

SLEEPING SITES OF GREEN ANOLES: THE CASE OF AN INTRODUCED POPULATION IN THE OGASAWARA ISLANDS, JAPAN

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Abstract.—Non-native predators sometimes trigger a dramatic decline in native prey species. In Japan, the introduced Green Anole (*Anolis carolinensis*) has caused catastrophic damage to endemic insect fauna on the Ogasawara Islands. The management plan attempts to catch the invasive Green Anoles and prevent their dispersion while focusing on their active daytime. These approaches, however, have not effectively reduced the established population. Understanding the natural history of Green Anoles during nighttime may be useful for their management, although basic natural histories at night are still lacking. We conducted a field survey to investigate the sleep ecology of Green Anoles. Through nighttime censuses at 11 field sites, we found that juveniles tended to sleep on lower grass (mean = 103 cm) than adults, which use higher perches for their sleeping sites (mean = 256.2 cm in males, and 261.7 cm in females). Moreover, juveniles and adults sleep on distinct plant species at night, suggesting an ontogenetic niche shift in terms of nighttime microhabitat use. Specifically, in anthropogenically modified environments, adult Green Anoles were clumped on two specific palm tree species. These findings could provide information needed to control the invasive Green Anole population.

Key Words.—*Anolis carolinensis*; invasive animal control; ontogenetic niche shift; perch height; sleep ecology.

INTRODUCTION

Invasive species can dramatically disrupt the balance of native ecosystems in various ways. Specifically, non-native predator animals can cause catastrophic damage to prey species that have evolved without these threats (Lockwood et al. 2013). Invasive reptilian predators are a particular concern on oceanic islands. For example, the introduction of the Brown Tree Snake (*Boiga irregularis*) caused the extinction of endemic bird species on the island of Guam, and similar risks are present in other Pacific islands (Rodda and Savidge 2007; Wiles et al. 2003). Another case of problematic invasive predators involves the introduction of the Green Anole (*Anolis carolinensis*) to the Ogasawara Islands in Japan (Toda et al. 2010). Since the introduction of Green Anoles to Chichi-jima in the 1960s, its population has dramatically increased and spread to neighboring islands. The original native ecosystem of these islands lacks arboreal insectivore lizards; therefore, the introduced Green Anoles occupy this niche and have significantly impacted the local insect fauna that is composed mainly of endemic species (Abe et al. 2008; Karube 2010). In addition, competition

between the invasive Green Anole and a native Ogasawara Skink (*Cryptoblepharus nigropunctatus*) is also of concern (Hasegawa et al. 1988).

To control invasive Green Anoles in the Ogasawara Islands since the 2000s, the management plan involves setting glue traps and installing barricade fences (Toda et al. 2010). These actions appear to slow the spread of Green Anoles in the targeted areas; however, flourishing populations are already out of control. For instance, in the focal area, the number of captures by traps ranges from 10 to 40K Green Anoles per year, compared to an estimated population size of 6.3 million individuals (Toda et al. 2010, see also the Policy for dealing with invasive alien species. 2023. Green Anole Control Plan for Ecosystem Conservation in the Ogasawara Islands (in Japanese). Ogasawara Islands World Natural Heritage Site Scientific Committee. Available from <https://ogasawara-info.jp/databank/guideline/> [Accessed 19 May 2025]). Because the Green Anole is a diurnal lizard, the ongoing management actions mainly aim to capture them and/or prevent their migration during active daytime. Nevertheless, their basic natural histories during the nighttime remain unclear (but see Kobayashi et al. 2025; Taylor et al. 2022), which may

be useful for developing new management strategies for the invasive Green Anoles.

Many diurnal species of arboreal lizard rest on leaves or branches at night (Mohanty et al. 2022). Studies on the sleep ecology of diurnal anoles have provided some insights into the microhabitat characteristics of their sleeping sites. For instance, Singhal et al. (2007) discovered that three anole species, the Stripefoot Anole (*A. lineatopus*), Graham's Anole (*A. grahami*), and Jamaican Twig Anole (*A. valencienni*), perch on higher and smaller twigs at night compared to their daytime habitats. Clark and Gillingham (1990) reported that two Puerto Rican anoles, the Gundlach's Anole (*A. gundlachi*) and the Puerto Rican Crested Anole (*A. cristatellus*), are found on large, simple-shaped leaves at night. Barnett (2023) noted inter- and intra-specific variation in perch height among four *Anolis* species on Caribbean islands. Regarding the sleep ecology of the Green Anole, Kobayashi et al. (2025) reported that 77.4 % ($n = 93$) slept on the leaves of Napiergrass (*Pennisetum purpureum*) at night, with the niche overlapping significantly with several native lizard species on Zamami-jima, Japan. These findings suggest consistent patterns in the sleep ecology of diurnal anoles, while also highlighting species-specific characteristics for sleeping sites (Mohanty et al. 2022; Shew et al. 2002). To leverage these insights for the management of the invasive Green Anoles, it is crucial to explore their nighttime microhabitat use in the Ogasawara populations.

We investigated the sleep ecology of invasive Green Anoles in the Ogasawara Islands, Japan. We made field surveys at night on Chichi-jima and Haha-jima in the summer breeding season. We collected data on the perch height and plant species where Green Anoles were observed and individual characteristics including sex, life stages, and body condition. Then we analyzed the sleeping site patterns with consideration of their sex (male vs female), life stages (juvenile vs adult), and local vegetation (artificially modified environment versus relatively natural vegetation). Based on prior knowledge about the sleep ecology of diurnal anoles (Barnett 2023; Clark and Gillingham 1990; Shew et al. 2002; Singhal et al. 2007), we anticipated that Green Anoles also would exhibit distinct spatial ecological characteristics between daytime and nighttime. Additionally, we discuss the implications of their sleep ecology for management strategies, particularly how these characteristics can be used for efficient population control.

MATERIALS AND METHODS

Field survey.—The Ogasawara Islands are located approximately 1,000 km south of mainland Japan. These islands feature vegetation commonly found in subtropical Asian regions, with a fauna rich in endemic species (Shimizu 2003). The vegetation of the Chichi-jima and Haha-jima is characterized by dry shrubland and subtropical rain forest, respectively (Shimizu 2003). We used 11 trails for the nighttime route census of Green Anoles, representing the typical vegetation of the focal area (Chichi-jima: seven sites, Haha-jima: four sites, Supplemental Information Fig. S1). The survey sites included natural forest areas with abundant native plant species and anthropogenically modified areas near farmlands and residential zones. The dominant plant species varied slightly between the survey sites (Supplemental Information Table S1).

Nighttime surveys (1930–2300) took place during the peak breeding season for Green Anoles, from 20 July to 9 August 2024. A single observer (KI) conducted the route census approximately one hour after sunset. The total survey effort covered 4.63 km in 10.45 h (Supplemental Information Table S1). The observer walked at a constant speed (10 m/min), thoroughly checking the vegetation on both sides of the route. The observer could recognize Green Anoles up to 8 m in the vegetation. The vegetation canopies were 10–20 m tall, depending on the survey site, so we did not survey the entire canopy. Upon spotting a Green Anole, the observer took a photograph and attempted to capture the lizard. We captured Green Anoles on low perches (< 2 m above ground) by hand, while those on high perches (> 2 m above ground) were captured using a net attached to an extendable rod. For each encounter, we measured the perch height using a pole with an accuracy scale of 10 cm. Additionally, we identified the plant species where we found Green Anoles.

We promptly transported the captured Green Anoles to the field station and euthanized the subjects using a cooling-then-freezing method. We temporarily stored the specimens in a freezer. Thereafter, we measured their snout-vent length (SVL) using a caliper and weighed their body weight using a digital balance. We categorized the specimens into two life stages (juvenile or adult) based on the size structure of the focal population in this season (Supplemental Information Fig. S2). We further classified adult Green Anoles into male or female based on morphological characteristics, such as the presence of enlarged

postnatal scales (Lovern et al. 2004). We calculated the body condition index (BCI), which is defined as the residual of a Linear Regression model for SVL against body weight (Jakob et al. 1996). There were significant BCI regressions for males ($F_{1-56} = 82.1$, $P < 0.001$, $r^2 = 0.587$; $n = 58$), females ($F_{1-64} = 20.4$, $P < 0.001$, $r^2 = 0.230$; $n = 66$), and juveniles ($F_{1-86} = 326.7$, $P < 0.001$, $r^2 = 0.789$; $n = 88$).

Data analysis.—First, we analyzed intra-specific variation in microhabitat use at night. Considering that some anole species exhibit inter-sexual separation and ontogenetic shifts in their sleeping sites (Barnett 2023), we compared perch heights among male, female, and juvenile. The data distributions deviated from the assumption of normality (Shapiro-Wilk test: Male, $W = 0.96$, $P = 0.041$; Female, $W = 0.91$, $P < 0.001$; Juvenile, $W = 0.82$, $P < 0.001$). Juvenile data were still non-normal even after log transformation, so we applied the non-parametric Wilcoxon Rank Sum Test to the dataset and adjusted statistical significance in pairwise comparisons between groups by the Bonferroni method (Bland and Altman 1995). Regarding the perch height data, we performed a further analysis focusing on four specific plant species on which both life stages were spotted. We used a Linear Mixed-effects Model (LMM) for the dataset of Giant Reed (*Arundo donax*), River Tamarind (*Leucaena leucocephala*), Chinese Silvergrass (*Miscanthus sinensis*), and Golden Cane Palm (*Chrysalidocarpus lutescens*). The model included life stage, perch type (one of the four plant species), and these interactions as fixed factors, as well as survey site as a random factor.

Second, we assessed the niche overlaps of plant species used by males, females, and juveniles. We employed Pianka's Niche Overlap Index among the groups (Pianka 1973) using the formula:

$$O_{jk} = \sum p_{ij} p_{ik} / (\sum p_{ij}^2 \sum p_{ik}^2)^{1/2}$$

where p_{ij} and p_{ik} represent the proportion of a specific plant species (i) used by the categories j and k, respectively. The overlap index (O_{jk}) ranges from 0 to 1, with higher score indicating greater consistency in the plant species used by both categories. For example, if males and females are assigned to the two categories (j and k), the index reflects inter-sexual niche overlap (or separation). Although arbitrary, an overlap score of 0.85, for instance, is generally accepted as indicating that males and females occupy similar niches for their sleeping sites at night, with 85% overlap in the composition of plant species.

Third, we analyzed whether any metrics of body size could predict perch height at night. In the daytime, larger male anoles, particularly dominant individuals, likely use higher perches and demonstrate display behaviors to neighbors during the breeding season (Jenssen and Nuez 1998; Ramírez-Bautista and Benabib 2001; Schoener and Schoener 1982; Yabuta and Suzuki-Watanabe 2011). Previous studies suggested that, in several anole species, spatial niches occupied during the day could reflect those at night (Mohanty et al. 2022; Singhal et al. 2007). We hypothesized that sex, body condition, and life stage affect the height at which lizards perch in the canopy. We predicted that larger-sized males with good body condition occupy higher perches at night than females and juveniles. To test this prediction, we used Spearman's Rank Correlation Test to check putative links between perch height at night and snout-to-vent length (SVL), body weight, and body condition index (BCI). We conducted all statistical analyses using R software version 4.3.0 (R Core Team 2023). Significance was set at $\alpha = 0.05$.

RESULTS

We observed 227 Green Anoles during our censuses and successfully captured 212 lizards, resulting in a capture rate of 93.4%. We found that all Green Anoles perched on leaves with their eyes closed, exhibiting a straight body posture and limbs folded along their sides (Supplemental Information Fig. S1). In five cases, multiple adult Green Anoles used the same tree and slept close to each other (Case 1: two males, two females, and one unknown sex; Case 2: three males and one female; Case 3: two males and two females; Case 4: two females; Case 5: two males). Green Anoles did not react to the presence of observer or the use of flashlights. Additionally, they showed delayed responses to tactile stimulations during capture attempts, such as being poked or grasped by hand. Based on these observations and situations, we inferred that the subjects were asleep on the leaves at night even without conducting physiological or neurological assessments.

The perch height did not significantly differ between males (Mean \pm standard deviation = 256.2 ± 112.2 cm, $n = 58$) and females (261.7 ± 123.5 cm, $n = 66$; $W = 1,929$, $P = 0.941$). In contrast, juveniles used significantly lower perches (103.0 ± 66.6 cm, $n = 93$) than those used by adults (male/juvenile: $W = 4,593$, $P < 0.001$; female/juvenile: $W = 5,323$, $P < 0.001$; Fig. 1). For the four plant species on

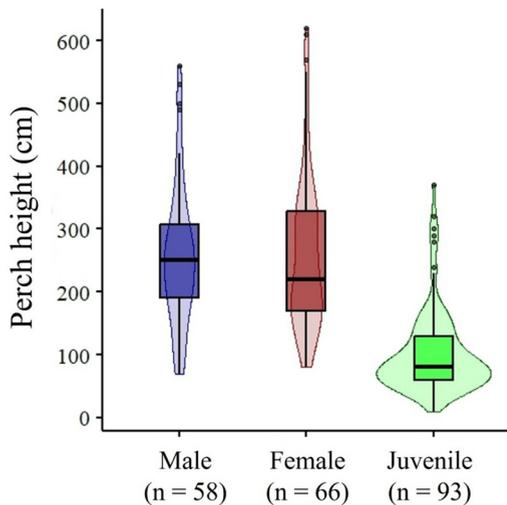


FIGURE 1. Comparison of perch height at night between male, female, and juvenile Green Anole (*Anolis carolinensis*) on the Ogasawara Islands, Japan. Box plot represents median (horizontal line), 1st–3rd quintiles (box), and outlier scores (dots). Violin plot represents 95% of the Kernell density of the data distributions.

which both juveniles and adults were found, there was a significant interaction between life stage and perch type (Supplemental Information Table S2). Specifically, the interaction was that there were large differences in perch height between juveniles

and adults when lizards were on River Tamarind (Estimate = -186.4, $t = -3.17$, $df = 87.7$, $P = 0.002$; Supplemental Information Fig. S3).

We found the majority (90%) of Green Anoles at night on 12 plant species, while the remaining 10% of observations were on 13 minor plant species. Males and females showed similar patterns in the variety of plant species used, with a niche overlap of 0.758. Specifically, adult Green Anoles predominantly used Formosa Palm (*Arenga ryukyuensis*) and Golden Cane Palm (Fig. 2). In contrast, juveniles used different plant species compared to those of adults, with low scores of the niche overlap (juvenile/males: 0.357; juvenile/females: 0.424). Generally, juveniles slept in lower vegetation such as Bracken Fern (*Pteridium aquilinum*), River Tamarind, and Chinese Silvergrass (Fig. 2). A comparison between two contrasting environments revealed that the plant species used by Green Anoles depended highly on local vegetation. In human-modified areas, 67% of adult Green Anoles were found on the two palm species. Conversely, in natural vegetation area, adult Green Anoles mostly used four plant species, showing no biased distribution (Fig. 3).

Males exhibited no significant correlation between perch height and SVL, body weight, or body condition

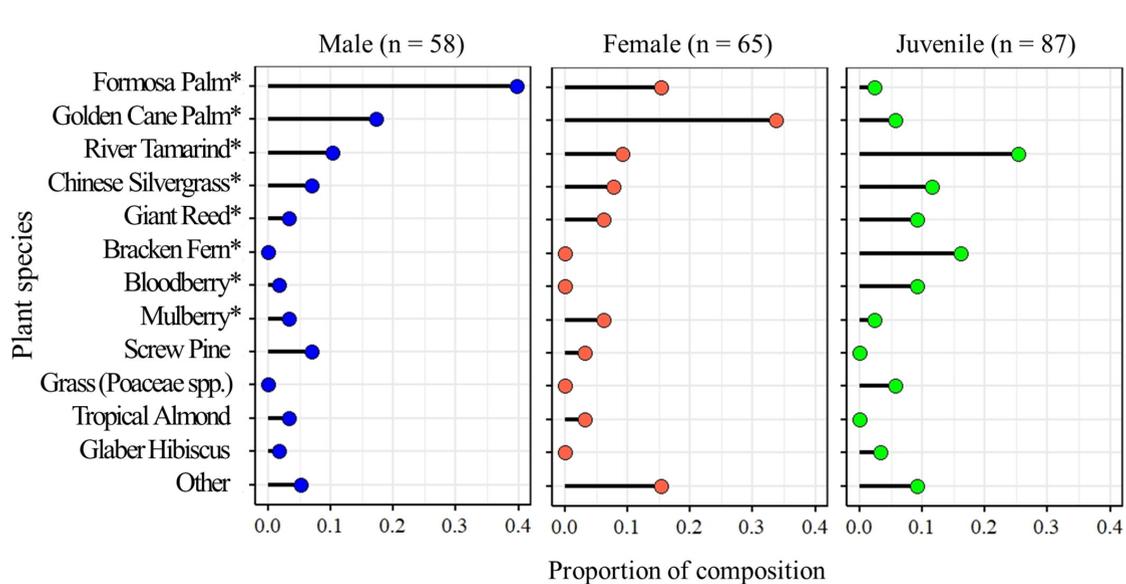


FIGURE 2. Variety of plant species used at night by Green Anole (*Anolis carolinensis*) on the Ogasawara Islands, Japan. Horizontal bars show the top 12 plant species that occupied 90% of all captured data including Formosa Palm (*Arenga ryukyuensis*)*, Golden Cane Palm (*Chrysalidocarpus lutescens*)*, River Tamarind (*Leucaena leucocephala*)*, Chinese Silvergrass (*Miscanthus sinensis*)*, Giant Reed (*Arundo donax*)*, Bracken Fern (*Pteridium aquilinum*)*, Bloodberry (*Rivina humilis*)*, Mulberry (*Morus australis*)*, Screw Pine (*Pandanus boninensis*), Grass (*Poaceae* spp.)*, Tropical Almond (*Terminalia catappa*), and Glaber Hibiscus (*Hibiscus glaber*). An asterisk (*) after scientific name represents non-native plant species on the Ogasawara Islands. The minor 13 plant species are grouped into Other category including Bishop Wood (*Bischofia javanica*)*, Shell Ginger (*Alpinia zerumbet*)*, Schima (*Schima wallichii*), Japanese Blood Grass (*Imperata cylindrica*), Fishtail Palm (*Caryota mitis*)*, Harlequin Glorybower (*Clerodendrum trichotomum*)*, Mango (*Mangifera indica*)*, Coastal She-Oak (*Casuarina equisetifolia*)*, Siebold ardisia (*Ardisia sieboldii*), Passion Fruit (*Passiflora edulis*)*, Sedge (*Cyperaceae* spp.), Japanese Cheesewood (*Pittosporum boninense*), and Asiatic Dayflower (*Commelina diffusa*)*.

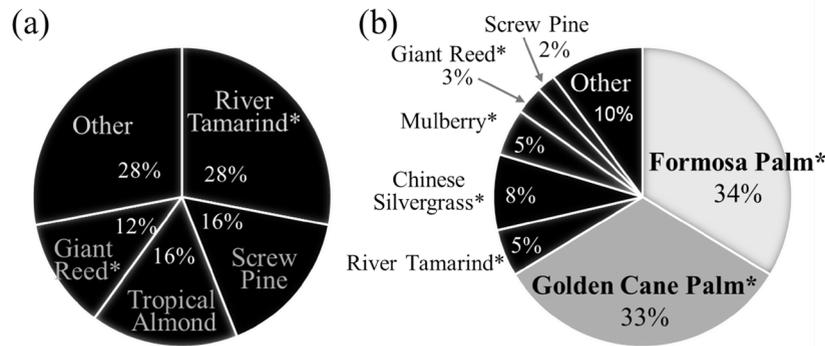


FIGURE 3. Comparison of plant species used by adult Green Anoles (*Anolis carolinensis*) on the Ogasawara Islands, Japan, in (a) natural vegetation ($n = 25$) and (b) human-modified environment ($n = 98$). Gray and white-gray areas represent major plant species that were occupied as over two thirds of the data, while black represents plant species that were occupied as less than 30% of the data. Scientific names of dominant plant species and Other plants are given in Fig 2. An asterisk (*) after scientific name represents non-native plant species on the Ogasawara Islands.

index (Table 1). On the other hand, females showed significant positive correlations between perch height and body weight ($r_s = 0.48$) and BCI ($r_s = 0.45$; Fig. 4). Juveniles showed a similar pattern as females, though albeit weaker, positive correlations that were significant (Perch height/Body weight: $r_s = 0.24$; Perch height/SVL: $r_s = 0.30$, Table 1).

DISCUSSION

Using nighttime surveys, we are able to shed light on the natural history of Green Anoles, particularly their sleep ecology. First, we revealed intra-specific variation in perch heights at night. Specifically, juveniles used significantly lower perches compared to adults though this trend varied by plant species. Our results are consistent with the pattern reported from Cayman Islands Blue-fanned Anole (*A. conspersus*) and Guadeloupe Anole (*A. marmoratus*; Barnett 2023). Although ecological reasons underlying this

TABLE 1. Correlations among perch height and several metrics of body size (Body weight in g and SVL in mm) and body condition index (BCI) of the Green Anole (*Anolis carolinensis*) on the Ogasawara Islands, Japan. Bold letters indicate significant correlations at $\alpha = 0.05$ level.

Category	Trait	ρ	P -value
Male ($n = 58$)	Body weight	0.01	0.945
	SVL	-0.07	0.620
	BCI	0.14	0.284
Female ($n = 66$)	Body weight	0.48	< 0.001
	SVL	0.30	0.015
	BCI	0.45	< 0.001
Juvenile ($n = 88$)	Body weight	0.24	0.023
	SVL	0.30	0.005
	BCI	0.02	0.868

pattern are unclear, several *Anolis* lizards seem to have similar sleep ecology; juveniles tend to sleep at lower perches than adults. In addition, previous studies compared perch heights between day and night, discussing the ecological significance of space use shift (Singhal et al. 2007). In the Ogasawara Islands, Green Anoles typically perch at lower than 100 cm during the day (Anzai et al. 2017; Mitani et al. 2020). These reports indicate that the focal Green Anoles tend to occupy a lower spatial niche during the daytime to forage ground dwelling arthropods (Toda et al. 2010). In contrast, we found that Green Anoles used significantly higher mean perch heights at night (Male = 256.2 cm, Female = 261.7 cm, Juvenile = 103.0 cm). In general, diurnal anoles sleep on leaves or twigs, and this habit allows them to detect vibrations caused by predators and swiftly evade threats (Mohanty et al. 2022; Singhal et al. 2007). During daytime, Green Anoles mostly rely on visual cues and partly on acoustic cues to detect approaching dangers and flee over long distances (Putman et al. 2020; Sakai and Iwai 2024). At night, however, they are more vulnerable to predation as they cease being alert to their surroundings (Mohanty et al. 2022; Singhal et al. 2007). Consequently, like other *Anolis* lizard species (Losos 2011), the preference for higher perches at night probably reflects a predator avoidance strategy as an arboreal species.

Another finding is that the Green Anoles used leaves of several plant species for their sleeping sites, and the variety of plant species differed between life stages but did not between sexes. The Green Anoles in Zamami-jima used 11 plant species for sleeping sites with notably high occupancy of Napiergrass (Kobayashi et al. 2025). In contrast, we found that

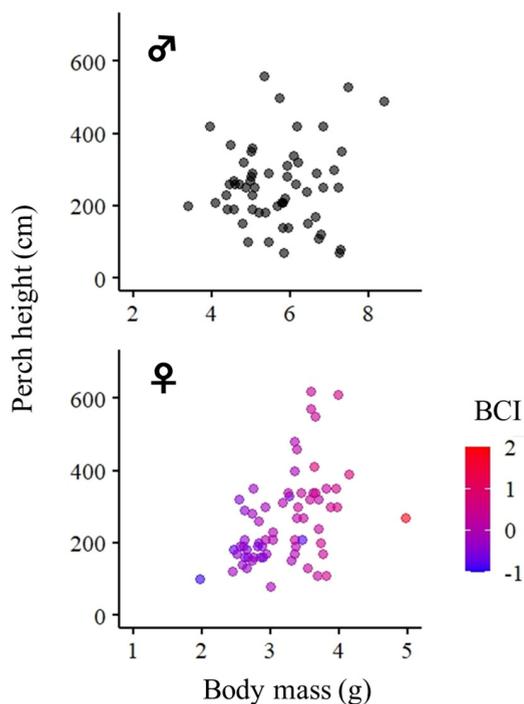


FIGURE 4. Correlations between perch height and body weight of the Green Anole (*Anolis carolinensis*) on the Ogasawara Islands, Japan, with a visualization of body condition. Male (♂) body weight was not correlated with perch height. In contrast, heavier females (♀) with better body condition tends to perch on higher leaves. Body condition index (BCI) for female is visualized with color gradient (blue to red).

Green Anoles in Chichi-jima use a greater variety of plant species (25 species in total) for sleeping sites, with the highest occupancy rates by adult lizards on Formosa Palm and Golden Cane Palm. Despite taxonomically different groups among these plant species, they share similar characteristics of leaves regarding their elongated, strap-like, parallel-fibred structure. These morphological characteristics of leaves may explain which plant species the Green Anoles select for their beds among the local vegetation in their non-native areas. Our findings suggest an ontogenetic niche shift in the plant species used for the sleeping sites, as the overlap index was small (0.36–0.42 between juveniles and adults). These scores, in terms of microhabitat use, can be interpreted as a weak overlap comparable to inter-specific niche participation reported in other lizard communities (Huey and Pianka 1977; Moreno-Arias et al. 2020; Pianka 1974). In general, animals select sleeping sites based on safety and comfort (Anderson 1984, 1998). The Comfort at Sleep Sites hypothesis may explain the ontogenetic niche shift of the sleeping sites of Green Anoles (Mohanty et al. 2022). Green

Anoles sleep by anchoring their bodies to leaf surfaces with their well-developed toe pads. Juveniles have smaller toe pads and lighter body weights than adults, suggesting that mechanical demands when anchoring their bodies to a surface probably differ with life stages (Donihue et al. 2020). The size and texture of leaves vary by plant species. These mechanical characteristics of leaves may explain the differences in comfort of beds between juvenile and adult Green Anoles although further evidence is needed for this idea.

Contrary to our prediction, the perch height at night in males did not correlate with any metrics of body size or body condition. In addition, unlike the original prediction, there was no significant differences of perch height between males and females at night. These results suggest that territoriality and social hierarchy may not influence the sleeping sites of Green Anoles, at least for the Ogasawara population. During the daytime in the breeding season, larger males typically use higher perches for demonstrating display behaviors, whereas body size no longer predicts perch height in the non-breeding season when male-male competition is alleviated (Jenssen et al. 1995; Ramírez-Bautista and Benabib 2001). This logic could also apply to the shift in territorial site defense from day to night. We found that, in some cases, multiple males used a single tree and slept in the vicinity of each other, suggesting a relaxed territoriality at night when social interactions are unnecessary. Conversely, an unexpected finding is that heavier females with better body condition tended to sleep on higher perches. Some females at our site were likely gravid, given the field surveys were during the breeding season. For female lizards, carrying large eggs imposes a physical burden on locomotion, increasing the risk of predation (Lecomte et al. 1993). For arboreal lizards, in general, sleeping at higher perches is a safer strategy against terrestrial predators climbing from the ground (Mohanty et al. 2022). Therefore, gravid females may use higher perches at night than during the day to decrease the chance of predation. Future studies should delve into the sleep ecology of particularly female Green Anoles, considering their gravidity status, reduced agility, and risk-averse tendency.

Our study also highlights implications for invasive animal management. The first notable point is that local vegetation may affect the sleep ecology of Green Anoles. Specifically, adult Green Anoles frequently perched on Formosa Palm and Golden Cane Palm. This trend was particularly detected in human-

modified environments, where the capture rate from the palm trees (67% of 98 captures) appeared to exceed the occupancy rate of these species in the vegetation (12% of the total census route; unpubl. data). These two palms are also exotic plant species on the Ogasawara Islands, primarily found in human-altered environments but not common in natural vegetation areas (Abe et al. 2018). A systematic investigation into the plant species that are potentially available to Green Anoles might differentiate between preference and availability of their sleeping sites. Second, the efficiency of nighttime capture trials is worth being addressed as was also suggested in a previous study (i.e., the introduced population of Green Iguana, *Iguana iguana*; Wasilewski et al. 2022). During our nighttime census, we spotted an average of 20.3 Green Anoles per hour, with a capture success rate of 93.4%. In contrast, during the daytime census, a single observer spotted 3.13 Green Anoles per hour with a capture success rate of 38.4% (Daisuke Suzuki et al., pers. comm.). These scores are difficult to compare directly due to being conducted by different researchers with different scientific goals; however, the notable point is that we can catch Green Anoles much easier at night compared to trials in the daytime. These implications could help develop more efficient management strategies for the invasive Green Anoles.

In conclusion, we provide basic insights into the sleep ecology of Green Anoles. Juveniles tend to sleep on lower grass while adults use higher perches for their sleeping sites, suggesting an ontogenetic niche shift in their sleeping sites. Moreover, in females, body weight and body condition partly predict perch height at night. The mechanisms underlying the positive correlation needs further testing because a priority target for population control should be gravid females (Lockwood et al. 2013). Comparisons between natural and artificially modified vegetations suggest that specific palm trees play a key role for sleeping sites of Green Anoles on the Ogasawara Islands. These findings contribute to the fundamental understanding of the natural history of invasive Green Anoles and could direct strategies for managing problematic invasive species in the focal area.

Acknowledgments.—Our study was conducted in accordance with the Guidelines of Permit and Use for Invasive Species (https://www.env.go.jp/nature/intro/1law/files/kihon_rev_all_r4.pdf). Field work and accommodation on the island were supported by the Ogasawara Research Station of Tokyo

Metropolitan University. In some areas, the field survey was conducted with the permission of the Ogasawara Subtropical Agriculture Center. Financial support for this study was provided by ESPEC Foundation for Global Environment Research and Technology (Charitable Trust for KI). We are grateful to Daisuke Suzuki, Fumiko Harakawa, and Adam Cronin of Tokyo Metropolitan University for sharing the daytime field survey data, and Naho Mitani of Nihon University for sharing the daytime perch height data. We are also grateful to Nayuta Yamamoto of the Ministry of Environment and Kou Ashizawa of the Japan Wildlife Research Center for their useful advice on the current management situation of the Green Anoles on the Ogasawara Islands.

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Supplemental Information: http://www.herpconbio.org/Volume_20/Issue_3/Inomori_etal_2025_Suppl.pdf



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