

Site Fidelity of *Gekko japonicus* to Artificially Lit Environments

Authors: Kobayashi, Kohei, and Mori, Akira

Source: Current Herpetology, 39(2) : 184-195

Published By: The Herpetological Society of Japan

URL: <https://doi.org/10.5358/hsj.39.184>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Site Fidelity of *Gekko japonicus* to Artificially Lit Environments

KOHEI KOBAYASHI* AND AKIRA MORI

*Department of Zoology, Graduate School of Science, Kyoto University,
Sakyo, Kyoto 606–8502, JAPAN*

Abstract: Several reptiles and amphibians frequently occur in environments exposed to artificial lights and appear to effectively hunt prey animals attracted to the light. Therefore, it would be beneficial for them to use such a habitat to survive in urban areas. In this paper, we examined site fidelity of a nocturnal gecko, *Gekko japonicus*, to a particular artificial light environment in the field. We observed short-term dependence on the same light environment by individual geckos for four to nine consecutive nights and also examined long-term site fidelity once every 10 days from March to November. The same individual frequently came to the particular light for several consecutive nights, but day and time of appearance varied among individuals. Over several months, 20% of marked individuals were repeatedly sighted at the same place although the number of their re-sightings was low (1–5 times). These results suggest that each *G. japonicus* may settle down in a certain artificially lit environment and use it repeatedly, but the dependence on lights not be so strong.

Key words: Artificial light; Dependence on light; *Gekko japonicus*; Site fidelity; Urban area

INTRODUCTION

As urban areas and human activities have expanded, the use of artificial lights has been increasing. An illuminated environment created by artificial lights may have many effects on wild animals. Negative influences caused by a light stimulus have been demonstrated: e.g., disruption of biological clocks, misorientation, and disorientation (Beier, 2006; Gauthreaux et al., 2006; Salmon, 2006). On the other hand, an artificial light environ-

ment sometimes leads to beneficial results for animals. Artificial lights may serve as a resource for thermoregulation by nocturnal ectotherms, such as reptiles (Perry et al., 2008). Because the absence of heat sources, such as sunlight, limits effective thermoregulation at night (Hitchcock and McBrayer, 2006), the subtle heat emitted from lights might be beneficial. In addition, insectivores increase their foraging efficiency in artificial light regimes because prey insects are attracted to the lights, and consequently food resources are clumped locally (Petren and Case, 1996; Zozaya et al., 2015; Mcmunn et al., 2019). It has been reported that several species of reptiles and amphibians come to

*Corresponding author.

E-mail address: kobayashi_bc@yahoo.co.jp

such artificially lit environments and use them as foraging sites (lizards: Perry et al., 2008; Maurer et al., 2019; frogs: Baker, 1990; Henderson and Powell, 2001; Van Grunsven et al., 2017). These animals are also able to use environments other than illuminated places (Baker, 1990; Powell and Henderson, 2008; Norval et al., 2011), but they are frequently found at lights. Moreover, use of artificial lights might increase the opportunity to encounter mates. Therefore, such artificial lights may play an important role for animals living in an anthropogenically influenced environment, and they may greatly depend on or settle down in the vicinity of lights.

Geckos are among the reptiles attracted to the artificial lights. Many reports have documented observations of nocturnal geckos frequenting artificial lights (Case et al., 1994; Thirakhupt et al., 2006; Williams and McBrayer, 2007; Perry et al., 2008; Martín et al., 2018). Various field studies of geckos in artificially lit environments have been conducted, focusing on their foraging activities, movement patterns, microhabitat selection, and interspecific interactions (Petren and Case, 1996; Werner et al., 1997; Thirakhupt et al., 2006; Williams and McBrayer, 2007; Paulissen et al., 2013; Kim et al., 2019; Park et al., 2019). However, detailed observations focusing on the daily appearance of a particular individual at a particular light are quite limited. Thus, sedentariness and dependence of individual geckos on artificial lights have not been well documented.

The Japanese gecko, *Gekko japonicus*, is frequently found in artificially lit environments at night, mainly in urban areas. This gecko is distributed throughout eastern China, southern Korea, and most regions of Japan (Ota and Tanaka, 1996). *Gekko japonicus* mainly inhabits houses or buildings in urban environments and often stays near artificial lights, such as houselights, at night although in rural and suburban areas this gecko is also found in dark places (Ota and Tanaka, 1996; Murai et al., 2013; Park et al., 2019). This gecko is considered a sit-and-wait

predator, waiting for insects and other arthropods at a feeding site (Ota and Tanaka, 1996; Werner et al., 1997). Few studies have observed the appearance patterns of *G. japonicus* at a particular light throughout the active season or during the entire night. Most previous research on *G. japonicus* in the field has been conducted for only a few days or only at a particular time of night (Caldwell, 2013; Caldwell et al., 2014; Kim et al., 2018, 2019), and observations were started when observers found geckos that were already present at the light and finished when geckos disappeared or hid (Werner et al., 1997). Therefore, the degree of the dependence of individual *G. japonicus* on artificially lit environments has not been clarified.

To evaluate the site fidelity to an artificially lit environment, it is necessary to investigate not only how frequently a given gecko visits it but also whether the gecko comes to the same light repeatedly in the long-term as well as in the short-term. This is because a gecko that comes to the same site repeatedly in the short-term does not necessarily visit the same place in the long-term. Therefore, in this study we conducted two types of field surveys of *G. japonicus*: short- and long-term surveys. The purpose of the short-term survey was to examine (1) repeated appearances of individuals at the same light environment throughout several consecutive nights and (2) persistence at a light environment during a night. For this survey we selected two restricted places that were illuminated with artificial lights throughout the whole night. The purpose of the long-term survey was to examine sedentariness over several months in the same artificially lit environment. We marked geckos and conducted a census every ten days for nine months. Combining results of these two surveys, we discuss the appearance patterns of *G. japonicus* in a particular artificially lit environment.

MATERIALS AND METHODS

Short-term Survey

Study site

The survey was conducted in the Ashiu Forest Research Station (Miyama-cho, Nantan City, Kyoto, Japan; 35°30'93" N, 135°71'69" E). At the base station area, where several houses, an accommodation for visitors, storage facilities, and an office lodge are present, we have confirmed a dense population of *G. japonicus* (Mori, unpublished data). We chose two observation points in 2018: the wooden walls of a particular storehouse and the office entrance. In 2019 we observed only the same storage wall as in 2018. The storage wall was basically flat and had one artificial light located at a height of 3.4 m. The wall of the office entrance was uneven because of several columns and door-casings. The office entrance had one artificial light located at the height of 2.5 m, immediately above the entrance door. These artificial lights provided a wide range of illumination levels. The observed light area at the storage facility was approximately 2.4 m² (1.25 m height×1.9 m width) in 2018 and 7.5 m² (2.2 m×1.9 m, 1.8 m×1.8 m) in 2019. The observed light area at the office was approximately 2.7 m² (1.1 m×2.5 m).

Observations

Observations on the geckos' daily use of the light environment were carried out for five nights (one night and four consecutive nights) from July to August 2018, and nine consecutive nights in August 2019. A video camera (Sony, HDR-SR12 or FDR-AX55) equipped with infrared light (invisible to geckos; Loew et al., 1996; Bowmaker, 2008; Liu et al., 2015) was placed in front of the observation point from dusk until around dawn, and behaviors of geckos that appeared on the wall were recorded. We did not approach the walls except to change batteries, to minimize disturbance to the geckos. Batteries were changed three times per night. Geckos were flipped down from a wall with a fishing rod

and were collected by hand two to five days before the observation period. They were marked with a combination of a few dots and a bar with an oil-based white marker pen on the back to identify each individual. They were released at the site of capture within two hours. Their snout-vent length (SVL), body mass (BM), sex, and maturity were recorded after collection. SVL was measured to the nearest 0.1 mm using a digital caliper (DT-150, Niigataseiki, Japan), and BM was measured to the nearest 0.1 g using a digital scale (Tanita, Japan). Sex was determined based on the size of post-cloacal spurs (spurs are larger in males than females). Geckos larger than 44.9 mm and 52.3 mm in SVL were considered to be mature males and females, respectively (Ikeuchi, 2004). It is unknown whether marked geckos in 2018 and 2019 included identical individuals.

Data analysis

Two variables were determined from the video data: (1) how many times each individual came to an illuminated area each night, and (2) how many times each individual ate prey during a night. Following Petren and Case (1996), a feeding attempt was defined as a movement toward an insect. Even if a target insect was not observed directly, the attempt was considered successful when jaw movements were observed following a lunge (Petren and Case, 1996). To evaluate the effects of previous foraging experiences on the gecko's appearance the subsequent night, a generalized linear mixed model (GLMM) with a binomial distribution and logit link was applied. The number of foraging attempts during the preceding night was the explanatory variable, and their appearance in the light environment during the subsequent night was the dependent variable (present: 1, absent: 0). Individual was included as random effect to avoid overdispersion of variance. Statistical calculation was conducted using the package glmmML in R version 3.6.1 (R Core Team, 2019).

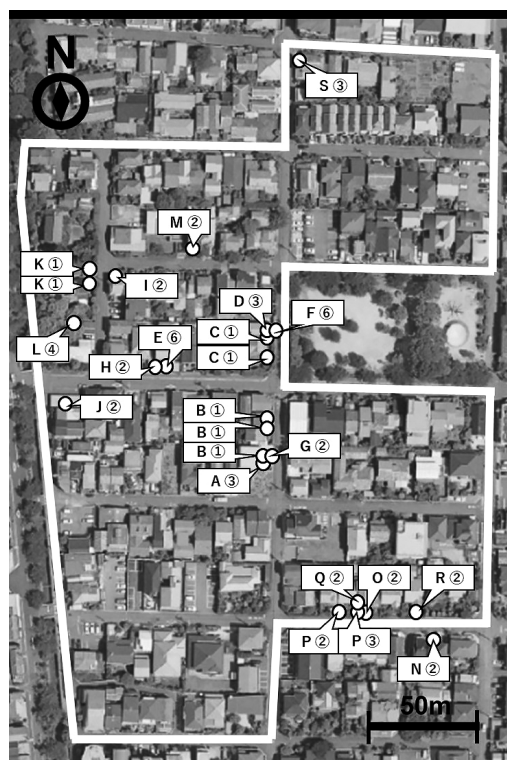


FIG. 1. A photograph of the survey site ($35^{\circ}03'48''$ N, $135^{\circ}79'06''$ E) located in Sakyo, Kyoto, Japan (© Geospatial Information Authority of Japan). Survey was conducted along almost all paths inside the white frame. Capture locations of geckos that were re-sighted at least once are shown. The locations of captures are indicated by white circles. Letters (A to S) inside a rectangle indicate the ID of geckos, and each circled numeral indicates the number of captures or sightings at the place.

Long-term Survey

Study site

The survey was conducted in a block of a residential area near Kyoto University, Sakyo, Kyoto, Japan ($35^{\circ}03'48''$ N, $135^{\circ}79'06''$ E; Fig. 1). This block mainly consisted of residential houses and parking lots. Houses were densely distributed, and several houses had vegetation, such as hedges or small gardens.

Field survey

In the long-term survey, we conducted a

route census along with an individual marking method. Hibernation of *G. japonicus* is considered to take place from around December to April (Hisai, 1997), and this gecko is active mainly from around April to late October (Xiang et al., 1991). Thus, we conducted the route census from March to November 2019, basically every ten days except for late September. Each census lasted for approximately two hours between 1900 h and 2200 h. The initiation of each census depended on sunset time because the peak activity period of *G. japonicus* was found to be 1–2 hours after lights-off in a laboratory experiment (Tawa et al., 2014). We walked along almost all paths slowly with a headlight and recorded the occurrence of *G. japonicus* on a map. We looked for geckos regardless of the brightness of the area, but mainly those on walls of houses along paths because it was prohibited to enter private houses. Censuses were not conducted at night when it rained heavily. At the beginning of the census and basically every hour, we measured air temperature with a digital thermometer (SK-1260, Sato Keiryoki MFG. Co., Ltd., Japan). We collected geckos whenever possible if they were not already marked (see below for the marking method). Marked geckos were basically identified by sighting, but they were captured if visual identification by sight was difficult. Upon capture and re-sight, we recorded the illumination level of the capture point and the occurrence of prey insects within 30 cm of the capture point. Illumination level was measured in lux (lumens/m²) to the nearest 0.01 Lx using a digital lux meter (ANA-F11, Tokyo Photoelectric Co., Ltd, Japan) held with the cosine correction dome (sensor) facing toward the light source. We looked for nearby insects visually. Geckos' SVL and BM were measured on the night of capture or next day. Sex, egg presence, and maturity were recorded at the same time.

A visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, USA) was used as a marking to identify geckos. Several previous studies in

which VIE tags were used for reptiles, including a gecko, indicated that they are retained at least for a year (Penney et al., 2001; Hutchens, 2008; Smith et al., 2012; Anderson et al., 2015). Six separate fixed positions (forelimbs, each side of midbody, hindlimbs) on the dorsal side of a gecko were chosen for marking, but the number of marks on an individual was limited to three. The VIE mark emits fluorescence against UV-black light, thus it is possible to check the gecko's ID easily without handling. Red VIE was injected subcutaneously with a syringe (Becton, Dickinson and Company, Franklin Lakes, New Jersey, USA). Geckos were released at the capture point within 24 hours. The census area was divided into nine sections, and geckos were marked in the same order within each section. Therefore, there were several individuals for which marking pattern overlapped in the study area. However, because an amount and a shape of VIE tags were slightly different between these individuals, we were able to distinguish them visually.

Data analysis

To characterize the capture points, we evaluated two environmental variables: (1) whether the point was a light place (Light) or a dark place (Dark), and (2) whether insects were present near the capture points (P: present, A: absent). Places in which illumination was less than 0.2 Lx were categorized as Dark because the illumination of the full moon is approximately 0.2 Lx (Cronin et al., 2014; Spitschan et al., 2016). Accordingly, we categorized the capture point into four types: "Light, P", "Light, A", "Dark, P", and "Dark, A."

RESULTS

Short-term survey

Seven individuals (two males and five females) from the storehouse and six individuals (three males and three females) from the office were marked in 2018 (SVL, mean \pm SD = 62.53 ± 5.45 mm; BM, 4.34 ± 1.05 g).

Thirteen individuals (four males, seven females, and two juveniles) from the storehouse were marked in 2019 (SVL, 60.69 ± 3.13 mm for adults and 45.25 ± 1.59 mm for juveniles; BM, 4.08 ± 0.65 g for adults and 1.55 ± 0.21 g for juveniles). On most nights, multiple individuals appeared. Although some geckos appeared almost every day (five out of 13 individuals in 2018 and three out of 13 individuals in 2019), the remaining geckos appeared once in several days (six individuals in 2018) or rarely appeared (two individuals in 2018 and 10 individuals in 2019) (Tables 1 and 2). The day on which a given gecko was observed appeared irregular, and its interval did not seem to be constant. Seventy-eight percent of geckos that appeared on the wall and retreated to a dark place reappeared there the same night. The individuals reappeared one to 46 times (8.3 times on average) per night. The time when geckos appeared and the number of individual's appearances during the night varied depending on day.

The number of feeding events by a gecko ranged from 0 to 10 per night in most cases, but in a few cases, geckos ate approximately 40 times (Tables 1 and 2). Geckos appeared again during the same night regardless of the number of feeding on that night (0 to 48 times). In addition, the number of previous foraging successes had no significant effect on geckos' appearances on the subsequent night (GLMM: Estimate coefficient = 0.04117, SE = 0.03652, $z = 1.1437$, $P = 0.253$).

Long-term survey

A total of 25 route censuses were conducted. In total, 132 records (46 males, 50 females, and 36 juveniles) were obtained from 96 individuals (31 males, 33 females, and 32 juveniles: SVL, 57.46 ± 4.62 mm, BM, 3.39 ± 0.77 g for adults; SVL, 37.41 ± 5.91 mm, BM, 0.36 ± 0.47 g for juveniles). Geckos were captured mainly from April to early August (Fig. 2), and the number of captures was small in September and October although the temperature in September and October was similar to that in May and June. Seventy-

TABLE 1. The number of foraging events observed each night in the office (O18) and the storehouse (S18) in 2018. Dash indicates that the individual did not come to the light environment on that night. M: male, F: female.

ID of gecko	Sex	SVL (mm)	Date				
			26 Jul	30 Jul	31 Jul	1 Aug	2 Aug
O18-A	M	64.2	—	—	—	—	
O18-B	F	69.53	—	18	—	—	
O18-C	M	62.1	—	—	0	2	
O18-D	F	63.07	6	6	0	—	
O18-E	F	74.4	—	0	—	1	
O18-F	M	65.09	—	7	30	8	
S18-A	F	61.92	1	5	—	2	0
S18-B	F	53.65	7	5	—	0	—
S18-C	M	55.1	—	40	17	—	4
S18-D	M	58.53	0	29	5	0	0
S18-E	F	60.59	—	48	45	7	0
S18-F	F	63.3	1	—	2	—	0
S18-G	F	61.35	—	—	—	2	10

No observation was conducted on 2 Aug in the office.

TABLE 2. The number of foraging events each night in the storehouse in 2019. Dash indicates that the individual did not come to the light environment that night. M: male, F: female.

ID of gecko	Sex	SVL (mm)	Date								
			17 Aug	18 Aug	19 Aug	20 Aug	21 Aug	22 Aug	23 Aug	24 Aug	25 Aug
S19-A	F	65.8	7	6	0	7	8	3	1	4	3
S19-B	F	64.6	—	27	—	—	—	—	—	—	—
S19-C	F	46.37	8	0	—	—	—	—	—	—	—
S19-D	M	55.5	0	—	—	—	—	—	—	—	—
S19-E	M	60.07	—	—	—	—	—	—	—	—	—
S19-F	M	61.45	1	—	—	—	—	—	—	—	—
S19-G	F	44.12	—	—	0	—	—	—	—	—	—
S19-H	F	61.18	—	—	—	—	—	—	—	—	—
S19-I	F	56.38	28	35	2	1	6	1	—	1	0
S19-J	M	59.81	48	12	—	1	5	0	—	—	2
S19-K	F	63.32	—	—	—	—	—	—	—	—	—
S19-L	F	60.23	—	—	—	—	—	—	—	—	—
S19-M	F	59.22	—	—	—	—	—	—	—	—	—

seven (80%) of the marked individuals were never re-sighted. The number of re-sighting events was 36, and the number of re-sighted individuals was 19 (eight males, 10 females, and one juvenile). There was no significant difference between males and females in the

number of captured individuals in each census (Wilcoxon rank-sum test, $W=252$, $P=0.8206$).

Geckos were re-sighted in almost the same places and light environments as their first capture points. Most of them were re-sighted

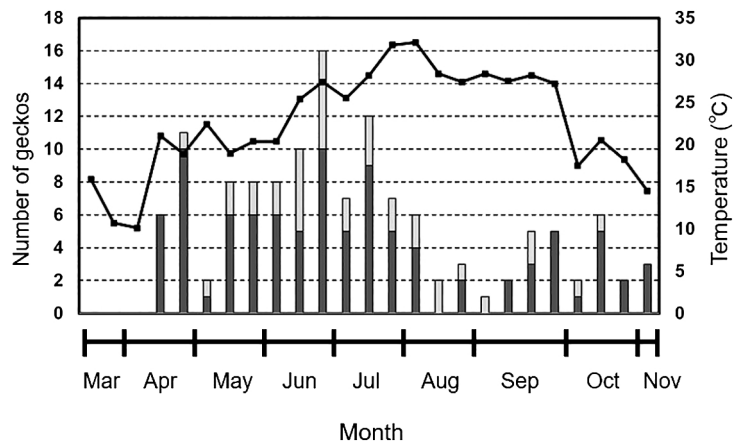


FIG. 2. Seasonal change of the number of *Gekko japonicus* observed in the long-term survey in Kyoto, Japan (n=132). Surveys were conducted twice to four times per month. Dark and light grey bars indicate first-captured geckos and re-sighted geckos, respectively. Black line graph indicates average air temperature (°C) measured during each survey.

once, and the maximum number of re-sightings was five (Fig. 1). The number of geckos found in a given environment near a light varied among places. In some places, two to seven individuals in total were found at the same place. However, in most cases, we observed one to two individuals at the same time in one place.

Capture points of 57% of all recorded geckos (n=155, including non-captured individuals) were categorized as “Light, P” (Fig. 3). These geckos were found close to the light equipment (within 15 cm on average). Most of the re-sighted individuals were also observed in “Light, P” repeatedly (Table 3). The range of illumination level in “Light” points was 0.21 to 3780 Lx (236.5 Lx on average). Thirty-one percent of the capture points were “Light, A”, and only 12% of the capture points were in a dark place (Fig. 3).

DISCUSSION

The result of the short-term survey suggests that *G. japonicus* seems to utilize the same light environment frequently within several nights although this is not necessarily every night. Because geckos usually reappeared

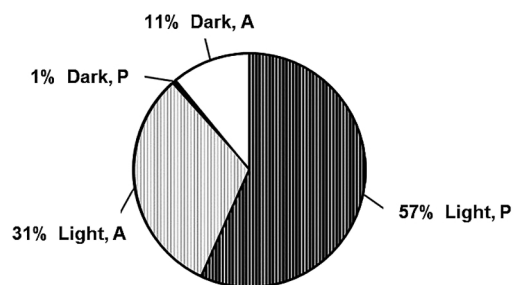


FIG. 3. Condition of brightness and prey occurrence of the points where geckos were found (n=155). “Light” indicates that the capture point was illuminated by nearby artificial lights, and “Dark” indicates that there was no light around the capture point. “P” indicates that insects were present near the capture point, and “A” indicates that insects were absent. See text for more detailed definitions. Twenty-three non-captured geckos are included in this graph.

several times during a night, they seem to persist at the particular artificially lit place during the night. Nonetheless, they did not stay in the light for a long time. By repeating visits and retreat several times, geckos might reduce encountering risks at the light, such as predation and conflict with conspecifics (Case et al., 1994; Perry and Fisher, 2006; Williams

TABLE 3. Microhabitat character of the capture points of geckos that were re-sighted at least once. The number of captures or sights is shown for each individual. “Light” indicates that the capture point was illuminated by nearby artificial lights, and “Dark” indicates that there was no light around the capture point. “P” indicates that insects were present near the capture point, and “A” indicates that insects were absent. See text for more detailed definitions. Each ID corresponds to that in Figure 1.

ID of gecko	Sex	Microhabitat			
		Light, P	Light, A	Dark, P	Dark, A
A	Female	2	0	0	1
B	Female	0	3	0	0
C	Male	1	1	0	0
D	Male	3	0	0	0
E	Male	4	2	0	0
F	Female	5	1	0	0
G	Male	1	1	0	0
H	Female	2	0	0	0
I	Female	2	0	0	0
J	Female	2	0	0	0
K	Male	1	0	0	1
L	Male	4	0	0	0
M	Male	0	2	0	0
N	Female	1	1	0	0
O	Female	2	0	0	0
P	Juvenile	2	3	0	0
Q	Male	2	0	0	0
R	Female	2	0	0	0
S	Female	3	0	0	0

and McBrayer, 2007). Physiological factors, such as fasting duration, would also affect geckos’ decision to stay in a dark place. However, there was no correlation between the number of the preceding feeding events and an appearance the next night. Thus, hunger level would not explain the various appearance patterns of the geckos within several nights. In future studies, effects of the presence of other individuals and recent experiences of interaction with conspecifics should be investigated as possible factors for decisions made by geckos.

In the long-term survey, the frequency of re-sightings of the same geckos was low, and they did not necessarily appear in every survey. However, re-sighted individuals were observed in association with the same lit place in most cases, even after an interval of one to

three months. Thus, it is likely that *G. japonicus* does not move far from one artificially lit place and is sedentary near a particular light at least during one active season. Small home range size of *G. japonicus* has been suggested in a previous study, in which its area of movement was reported to be less than 100 m² (Park et al., 2019). Therefore, at our study site it seems rare that one individual would visit separate lighted places on different houses. Fifty-seven percent of the geckos were found at a light with nearby prey, indicating that a light environment actually provides food resources and that *G. japonicus* uses such light environments at a moderately high rate. On the other hand, 31% of the geckos were observed in light places without prey. This might reflect the fact that species of geckos are generally sit-and-wait predators that

remain at efficient feeding sites, such as those near light sources, for a while, waiting for approaching insects (Petren and Case, 1996; Cooper, 2005; Thirakhupt et al., 2006). Actually, geckos in our short-term survey occasionally stayed on the wall without the presence of nearby insects. *Gekko japonicus* might learn that a particular light environment where insects are clumped is a suitable foraging site and visit it frequently.

Although *G. japonicus* seems sedentary at a particular place, the frequency of re-sighting in the long-term survey was low. This may be, at least partially, due to the underestimation of its reappearance in the light environment. There are two possibilities. First, the census time of our survey may not have corresponded to the active time of geckos because the duration when geckos are active was limited. Thirakhupt et al. (2006) reported that the appearance time of individual *G. gekko* varied depending on the survey and that this gecko did not necessarily stay in the light environment all night. Such an appearance pattern was also observed in *G. japonicus* in the short-term survey. Second, *G. japonicus* may not have stayed in observable areas despite being active throughout the whole night. Because the long-term survey was conducted in a residential block, our search areas were restricted to the outside of houses and did not cover all areas available for geckos, including dark places. Actually, previous studies show that *G. japonicus* uses also dark places (Murai et al., 2013; Park et al., 2019). Therefore, it is likely that *G. japonicus* in the present census area might have used light environments more frequently than our results indicate.

In both the short- and long-term surveys, multiple individuals were found at a particular artificially lit place. However, the day and time-of-day of their appearance varied among individuals, and their activity did not seem to be synchronized. This alternate visitation of a particular light place by several individuals would lead to a misunderstanding that a single gecko continuously occupies a particu-

lar light environment in urban areas. To reveal the appearance pattern of each *G. japonicus* in the field, an individual tracking survey will be necessary.

The present results suggest that *G. japonicus* may have site fidelity and settle down in a particular light environment. Such a persistent use implies that an environment illuminated with artificial lights, where prey insects are easily available, is useful and important for *G. japonicus* to survive in urban areas. Nonetheless, individual geckos did not stay in the light environment continuously, and several individuals alternately appeared even within a night. Therefore, *G. japonicus* may not depend completely on the artificial light environment. It is still unclear how *G. japonicus* establishes site fidelity to a particular light environment, thus future research should examine its mechanism. In addition, the advantage of light environment use has not been quantitatively demonstrated. Comparing stomach contents or body condition index between individuals that inhabit different light conditions may help us to evaluate whether *G. japonicus* is able to increase energy intake by using a light environment in urban areas.

ACKNOWLEDGMENTS

We are grateful to the staff of the Ashiu Forest Research Station for allowing us to observe geckos in the station area. We also express our appreciation to two anonymous reviewers for insightful comments that helped to improve the manuscript. The present study was carried out in compliance with the guidelines of the Animal Care and Use Committee of Kyoto University.

LITERATURE CITED

- ANDERSON, K. P., BYER, N. W., MCGEHEE, R. J., AND RICHARDS-DIMITRIE, T. 2015. A new system for marking hatchling turtles using visible implant elastomer. *Herpetological Review* 46: 25–27.
- BAKER, J. 1990. Toad aggregations under street

- lamps. *British Herpetological Society Bulletin* 31: 26–27.
- BEIER, P. 2006. Effects of artificial night lighting on terrestrial mammals. p. 19–42. In: C. Rich and T. Longcore (eds.), *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington, DC.
- BOWMAKER, J. K. 2008. Evolution of vertebrate visual pigments. *Vision Research* 48: 2022–2041.
- CALDWELL, K. R. 2013. *Gekko japonicus* (Japanese gecko). Cold weather aggregations. *Herpetological Review* 44: 672.
- CALDWELL, K. R., HONG, X., BRINKER, A. M., AND YURK, D. J. 2014. Utilisation of weep holes in retaining walls by the Japanese gecko (*Gekko japonicus* Duméril and Bibron, 1836) in Fukuoka, Japan. *Herpetological Notes* 7: 235–240.
- CASE, T. J., BOLGER, D. T., AND PETREN, K. 1994. Invasions and competitive displacement among house geckos in the tropical Pacific. *Ecology* 75: 464–477.
- COOPER, W. E., JR. 2005. Duration of movement as a lizard foraging movement variable. *Herpetologica* 61: 363–372.
- CRONIN, T. W., JOHNSEN, S., MARSHALL, N. J., AND WARRANT, E. J. 2014. *Visual Ecology*. Princeton University Press, Princeton.
- GAUTHREAUX, S. A., JR., BELSER, C. G., RICH, C., AND LONGCORE, T. 2006. Effects of artificial night lighting on migrating birds. p. 67–93. In: C. Rich and T. Longcore (eds.), *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington, DC.
- HENDERSON, R. W. AND POWELL, R. 2001. Responses by the West Indian herpetofauna to human-influenced resources. *Caribbean Journal of Science* 37: 41–54.
- HITCHCOCK, M. A. AND MCBRAYER, L. D. 2006. Thermoregulation in nocturnal ectotherms: Seasonal and intraspecific variation in the Mediterranean gecko (*Hemidactylus turcicus*). *Journal of Herpetology* 40: 185–195.
- HISAI, N. 1997. Ecological observation on hibernation of Japanese common gecko, *Gekko japonicus* (Duméril et Bibron). *Report of Institute for Nature Study* 28: 1–3.
- HUTCHENS, S. J. 2008. Visible implant fluorescent elastomer: A reliable marking alternative for snakes. *Herpetological Review* 39: 301.
- IKEUCHI, I. 2004. Male and female reproductive cycles of the Japanese gecko, *Gekko japonicus*, in Kyoto, Japan. *Journal of Herpetology* 38: 269–274.
- KIM, D., CHOI, W., PARK, I., KIM, J., KIM, I., AND PARK, D. 2018. Comparisons of microhabitat use of Schlegel's Japanese gecko (*Gekko japonicus*) among three populations and four land cover types. *Journal of Ecology and Environment* 42: 24.
- KIM, D., PARK, I., KIM, J., OTA, H., CHOI, W., KIM, I., AND PARK, D. 2019. Spring and summer microhabitat use by Schlegel's Japanese gecko, *Gekko japonicus* (Reptilia: Squamata: Gekkonidae), in urban areas. *Animal Cells and Systems* 23: 64–70.
- LIU, Y., ZHOU, Q., WANG, Y., LUO, L., YANG, J., YANG, L., LIU, M., LI, Y., QIAN, T., ZHENG, Y., LI, M., LI, J., GU, Y., HAN, Z., XU, M., WANG, Y., ZHU, C., YU, B., YANG, Y., DING, F., JIANG, J., YANG, H., AND LI, M. 2015. *Gekko japonicus* genome reveals evolution of adhesive toe pads and tail regeneration. *Nature Communications* 6: 1–11.
- LOEW, E. R., GOVARDOVSKII, V. I., RÖHLICH, P., AND SZÉL, Á. 1996. Microspectrophotometric and immunocytochemical identification of ultraviolet photoreceptors in geckos. *Visual Neuroscience* 13: 247–256.
- MARTÍN, B., PÉREZ, H., AND FERRER, M. 2018. Effects of natural and artificial light on the nocturnal behaviour of the wall gecko. *Animal Biodiversity and Conservation* 41: 209–215.
- MAURER, A. S., THAWLEY, C. J., FIREMAN, A. L., GIERY, S. T., AND STROUD, J. T. 2019. Nocturnal activity of Antiguan lizards under artificial light. *Herpetological Conservation and Biology* 14: 105–110.
- MCMUNN, M. S., YANG, L. H., ANSALMO, A., BUCKNAM, K., CLARET, M., CLAY, C., COX, K., DUNGEY, D. R., JONES, A., KIM, A. Y., KUBACKI, R., LE, R., MARTINEZ, D., REYNOLDS, B., SCHRODER, J., AND WOOD, E. 2019. Artificial light increases local predator abundance, predation rates, and herbivory. *Environmental*

- Entomology* 48: 1331–1339.
- MURAI, S., JONO, T., AND HONGO, Y. 2013. *Gekko japonicus* (Japanese gecko). Sap feeding. *Herpetological Review* 44: 323–324.
- NORVAL, G., DIECKMANN, S., HUANG, S. C., MAO, J. J., CHU, H. P., AND GOLDBERG, S. R. 2011. Does the tokay gecko (*Gekko gecko* [Linnaeus, 1758]) occur in the wild in Taiwan? *Herpetology Notes* 4: 203–205.
- OTA, H. AND TANAKA, S. 1996. Gekkonidae and Eublepharidae. p. 65–71. In: S. Sengoku, T. Hikida, M. Matsui and K. Nakaya (eds.), *The Encyclopaedia of Animals in Japan 5, Amphibians, Reptiles, Chondrichthyes*. Heibonsha, Tokyo.
- PARK, I-K., KIM, D., FONG, J., AND PARK, D. 2019. Home range size and overlap of the small nocturnal Schlegel's Japanese gecko (*Gekko japonicus*), introduced into a city park in Korea. *Asian Herpetological Research* 10: 261–269.
- PAULISSEN, M. A., MEYER, H. A., AND HIBBS, T. S. 2013. Movement patterns and sociality of the Mediterranean gecko, *Hemidactylus turcicus*, in southwestern Louisiana. *The Southwestern Naturalist* 58: 344–350.
- PENNEY, K. M., GIANOPULOUS, K. D., MCCOY, E. D., AND MUSHINSKY, H. R. 2001. The visible implant elastomer marking technique in use for small reptiles. *Herpetological Review* 32: 236.
- PERRY, G. AND FISHER, R. N. 2006. Night lights and reptiles: Observed and potential effects. p. 169–191. In: C. Rich and T. Longcore (eds.), *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington, DC.
- PERRY, G., BUCHANAN, B. W., FISHER, R. N., SALMON, M., AND WISE, S. E. 2008. Effects of artificial night lighting on amphibians and reptiles in urban environments. p. 239–256. In: J. C. Mitchell, R. E. Jung, and B. Bartholomew (eds.), *Urban Herpetology* 3. Society for the Study of Amphibians and Reptiles, Salt Lake City.
- PETREN, K. AND CASE, T. J. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77: 118–132.
- POWELL, R. AND HENDERSON, R. W. 2008. Urban herpetology in the West Indies. p. 389–404. In: J. C. Mitchell, R. E. Jung, and B. Bartholomew (eds.), *Urban Herpetology* 3. Society for the Study of Amphibians and Reptiles, Salt Lake City.
- R CORE TEAM. 2019. *R: A Language and Environment for Statistical Computing, version 3.6.1*. Available via <https://www.r-project.org/>
- SALMON, M. 2006. Protecting sea turtles from artificial night lighting at Florida's oceanic beaches. p. 141–168. In: C. Rich and T. Longcore (eds.), *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington, DC.
- SMITH, A. L., BULL, C. M., AND DRISCOLL, D. A. 2012. Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biological Conservation* 145: 139–147.
- SPITSCHAN, M., AGUIRRE, G. K., BRAINARD, D. H., AND SWEENEY, A. M. 2016. Variation of outdoor illumination as a function of solar elevation and light pollution. *Scientific Reports* 6: 26756.
- TAWA, Y., JONO, T., AND NUMATA, H. 2014. Circadian and temperature control of activity in Schlegel's Japanese gecko, *Gekko japonicus* (Reptilia: Squamata: Gekkonidae). *Current Herpetology* 33: 121–128.
- THIRAKHUPT, K., AOWPHOL, A., VORIS, H., AND NABHITABHATA, J. 2006. Foraging ecology of the Tokay gecko, *Gekko gecko* in a residential area in Thailand. *Amphibia-Reptilia* 27: 491–503.
- VAN GRUNSVEN, R. H., CREEMERS, R., JOOSTEN, K., DONNERS, M., AND VEENENDAAL, E. M. 2017. Behaviour of migrating toads under artificial lights differs from other phases of their life cycle. *Amphibia-Reptilia* 38: 49–55.
- WERNER, Y. L., OKADA, S., OTA, H., PERRY, G., AND TOKUNAGA, S. 1997. Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetological Research* 7: 153–165.
- WILLIAMS, S. C. AND MCBRAYER, L. D. 2007. Selection of microhabitat by the introduced Mediterranean gecko, *Hemidactylus turcicus*: Influence of ambient light and distance to refuge. *The Southwestern Naturalist* 52: 578–585.
- XIANG, J., WANG, P., AND HONG, W. 1991. The reproductive ecology of the gecko *Gekko japonicus*.

nicus. Acta Zoologica Sinica 37: 185–192.
ZOZAYA, S. M., ALFORD, R. A., AND
SCHWARZKOPF, L. 2015. Invasive house geckos
are more willing to use artificial lights than are

native geckos. *Austral Ecology* 40: 982–987.

Accepted: 1 July 2020