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Population Density of a Clonal Gecko Species in Its Northernmost Range, the Ryukyus in Japan

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Abstract: Many species of organisms are known to have expanded their distributional ranges and established highly dense populations in their non-native areas due to human activities. Several gecko species have been introduced from tropics to seasonal subtropics with the aid of artificial transportations. However, it has not yet been well-documented as to whether invasive tropical geckos flourish in extra-tropical cooler areas outside their native range. Here, I report demographic information of the mourning gecko, *Lepidodactylus lugubris*, in its northernmost distribution, the Ryukyu Archipelago in Japan. I conducted a mark-recapture survey of mourning geckos inhabiting a coastal vegetation habitat and estimated their population size using the Jolly-Seber open population model. An estimated 94–284 individuals lived in a small beachfront forest. The population showed a high density (880–2,656 geckos/ha), which is comparable to that of other invasive gecko populations in tropical areas. The results imply a successful colonization of clonal geckos at their northernmost invasion front.

Key words: Climate shift; Invasive species; *Lepidodactylus lugubris*; Population abundance; Subtropics

Introduction

Many animal species are introduced outside their native range because of intentional or accidental artificial transportations by humans (Sakai et al., 2001; Parker et al., 2013). In some cases, invasive reptiles and amphibians flourish in non-native ranges, causing serious impacts on local ecosystems (Bomford et al., 2009; Kraus, 2009). Several gecko species frequently invade new areas in association with human activities and colonize both urban and natural habitats (Rödder et al., 2008; Rödder and Lötters, 2009; Hoskin, 2011). For example, the Mediterranean house gecko, *Hemidactylus turcicus*, invaded the United States where it has established dense populations in Florida (479–1,476 geckos/ha; Punzo, 2001) and in Oklahoma (478 geckos/ha; Locey and Stone, 2006). In the case of *H. turcicus*, its climatic environments are similar between the native and non-native temperate zones (Rödder and Lötters, 2009; but see Wessels et al., 2018). In other cases, invasions are also observed across different climatic environments (e.g., from wet tropics to seasonal subtropics). However, it remains

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unclear whether introduced geckos from tropics can flourish in non-native, cooler, subtropical areas.

The mourning gecko, *Lepidodactylus lugubris* (Duméril and Bibron, 1836), is one of the most widely distributed terrestrial reptile species, commonly occurring on most tropical and subtropical Pacific and Indian Ocean islands (Ineich, 1999). The success of *L. lugubris* is partially due to parthenogenetic reproduction: an all-female population produces clones (genetically uniform individuals) without mating. Because parthenogenetic reproduction allows establishment of a sustainable population from only a single individual, *L. lugubris* is a successful colonizer, particularly in island ecosystems where competition is reduced and food is abundant (Ineich, 2010). The geographical origin of unisexual *L. lugubris* is assumed to be tropical islands in Micronesia (Radtkey et al., 1995). In addition, further clonal diversity has been generated in other areas, and several endemic clonal types are reported in small isolated islands (e.g., the Daito Islands, Japan: Yamashiro et al., 2000; Murakami and Hayashi, 2019). Recently, several additional populations have been introduced and established in South and Central America, Australia, and Asia (Bauer and Henle, 1994; Hoogmoed and Avila-Pires, 2015; Lapwong and Juthong, 2018).

The Ryukyu Archipelago of Japan represents the northernmost distributional range of *L. lugubris*, where the species experiences a cold winter season compared to the tropics (Ota, 1994; Ineich, 1999; Sakai, 2016). In this area, populations of *L. lugubris* are divided into two groups based on their different endemicity and occurrence. In the Daito Islands, populations consist of several clones endemic to this isolated island group (Yamashiro et al., 2000; Murakami and Hayashi, 2019). They are considered to be native in these small islands, and their occurrence there was already recognized by the mid-1930s (Okada, 1936; Ota and Toyama, 1992). In other island groups in the Ryukyu Archipelago, *L. lugubris* was first recorded in the early 1970s and has been reported from most islands belonging to Okinawa Prefecture since then (Shibata et al., 1972; Maenosono and Toda, 2007). These non-Daito Ryukyu populations, reportedly predominated by the widely distributed triploid Clone C, are considered to have originated from recent accidental artificial transportations (Ota et al., 2004). In spite of several distributional reports of *L. lugubris* in the Ryukyu Archipelago, there is no demographic information of the invasive populations. During an ecological survey of *L. lugubris* on Okinawa-jima Island, I found a dense population in a coastal vegetation habitat where I conducted a mark-recapture survey and estimated their population density.

Materials and Methods

Field survey

I conducted a field survey at a small, elongated beachfront forest (100 m length, 6–11 m width, 1,068 m^2 area) on Okinawa-jima Island, Japan (26°44'34"N, 128°10'31"E) (see figure in Sakai, 2019). This forest mainly consists of sea hibiscus (*Hibiscus tiliaceus*: 8 m mean height), tropical almond (*Terminalia catappa*: 11 m mean height), screw pine (*Pandanus odorifer*: 8 m mean height), and beach cabbage (*Scaevola taccada*: 1 m mean height). The forest boundaries faced two types of environments: a beach 60–80 m width from the shore line, and a town area where pedestrians and cars pass both day and night. The nearlest street lamps were located over 50 m away and the study area had less than 3 lx of ambient light at night.

A total of four mark-recapture surveys were conducted over three years (September 2013, June and September 2014, and September 2015). In each survey period, I usually conducted five to six sampling efforts at three-day intervals. However, I sometimes conducted sampling efforts for two consecutive days while keeping previously collected geckos in captivity (28% of all sampling efforts), which I refer to as "consecutive

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samples" in the following analysis. I found three gecko species (*Lepidodactylus lugubris*, *Gekko hokouensis*, and *Hemidactylus frenatus*) in the habitat but collected only *L. lugubris* during the field survey. In each sampling day, I searched for geckos from sunset to midnight (for approximately five hours) by walking along the outer edge of the forest. I collected geckos by hand and placed them in small Ziploc bags (10×7 cm), that were punctured with several small holes to allow air exchange. I immediately transported geckos to an indoor field-laboratory close to the field site (<1 km). In the day following capture, I measured their snout-vent length and weighed them. I marked them with a toe clipping method and then photographed each gecko for complementary individual identification. After the measurements and manipulations, each gecko was released at its precise capture point.

Population analysis

I applied capture and recapture data to the Jolly-Seber open population model (White and Burnham, 1999). I used the formulation POPAN of the software MARK Version 8.0. The formulation POPAN allows the estimation of four demographic parameters: apparent survival rate (Phi), capture rate (P), probability of entrance (Pent), and population size (N). Considering numerical features of these demographic parameters, the following link functions were used in all models: logit for Phi and P, multinominal logit for Pent, and identity for N (see details in White and Burnham, 1999). The parameter Pent was considered to be time dependent (given parameter was changing during a survey period). On the other hand, the parameters Phi and P were considered as either time dependent or constant (given parameters were stable during a survey period). Therefore, I built four models with different combinations of demographic parameters (time dependent or constant) and selected the best ones in each survey period. Model selection was carried out based on the lowest Akaike Information Criterion corrected for small samples (AICc).

Time intervals between separate sampling efforts were set on a daily basis. In the case of consecutive samples, I started the next sampling effort while keeping previously collected geckos in captivity. Such consecutive samples were pooled as "one sampling occasion" that was regarded to be conducted on the intermediate day (Schwarz and Arnason, 2009). For example, if I conducted sampling efforts on days 3, 4, and 9, I pooled days 3 and 4 as one sampling event that was conducted on day 3.5 (intermediate between days 3 and 4). Then, I calculated the time interval between separate sampling efforts as 5.5 days (the interval between days 3.5 and 9).

Results

I collected 369 individuals in a total of 626 captures during four survey periods (the number of captures: 223 in September 2013 [6 sampling days], 91 in June 2014 [5 sampling days], 156 in September 2014 [5 sampling days], and 156 in September 2015 [6 sampling days]). Out of these 369 geckos, 131 individuals (35.5%) were captured multiple times; the mean number of captures per individual was 1.70±1.17 (1–10) (mean±SD, range). The mean time interval between capture and recapture was 6.9±4.4 (4–23) days within each survey period (n=207) and 278.5±129.7 (71–477) days across survey periods (n=50).

The best models had different combinations of demographic parameters among survey periods (Table 1). In September 2013 and June 2014, the models with constant survival rate (Phi) and constant capture rate (P) showed the lowest AICc. On the other hand, in September 2014 and September 2015, the models with constant survival rate (Phi) and time dependent capture rate (P) showed the lowest AICc. According to the best models in each survey period, total population size was estimated as 94–284 individuals (Table 2). Given that the beachfront forest is approximately 1,068 m^2, the density of the

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TABLE 1. Results of model selection in population analyses. Models with different combinations of demographic parameters (Phi: apparent survival rate, P: capture rate, Pent: probability of entrance) were compared by AICc. Parameters Phi and P were considered as either time dependent (changing during a survey period) or constant (stable during a survey period). "t" indicates time dependent parameters, and "c" indicates constant parameters.

Survey period	Model (Phi/P/Pent)	AICc	ΔAICc	No. of parameters
Sep 2013	c/c/t	405.1	—	8
	c/t/t	410.8	5.7	13
	t/t/t	419.6	14.5	17
	t/c/t	420.2	15.1	12
Jun 2014	c/c/t	177.4	—	7
	t/c/t	183.8	6.4	10
	c/t/t	185.9	8.5	11
	t/t/t	190.5	13.1	14
Sep 2014	c/t/t	314.4	—	11
	c/c/t	315.1	0.7	7
	t/c/t	320.6	6.2	10
	t/t/t	321.1	6.7	14
Sep 2015	c/t/t	316.3	—	13
	t/c/t	316.5	0.2	12
	c/c/t	318.8	2.5	8
	t/t/t	325.0	8.7	17

TABLE 2. Population size and density of mourning geckos. Population size was estimated by the best models in each survey period (see details in Table 1). Population density was calculated as the number of individuals divided by the field area (1,068 m^2).

Survey period	No. of individuals		Density (individuals/ha)	
	Estimate	95% CI	Estimate	95% CI
Sep 2013	283.7	238.7–352.5	2,656	2,235–3,301
Jun 2014	94.0	77.3–129.1	880	724–1,209
Sep 2014	146.2	124.3–187.8	1,369	1,164–1,758
Sep 2015	175.4	148.4–220.9	1,642	1,390–2,068

focal population was calculated as 880–2,656 geckos/ha (i.e., 0.09–0.27 geckos/m^2).

DISCUSSION

The population analysis demonstrates that *L. lugubris* established a dense population on subtropical Okinawa-jima Island. Conspecifics in tropical areas show population densities of 8,600 geckos/ha in Oahu, Hawaii (Jarecki and Lazell, 1987), 7,600 geckos/ha in Moorea, French Polynesia (Ineich, 1988), and 1,000–2,700 geckos/ha in Suva, Fiji (Case et al., 1994). Another invasive gecko species, *Hemidactylus frenatus*, established a dense population of 1,000–3,000 geckos/ha in Suva, Fiji (Case et al., 1994). It should be noted that these population densities were estimated by different survey efforts and methods. However, the density of the focal subtropical

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population of *L. lugubris* seems to be as high as that of many tropical populations. This result implies a successful colonization of invasive *L. lugubris* in a cooler non-native subtropical area.

However, considering spatial ecological features of *L. lugubris*, the population size of the present survey may possibly be underestimated. Mourning geckos in the focal population show a high level of site fidelity and a small home range (Sakai, 2019). If some geckos inhabit areas where they are difficult to be captured (e.g., dense bushes or high perch site), sampling would be biased to individuals inhabiting areas where they are easily captured. In this case, the survey area is only a part of the actual occupied area by the geckos. It should be noted that the Jolly-Seber open population model assumes no sampling bias between marked and unmarked individuals (Pledger and Efford, 1998). Given that unidentified individuals of *L. lugubris* were also observed in areas where they were impossible to capture, it is most likely that the actual population size of *L. lugubris* could be much larger than the present estimation.

In conclusion, this study shows that *L. lugubris* flourishes at the northernmost extremity of its range at similar densities as those observed in tropical populations. This is the first report that quantifies the population density of a tropical gecko species that invaded the seasonal subtropics. Further demographic investigation in other non-native populations, as well as native Daito populations, of *L. lugubris* would help to understand why and how highly dense clonal populations occur in cooler areas. In addition, the occurrence of dense populations of a non-native predator may impact potential prey species, such as native small insects, and create competition with native insectivorous lizards. However, the potential threat of *L. lugubris* to local ecosystem is still unclear in the Ryukyu Archipelago. In the future, comparative ecological surveys between areas with and without invasive *L. lugubris* would be informative.

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