. and Bauwens, D. 2002. An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. *Animal Behaviour* 63: 1037–1046.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80: 238–251.

Huxel, G. R. 1999. Rapid displacement of native species by invasive species: effects of hybridization. *Biological Conservation* 89: 143–152.

Ishikawa, T., Abe, S., Hayasegawa, N., Takayanagi, K., Imamura, M., Nishihira, A., and Toume, M. 2011. Distribution of nonnative green anole *Anolis carolinensis* on Okinawajima Island, southern Japan. *The Biological Magazine Okinawa* 49: 9–13.

Iwao, K. 2015. Immigrants of Kerama Islands. *Midoriishi: report of Akajima Marine Science Laboratory* 26: 24–34.

Jenssen, T. A., Greenberg, N., and Hovde, K. A. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs* 9: 41–62.

Karube, H. 2005. The influence of the introduced lizard, *Anolis carolinensis* on the native insect fauna of the Ogasawara Islands. *Bulletin of the Herpetological Society of Japan* 2005: 163–168.

Krebs, C. J. 2001. *Ecology: The Experimental Analysis of Distribution and Abundance. 5th Edition*. Benjamin Cummings, San Francisco.

Kupferberg, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. *Ecology* 78: 1736–1751.

Lima, S. L., Rattenborg, N. C., Lesku, J. A., and Amlaner, C. J. 2005. Sleeping under the risk of predation. *Animal Behaviour* 70: 723–736.

Maenosono, T. and Toda, M. 2007. Distributions of amphibians and terrestrial reptiles in the Ryukyu Archipelago: A review of published records. *AKAMATA* 18: 28–46.

Makihara, H., Kitajima, H., Goto, H., Kato, T., and Makino, S. 2004. An evaluation of predation impact of the introduced lizard *Anolis carolinensis* on the endemic insect fauna of the Ogasawara Islands based on insect collection records and feeding experiments, with special reference to longicorn beetles (Insecta: Coleoptera: Cerambycidae). *Bulletin of Forestry and Forest Products Research Institute* 3: 165–183.

Ministry of the Environment, Government of Japan. 2023. *Alien Species Control Project within the Jurisdiction*. https://kyushu.env.go.jp/okinawa/wildlife/gairai.html (accessed 13 July 2024)

Mitani, N., Kishimoto, T., Sugo, N., Odaohara, F., and Ito, Y. 2020. Tree species preference of the green anole (*Anolis carolinensis*) and perch selection. *Current Herpetology* 39: 137–146.

Nature Conservation Division, Department of Environmental Affairs, Okinawa Prefectural Government (NCDDEAO). 2024. Anolis carolinensis—*Okinawa Prefecture Invasive Species Information Network*. https://okinawa-gairaisyu.com/zukan/green-anole/ (accessed 13 July 2024)

Norval, G., Mao, J.-J., and Goldberg, S. R. 2012. A record of a green anole (*Anolis carolinensis* Voigt 1832), from the wild in southwestern Taiwan. *Herpetology Notes* 5: 95–97.

Okinawa Prefectural Government. 2023. *Reports on Control of Invasive Species (Reptiles and Amphibians) in 2022*. https://www.pref.okinawa.lg.jp/kurashikankyo/shizenseibutsu/1018702/1004814/1004816/1004826.html (accessed 13 July 2024)

Ota, H. 2002. *Anolis carolinensis*. p. 99. *In*: M. Murakami and I. Washitani (eds.), *Handbook of Alien Species in Japan*. Chijinshokan, Tokyo.

Ota, H. and Hamaguchi, T. 2003. *Series of Natural Monument in Okinawa No. 41. Survey Report of the Actual Situation of* Geoemyda japonica *and* Cuora flavomarginata evelynae. Okinawa Prefectural Board of Education, Naha.

Pacala, S. and Roughgarden, J. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science* 217: 444–446.

Petren, K. and Case, T. J. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77: 118–132.

Pianka, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53–77.

Pianka, E. R. 1986. *Ecology and Natural History of Desert Lizards*. Princeton University Press, Princeton.

Pintor, L. M., Sih, A., and Kerby, J. L. 2009. Behavioral correlations provide a mechanism for explaining high invader densities and increased impacts on native prey. *Ecology* 90: 581–587.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rodda, G. H. and Fritts, T. H. 1992. The impact of the introduction of the brown tree snake, *Boiga irregularis*, on Guam's lizards. *Journal of Herpetology* 26: 166–174.

Rodda, G. H., Fritts, T. H., and Campbell III, E. W. 1999. The feasibility of controlling the brown treesnake in small plots. p. 468–477. *In*: G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka (eds.), *Problem Snake Management: The Habu and the Brown Treesnake*. Cornell University Press, New York.

Rogers, H., Buhle, E., Hillerislambers, J., Fricke, E. C., Miller, R. H., and Tewksbury, J. J. 2017. Effects of an invasive predator cascade to plants via mutualism disruption. *Nature Communications* 8: 14557.

Rushton, S. P., Lurz, P. W. W., Gurnell, J., Nettleton, P., Brumemmer, C., Shirley, M. D. F., and Sainsbury, A. W. 2006. Disease threats posed by alien species the role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiology and Infection* 134: 521–533.

Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68: 660–668.

Singhal, S., Johnson, M. A., and Ladner, J. T. 2007. The behavioral ecology of sleep: Natural sleeping site choice in three *Anolis* lizard species. *Behaviour* 144: 1033–1052.

Spatz, D. R., Zilliacus, K. M., Holmes, N. D., Butchart, S. H. M., Genovesi, P., Ceballos, G., Tershy, B. R., and Croll, D. A. 2017. Globally threatened vertebrates on islands with invasive species. *Science Advances* 3: e1603080.

Suzuki, A. and Nagoshi, M. 1999. Habitat utilization of the native lizard, *Cryptoblepharus boutonii nigropunctatus*, in areas with and without the introduced lizard, *Anolis carolinensis*, on Haha-jima, the Ogasawara Islands, Japan. p. 155–168. *In*: H. Ota (ed.), *Tropical Island Herpetofauna*. Elsevier Science, Amsterdam.

Suzuki-Ohno, Y., Morita, K., Bagata, N., Mori, H., Abe, S., Makino, T., and Kawata, M. 2017. Factors restricting the range expansion of the invasive green anole *Anolis carolinensis* on Okinawa Island, Japan. *Ecology and Evolution* 7: 4357–4366.

Takahashi, H., Yamaki, A., Akita, K., Kishimoto, T., and Toda, M. 2014. Feeding habits of the green anole in the Ogasawara Islands and its impact on the native insect community. *Bulletin of the Herpetological Society of Japan* 2014: 158–167.

The Herpetological Society of Japan. 2021. *Amphibians and Reptiles of Japan*. Sunrise Publishing, Hikone.

Toda, M. 2022. Problems and countermeasures of green anole in Ogasawara Islands, Japan. *Insects and Nature* 57: 15–19.

Toda, M., Nakagawa, N., and Sukigara, N. 2009. Ecology and control of green anole *Anolis carolinensis*, invasive alien species in the Ogasawara Islands. *Chikyu Kankyo* 14: 39–49.

Watson, M. and Gough, L. 2012. The role of temperature in determining distributions and coexistence of three species of *Plestiodon*. *Journal of Thermal Biology* 37: 374–379.

Wiles, G. J., Bart, J., Beck, R. E., Jr., and Aguon, C. F. 2003. Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. *Conservation Biology* 17: 1350–1360.

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