

VARIATION IN COLD TOLERANCE OF NORTHERN EDGE POPULATIONS OF THE COMMON HOUSE GECKO (*HEMIDACTYLUS FRENATUS*)

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Abstract.—The Common House Gecko (*Hemidactylus frenatus*) is one of the most successful colonizers among squamates and is widely distributed in tropical and subtropical regions of the world. Recently, this species has been found on the island of Amamioshima, Japan, extending its previous northern range limit, and it has quickly spread throughout the island within two decades. Possible explanations for this rapid northward range expansion might be because of climate change or to adaptation of the gecko to the cooler weather on the island. We examined meteorological data and inter-population variation in cold tolerance of this species near the northern edge to test these hypotheses. We also compared the cold tolerance of this gecko between urban/rural populations on islands at different latitudes. We found that rural populations consistently have lower CT_{min} compared to their counterpart urban populations on all islands. The higher latitude populations tended to have lower CT_{min} , but the lowest CT_{min} was found in the rural population of Okinawajima instead of the northernmost on Amamioshima, despite that weather on the latter island is apparently colder than that of the former. Meteorological data also showed an increase in temperature on all three islands, and the average temperature of Amamioshima after 2000 is similar to the temperature of Okinawa before 1955. These results suggest that the recent range expansion at the northern edge of this species is chiefly attributable to climate change, but the significant geographic difference in cold tolerance suggests a contribution from local adaptation.

Key Words.—climate change; cold tolerance; range expansion; latitude; global warming

INTRODUCTION

Biological invasion is one of the most serious threats to biodiversity conservation worldwide (Gurevitch and Padilla 2004; Bellard et al. 2016; Pyšek et al. 2020). Invasions by non-native species can be divided into several phases, including transportation of individuals, establishment of a population, and range expansion to a new location (Sakai et al. 2001). Human activities have facilitated these phases of biological invasion in various ways. The rapid development of the global transportation network has enhanced the chance that individuals will disperse across geographic barriers (Simberloff et al. 2013; Lewis and Maslin 2015). Worldwide climatic change is considered to have increased the chances of establishment of invasive populations and promoted further spread to new locations (Hellmann et al. 2008). Human activities have made vast spaces with novel environments, such as urban areas, and certain species that have some pre-adaptive physiological and ecological traits successfully invade these

spaces (Santana Marques et al. 2020). After invasive populations have established themselves in a novel region or environment, natural selection can facilitate populations acquiring ecological and behavioral traits that enhance dispersal ability allowing animals to expand their range (Narimanov et al. 2022). It is important to understand the factors that contribute to establishment of a population, population growth, and subsequent range expansion in biological invasions.

The Common House Gecko (*Hemidactylus frenatus*) is one of the most successful squamate colonizers and has spread widely in tropical and subtropical regions (Lever 2006; Rödder et al. 2008; Hoskin 2011). This species has also successfully colonized multiple temperate regions, such as Mexico, Australia, and East Asia (Farr 2011; Hoskin 2011; Kurita 2013). In East Asia, the northern distribution edge of *H. frenatus* is in the Ryukyu Archipelago, Japan (Fig. 1), in which the islands align in a northeast–southwest direction, across a temperate to subtropical transition zone. Within the archipelago, the distribution of this species had long

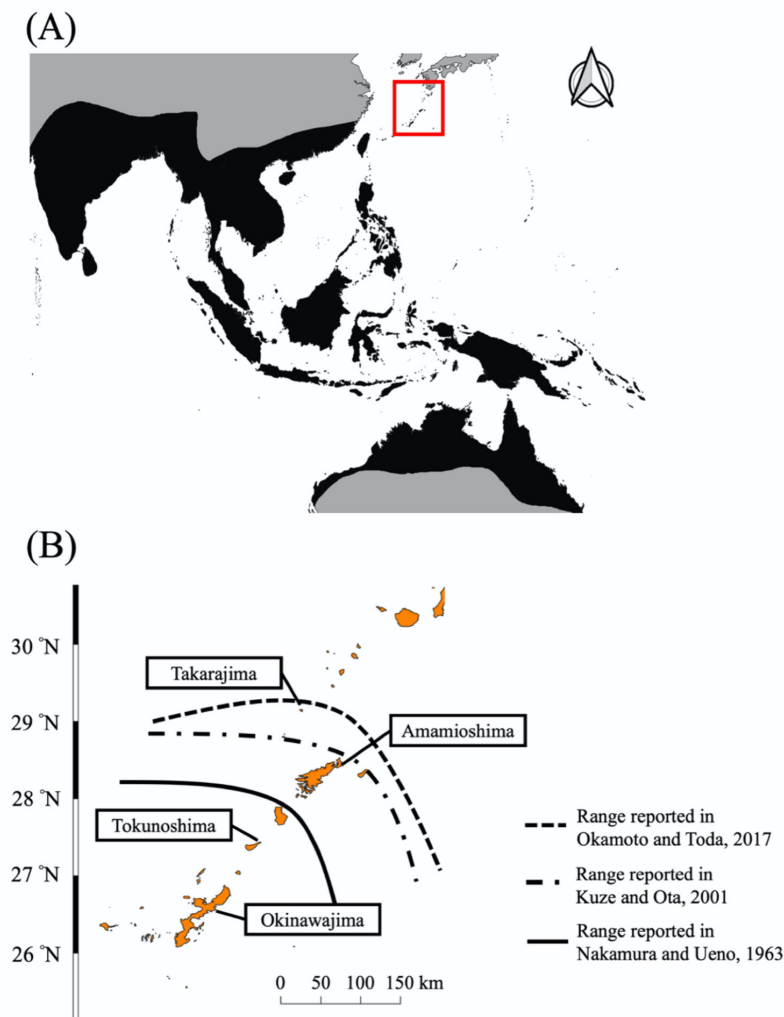


FIGURE 1. (A) Known distribution of the Common House Gecko (*Hemidactylus frenatus*) in Asia and Australia. The black area represents the known distribution of this species recreated from the occurrence data (Global Biodiversity Information Facility; GBIF.org 18 July 2023 GBIF Occurrence Download <https://doi.org/10.15468/dl.gk5nju>). The red square indicates the area shown in (B), showing the recent northern range expansion within the Ryukyu Archipelago.

been limited to Tokunoshima and more southern islands, such as Okinawajima (Nakamura and Ueno 1963; Maenosono and Toda 2007; Fig. 1). In 2000, however, *H. frenatus* was reported to have established a population near the major harbor in northern part of Amamioshima, an island located about 60 km north of Tokunoshima (Kuze and Ota 2001). Thereafter, this species rapidly spread across the island until 2013 (Kurita 2013). In 2016, Okamoto et al. (2017) reported the occurrence of *H. frenatus* in Takarajima, a small island about 100 km farther north than Amamioshima (Fig. 1).

The colonization of islands by *H. frenatus* is considered to be facilitated by human transport

(Carranza and Arnold 2006). Takahashi (2005) observed three live *H. frenatus* on walls of cargo containers in a passenger boat connecting Okinawajima, Tokunoshima, Amamioshima, and more northern regions, operating on a daily basis. Despite the putative frequent opportunities for human transport, *H. frenatus* had not colonized Amamioshima until the 2000s (Kuze and Ota 2001). Temperatures of the coldest month in Amamioshima occasionally drop below the known critical minimum for the species of 11.9° C (Huey et al. 1989). Empirical research also suggests that *H. frenatus* stops feeding when the ambient temperature drops below 17° C (Lei and Booth 2014). A few previous

authors reported that free ranging *H. frenatus* had lost their righting reflex (Toda and Jono 2017) and even die (Toyama 1984) in extremely low temperature in winter even on Okinawajima. These anecdotal observations suggest that a limiting factor for the distribution of *H. frenatus* in this region may be cold winter temperatures.

Possible explanations for the recent range expansion of *H. frenatus* in the Ryukyu Archipelago might be the thermal environment becoming suitable for *H. frenatus* due to climate change and/or that the species has gained greater cold tolerance, allowing them to survive at a higher latitude. In the case of *Anolis* lizards, range expansion into higher latitudes in North America may result from the evolution of greater tolerance of low temperatures (Kolbe et al. 2014; Campbell-Staton et al. 2016, 2018). Recent studies in southern edge populations of *H. frenatus* in Australia suggest that it not only shows stronger cold tolerance (Lapwong et al. 2021) but also a preference (Lapwong et al. 2020) for lower temperatures compared to native populations in Thailand.

It is reasonable to assume that the range expansion in the northern populations of *H. frenatus* in the Ryukyu Archipelago may result from the species gaining stronger cold tolerance. On the other hand, the climate change hypothesis predicts no difference in cold tolerance of *H. frenatus* along latitudinal gradient in the Ryukyu Islands. Temperatures in urban areas are considerably higher compared to rural or natural environments even at the same latitude, which is known as the Urban Heat Island Effect (Heisler and Brazel 2010). This thermal condition of urban environments may also influence the range expansion of *H. frenatus* because of the highly human commensal nature of this gecko. Our main purpose is to determine whether there is any difference in cold tolerance along the latitudinal and rural–urban gradients near the northern edge of the distribution of *H. frenatus*. These results may shed light on possible causes of the rapid expansion of the range of this species since 2000

MATERIALS AND METHODS

Climatic data.—To understand the temporal changes in air temperatures in relation to regional differences within the Ryukyu Islands, we chose three islands along a latitudinal gradient; Ishigakijima, Okinawajima, and Amamioshima. We selected Okinawajima as a substitute for Tokunoshima in our comparisons with Ishigakijima and Amamioshima

due to the incompleteness in the past climate data for Tokunoshima, which was the exact northern limit before 2000 (Kuze and Ota 2001). Among the three islands, Okinawajima and Ishigakijima have had stable populations of *H. frenatus* since at least 1907 (Stejneger 1907), whereas Amamioshima lacked that species before 2000 (Kuze and Ota 2001). These three islands should adequately represent the latitudinal thermal gradient in the Ryukyu Islands.

We used average daily minimum temperature for the entire year (ADMTY) and average daily minimum temperature of the coldest month (ADMTC) at the representative weather stations taken from the Japanese Meteorological Agency (<https://www.data.jma.go.jp/obd/stats/etrn/index.php>) for those three islands; Ishigaki weather station (24.337°N, 124.163°E), Naha weather station in Okinawajima (26.207°N, 127.687°E), and Naze weather station in Amamioshima (28.378, 129.495). We separated the meteorological data into three time periods for statistical comparisons: (1) before 1955; (2) 1955–1999; and (3) after 2000. These records cover the years 1897 to 2021, with missing data for Okinawajima (Naha) between 1944 to 1951. We used the Shapiro-Wilk Test to check the normality and Levene's Test for variances homogeneity of our data to determine whether they meet the assumptions for parametric analysis. Our original data for urban and rural climate comparison met the assumption of variance homogeneity, but data for ADMTC deviated from the assumption of normality while ADMTY did not (Supplemental Information Table S2). Thus, the differences in ADMTY between urban and rural area within Okinawajima were analyzed using Analysis of Variance (ANOVA) with Tukey Honestly Significant Differences (HSD) *post hoc* Tests. All comparisons of ADMTC and comparisons for islands and between different periods of time for ADMTY did not meet parametric assumptions (Supplemental Information Table S2), and we used Kruskal-Wallis Tests for overall significant and Pairwise Wilcoxon Tests with sequential Bonferroni correction for pairwise comparison instead of ANOVA. All statistical analysis was performed by using R version 3.6.2 (R Core Team 2019).

In addition, we compared temperature data between rural and urban regions to see the effect of environment on the local climate. We examined data of the same two variables shown above at four weather stations in Okinawajima, Naha weather station (26.207°N, 127.687°E as representative of urban environment in southern part of the island), Itokazu

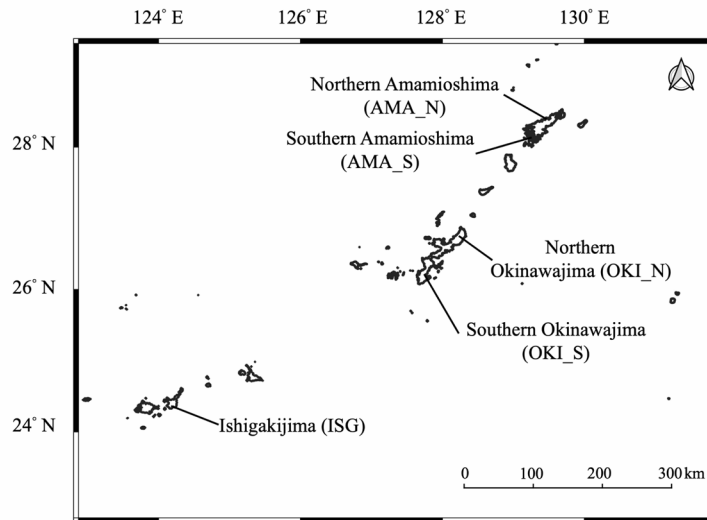


FIGURE 2. Five sampling sites of the Common House Gecko (*Hemidactylus frenatus*) on the three islands along a latitudinal gradient. Each site is indicated by both an urban and rural sampling sites.

station (26.153°N, 127.765°E, of rural environment in southern part of the island), Nago station (26.593°N, 127.965°E, of urban in the northern part), and Oku station (26.835°N, 128.272°E, of rural in the northern part). Because available meteorological data for the rural weather stations are limited, we used data from 2013 to 2021 for this comparison. We analyzed the differences among selected weather stations using the same statistical methods mentioned above.

Study sites.—To assess a change in cold tolerance in *H. frenatus*, we selected five regions along the latitudinal gradient: (1) Ishigakijima (ISG); (2) southern Okinawajima (Naha, OKI_S); (3) northern Okinawajima (Kunigami, OKI_N); (4) southern Amamioshima (Koniya, AMA_S); and (5) northern Amamioshima (Naze, AMA_N; Fig. 2). Previous studies have documented the changes in thermal tolerance of ectotherms in urban area through plastic or evolutionary change (Diamond et al. 2017, 2018; Campbell-Staton et al. 2020). We considered that populations of *H. frenatus* in urban and rural areas may experience different thermal environments. Therefore, we distinguished between the thermal effects related to latitude alone and those related to the local environment. We set a pair of urban and rural sites in each region along the latitudinal gradient. We determined the urban-rural division following GIS data for 1:25,000 vegetation map released by the Biodiversity Center of Japan, Ministry of the Environment (<http://gis.biodic.go.jp/webgis/index.html>), and chose some representative sites for sampling of the geckos. The urban sites we

sampled were: (1) Ishigaki City (ISG-UA: 24.341°N, 124.154°E); (2) Matsuyama (OKI_S-UA: 26.218°N, 127.677°E); (3) Kunigami (OKI_N-UA: 26.747°N, 128.173°E); (4) Koniya (AMA_S-UA: 28.148°N, 129.311°E); and (5) Naze (AMA_S-UA: 28.388°N, 129.493°E). As for rural sites along the latitudinal gradient, we chose: (1) Banna (ISG-RA: 24.368°N, 124.157°E); (2) University of the Ryukyus (OKI_S-RA: 26.250°N, 127.766°E); (3) Benoki (OKI_N-RA: 26.798°N, 128.233°E); (4) Seisui (AMA_S-RA: 28.142°N, 129.330°E); and (5) Yamato Harbor (AMA_S-RA: 28.356°N, 129.399°E).

Sampling geckos and treatment in captivity.—We captured 231 geckos by hands from July to October, 2019 and 2020 (Supplemental Information Table S1). We transported geckos to the University of the Ryukyus, Okinawa, Japan, where we measured snout-vent length (SVL) with a ruler to the nearest 1 mm and body mass (Mb) to the nearest 0.01 g using a balance. Because our data did not meet assumptions for parametric analysis, we used Kruskal-Wallis Tests to determine if there were sexual differences in SVL or body weight, respectively. We maintained geckos at room temperature (about 27° C) in individual transparent plastic boxes (206 × 106 × 64 mm) with a vented plastic lid and a folded paper towel for substrate and shelter. Each gecko received water with a supplement (including vitamin and calcium) *ad libitum* and a live cockroach every 2–3 d. The natural ambient light regime provided an approximate 13:11 light:dark cycle. We fasted individuals for at least 24 h before measuring their cold tolerance.

Critical thermal minimum temperature.—We determined critical thermal minimum (CT_{min}) as the body temperature at which the gecko lost its righting response or showed a morbid response (Qu et al. 2011; Phillips et al. 2016). We moved each gecko into a transparent, sealed chamber ($197 \times 257 \times 89$ mm) and cooled them using an incubator (Model MIR-153; Sanyo Electric Company, Ltd., Osaka, Japan) set to 5° C. Using a digital thermometer (Model D717; Tateyama Kagaku Ind., Toyama, Japan) with hand-made glass coated thermocouples inserted into the cloaca, we measured the starting body temperature for each individual. We placed another ethanol-filled thermometer inside the chamber, which allowed us to ensure that the rate of air temperature decrease was $< 1^\circ$ C per minute inside of the chamber, starting from 27° C. We confirmed in the preliminary experiments that the body temperature of geckos decreased almost the same as the air temperature by monitoring the former temperature with thermocouples kept inside their cloaca. We covered all surfaces inside the experimental chamber with unscented baby powder to prevent the geckos from sticking to the surfaces.

We checked the righting reflex of individuals every minute starting from 10 min after the start of incubation, and we measured the body temperature immediately after the gecko had lost the righting reflex. After each trial, we placed every gecko back to its husbandry cages with newly supplied food and water. We tested each gecko three times, with an interval of at least 24 h between each trial. We selected the lowest CT_{min} of each individual as indicator of the cold tolerance in *H. frenatus* and combining data point of male and females in all of the following analyses. To prevent possible acclimatization to the captive environment, we completed all trials within a week of capture. We euthanized all geckos following procedures approved in the animal experiment guidelines of the University of the Ryukyus. We calculated the Pearson Product-moment Correlation Coefficient between SVL or body weight with CT_{min} . We analyzed the differences in CT_{min} among populations from different latitudes and habitats (urban/rural) using the same statistical methods as for climatic data.

RESULTS

Climatic data.—Average daily minimum temperatures throughout the year varied from 17.76° C to 22.52° C depending on time period and island and average daily minimum temperatures for

the coldest month varied from 10.80° to 16.35° C, depending on time period and island (Table 1). There were significant differences between islands and between different periods of time for both ADMTY ($H = 300.07$, $df = 8$, $P < 0.001$) and ADMTC ($H = 259.47$, $df = 8$, $P < 0.001$). For annual average, Ishigakijima had significantly higher ambient minimum temperatures among the three islands in each time period (Supplemental Information Table S3; Fig.3). Conversely, Amamioshima had the lowest ambient temperature among the three islands (Supplemental Information Table S3). It should be noted that, although the average ambient temperature was consistently colder in Amamioshima than Okinawajima in all three time periods, the annual average temperature of Amamioshima after 2000 was relatively less different from the past temperature of Okinawajima before 1955 (Supplemental Information Table S3). The average daily minimum temperature in the coldest month in Amamioshima after 2000 is still lower than that of the past for Okinawajima (Supplemental Information Table S4) because of the magnitude of increase is smaller in Amamioshima than Okinawajima (Fig. 4), but the former has become apparently closer to the latter (Fig. 4).

There were significant differences in the annual average and average of the coldest month among the weather stations represented the urban and rural ambient temperature within Okinawajima (ADMTY, $F_{3,32} = 119.6$, $P < 0.001$, Supplemental Information Table S5; ADMTC, $H = 21.81$, $df = 3$, $P < 0.001$). Itokazu (annual average: $19.60^\circ \pm 0.29^\circ$ C; coldest

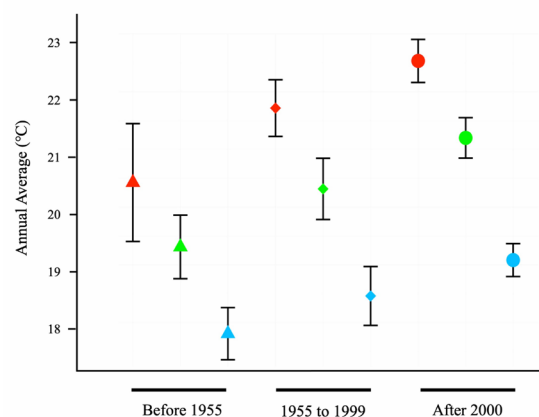


FIGURE 3. Annual average of daily minimum temperature on three islands before 1955 (1897–1955), 1955–1999, and after 2020 from weather stations for three islands; Ishigakijima (ISH; red), Okinawajima (OKI; green) and Amamioshima (AMA; blue). Different time periods are indicated by different legend: before 1955 (triangles), 1955–1999 (diamonds), and after 2020 (dots)

TABLE 1. Mean daily minimum temperatures throughout the year and for the coldest months (mean \pm standard deviation) of the three study islands.

Time	Amamioshima	Okinawajima	Ishigakijima
Yearly			
Before 1955	17.76° \pm 0.72° C	19.35° \pm 0.61° C	20.50° \pm 0.97° C
1955–1999	18.46° \pm 0.51° C	20.32° \pm 0.53° C	21.72° \pm 0.49° C
After 2000	19.08° \pm 0.29° C	21.20° \pm 0.35° C	22.53° \pm 0.37° C
Coldest Months			
Before 1955	10.80° \pm 0.87° C	12.81° \pm 1.14° C	14.43° \pm 1.44° C
1955–1999	11.01° \pm 0.96° C	13.51° \pm 1.06° C	15.34° \pm 1.20° C
After 2000	11.74° \pm 0.74° C	14.50° \pm 0.79° C	16.35° \pm 0.86° C

month: 13.07° \pm 0.68° C) and Oku (annual average: 18.89° \pm 0.28° C; coldest month: 12.23° \pm 0.65° C) as representatives of rural environments had significantly lower temperatures than Naha (annual average: 21.43° \pm 0.30° C; coldest month: 14.72° \pm 0.72° C) and Nago (annual average: 20.68° \pm 0.35° C; coldest month: 13.64° \pm 0.72° C) with urban environments in both ADMTY (Tukey HSD, $P < 0.010$, Supplemental Information Table S6) and ADMTC (Supplemental Information Table S7).

Cold tolerance.—Mean SVL of lizards in urban areas varied from 49.6–55.4 mm and in rural areas from 44.6–53.4 (Table 2). Mean weight of lizards varied from 2.04–3.45 g in urban areas and 2.03–3.58 g in rural areas (Table 2). In urban areas, mean CT_{min} varied from 10.95°–11.73° C and in rural areas, from 9.48°–10.98° C (Table 3). The correlation between CT_{min} and SVL was significant ($r = 0.17$, $t = 2.54$, $P = 0.012$) as was CT_{min} with body weight ($r = 0.28$, $t = 4.38$, $P < 0.001$), but SVL was not significantly correlated with body weight ($r = 0.02$, $t = 0.25$, $P = 0.803$). Mean body weight of males was (3.25 \pm 0.97 g) significantly larger ($H = 44.79$, $df = 1$, $P < 0.001$) than females (2.43 \pm 0.68 g). Also, SVL of males (53.5 \pm 4.73 mm) was significantly larger ($H = 42.63$, $df = 1$, $P < 0.001$) than that of female (49.5 \pm 3.95 mm).

Differences in cold tolerance did not differ significantly between sexes ($H = 2.60$, $df = 1$, $P = 0.107$) or the order of trials ($H = 5.22$, $df = 2$, $P = 0.073$). The CT_{min} of *H. frenatus* differed significantly among populations from different habitats in different latitude ($H = 128.76$, $df = 9$, $P < 0.001$). CT_{min} of *H. frenatus* from the rural habitat was consistently lower than for the urban habitat for each pair of sites at each latitude (Supplemental Information Table S8). The CT_{min} of *H. frenatus* from urban population of Ishigakijima (Fig 5) was significantly higher than

the other islands in both urban and rural populations (Supplemental Information Table S8). There were no significant differences were found in locations between Amamioshima and Okinawajima either in urban or rural in northern Okinawajima, except for the rural population from southern Amamioshima (Supplemental Information Table S8). The rural population of *H. frenatus* in southern Okinawajima showed the lowest CT_{min} (9.48° \pm 0.55° C) of all populations we examined (Supplemental Information Table S8), rather than the northernmost rural population from Amamioshima (10.36° \pm 0.54° C; Fig. 5).

DISCUSSION

We found differences in cold tolerance of *H. frenatus* populations from sites in different latitude and habitats. CT_{min} was consistently lower in rural

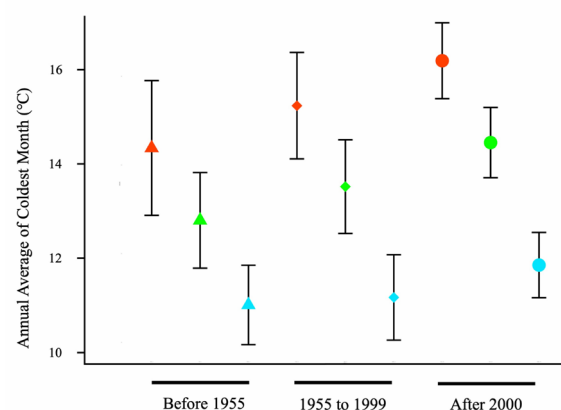


FIGURE 4. Average of daily minimum temperature of the coldest month on three islands before 1955 (1897–1955), 1955–1999, and after 2000 from weather stations for three islands; Ishigakijima (ISH; red), Okinawajima (OKI; green) and Amamioshima (AMA; blue). Different time periods are indicated by different legend: before 1955 (triangles), 1955–1999 (diamonds), and after 2000 (dots).

TABLE 2. Mean (\pm standard deviation) of snout-vent lengths (SVL, mm) and weights (g) of the Common House Gecko (*Hemidactylus frenatus*) in different habitats among three islands. Islands are AMA_N = northern Amamioshima; AMA_S = southern Amamioshima; OKI_N = northern Okinawajima; OKI_S = southern Okinawajima; ISG = Ishigakijima.

Island	Urban	Rural
SVL		
AMA_N	54.03 \pm 3.23 mm	53.42 \pm 4.36 mm
AMA_S	53.74 \pm 4.29 mm	51.57 \pm 5.34 mm
OKI_N	55.42 \pm 2.94 mm	51.23 \pm 3.72 mm
OKI_S	50.81 \pm 3.08 mm	44.59 \pm 3.80 mm
ISG	49.64 \pm 3.52 mm	48.76 \pm 4.75 mm
Weight		
AMA_N	2.04 \pm 0.60 g	2.03 \pm 0.66 g
AMA_S	2.22 \pm 0.57 g	2.15 \pm 0.36 g
OKI_N	3.45 \pm 0.78 g	3.58 \pm 0.38 g
OKI_S	2.66 \pm 0.57 g	2.52 \pm 0.68 g
ISG	3.26 \pm 0.73 g	2.39 \pm 0.39 g

populations compared to their counterpart urban sites throughout the latitudinal gradient we investigated. Urban areas not only provide more suitable thermal environment for introduced species (Battles and Kolbe 2019), but also serve as sources of new individuals to the adjacent rural area. In fact, all our urban sampling sites are in major cities or large towns, which are also the location of large harbors on the three islands. Because the dispersal of *H. frenatus* is highly dependent upon human transport, *H. frenatus* may first colonize urban areas where major harbors are located, and subsequently acclimatize or adapt to the colder environments of adjacent rural areas. In the case of *H. frenatus* in Australia, populations with longer invasion histories and higher population abundances in urban areas facilitated further dispersal and establishment of new population in adjacent rural areas (Barnett et al. 2017).

TABLE 3. Mean (\pm standard deviation) critical thermal minimum (CT_{min}) of the Common House Gecko (*Hemidactylus frenatus*) in different habitats along a latitudinal gradient in the Ryukyu Islands, Japan. Islands are AMA_N = northern Amamioshima; AMA_S = southern Amamioshima; OKI_N = northern Okinawajima; OKI_S = southern Okinawajima; ISG = Ishigakijima

Island	Urban	Rural
AMA_N	10.95° \pm 0.44° C	10.36° \pm 0.55° C
AMA_S	11.11° \pm 0.57° C	10.27° \pm 0.56° C
OKI_N	11.31° \pm 0.54° C	10.66° \pm 0.44° C
OKI_S	10.70° \pm 0.51° C	9.48° \pm 0.56° C
ISG	11.73° \pm 0.25° C	10.98° \pm 0.40° C

A previous study reported the CT_{min} for *H. frenatus* in Hawaii as 11.9° C (Huey et al. 1989). All population we examined had lower CT_{min} except for the urban population in Ishigakijima (11.73° \pm 0.25° C). In general, cold tolerance is expected to reflect the lowest temperature experienced by a population (Sunday et al. 2011). The lowest CT_{min} of *H. frenatus* that we found was not in the northernmost Amamioshima population with the lowest ambient temperature, but rather observed in the rural population from southern Okinawa. Although CT_{min} in the rural population of southern Amamioshima was significantly lower than the northern Okinawajima populations, there were no significant difference between the population from northern Amamioshima and the latter. On the other hand, the ambient temperature has been gradually rising throughout the past several decades among all three islands, which may be attributable to urbanization and global warming. Combining the climatic data and the geographic variation in cold tolerance of *H. frenatus*, the recent northward range expansion of the species in the Ryukyu Islands may result from climate change, rather than increased cold tolerance.

The mechanism responsible for the highest cold tolerance of *H. frenatus* in the rural population in Okinawajima remains unclear at the moment. Other empirical research suggests, however, that not only acclimation but also genetic adaptation can shape the thermal tolerance of an invasive species (Kolbe et al. 2014; Campbell-Staton et al. 2018). Although it is difficult to separate the effect of acclimation and local

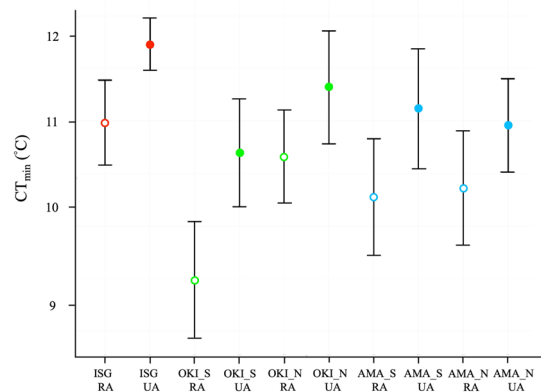


FIGURE 5. Critical minimum temperature (CT_{min}) of the Common House Gecko (*Hemidactylus frenatus*) from urban (UA)/rural (RA) sites at the five localities along the latitudinal gradient in the Ryukyu Islands, Japan. Solid dots indicate urban and hollow dots indicate rural samples, respectively. Island are indicated by different colors: Ishigakijima (red); Okinawajima (green); Amamioshima (blue). Sample sites are indicated as abbreviations: ISG = Ishigakijima, OKI_S = southern Okinawajima, OKI_N = northern Okinawajima, AMA_S = southern Amamioshima, and AMA_N = northern Amamioshima.

adaptation, at one point in time, the occurrence of the lowest CT_{min} in the rural Okinawa population where the ambient temperature was not the lowest among the study sites is difficult to explain by the acclimation hypothesis alone.

The theory of range expansion predicts that, if the edge population is highly fragmented, random effects will be too great for a population to adapt successfully to a novel environment (Courchamp et al. 1999; Holt and Keitt 2000, 2005), whereas a highly connected population cannot achieve fixation of a locally adaptive gene due to continuous influx of less adaptive genes from the source population (Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997; Lenormand 2002). Previous research on other highly invasive congeners of *H. frenatus*, such as the Tropical House Gecko (*H. mabouia*) and the Mediterranean House Gecko (*H. turcicus*), suggested this genus has limited self-dispersal abilities (Klawinski 1991; Locey and Stone 2006; Short and Petren 2011). We can reasonably assume that the migration rate of *H. frenatus* into rural areas is relatively limited, which may promote local adaptation to colder conditions in *H. frenatus*. The parallel acclimatization or adaptation of *H. frenatus* to the colder environment in rural areas across a latitudinal gradient provides an excellent opportunity to examine the underlying theory in the future. Species with tropical origins, such as *H. frenatus*, are predicted to have relatively narrow thermal tolerances because they evolved in stable thermal environments (Addo-Bediako et al. 2000; Janzen, 1967; Kingsolver, 2009); however, the global distribution of *H. frenatus* is predicted to expand as a consequence of global warming (Rödder et al. 2008). Our current results demonstrate that both urbanization and global warming act synergistically to promote the range expansion of a tropical invasive species at its northern edge and that the exposure of the species to novel climate might further facilitate widening of its thermal tolerance through phenotypic plasticity or local adaptation under certain conditions.

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