



# Shifts in thermal tolerance of the invasive Asian house gecko (*Hemidactylus frenatus*) across native and introduced ranges

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**Abstract** The ability to rapidly adjust thermal tolerance in response to variable temperatures may facilitate the success of invasive species in non-native ranges. The Asian house gecko *Hemidactylus frenatus* is native to the tropics of South and Southeast Asia. This small lizard has spread across the globe and has also successfully invaded colder regions of Australia. In this study, we investigated whether this species displays plasticity in thermal tolerance in its introduced range. We measured cold tolerance ( $CT_{\min}$ ) and heat tolerance ( $CT_{\max}$ ) of *H. frenatus* from two native tropical populations in Thailand, and two introduced subtropical populations in southeastern Australia. We also explored seasonal variation in the thermal tolerance of the introduced populations. We found that heat tolerance ( $CT_{\max}$ ) of geckos did not differ among four populations in Thailand and Australia (range = 43.4–43.7 °C). By contrast, geckos from southeastern Australia had lower cold tolerance ( $CT_{\min}$ ) (mean =

10.43 °C) than geckos from Thailand (mean = 11.57 °C). We also documented seasonal shifts in cold tolerance of *H. frenatus* from southeastern Australia. Geckos captured in winter had cold tolerances 1–2 °C lower than those captured in summer. Unexpectedly, this shift in cold tolerance was accompanied by a 1–2 °C upward shift in heat tolerance. Our results support a growing body of evidence showing that tropical invaders can adjust cold tolerance downwards via plasticity or acclimation. Such changes may allow tropical invaders to expand their geographic range into colder regions of non-native ranges.

**Keywords** Invasive species · Ectotherm · Thermal biology · Critical thermal · Adaptation · Acclimation

## Introduction

Invasive species cause ecological and economic impacts worldwide and have become a significant concern in recent decades (Jardine and Sanchirico 2018; McNeely et al. 2001; Pimentel et al. 2005). Once invasive species become established, controlling or eradicating them is costly and difficult (Leung et al. 2002). However, knowledge about the future spread of invaders can help to inform managers about future impacts, and may help to buy time to develop practical tools to mitigate such impacts. To predict the future

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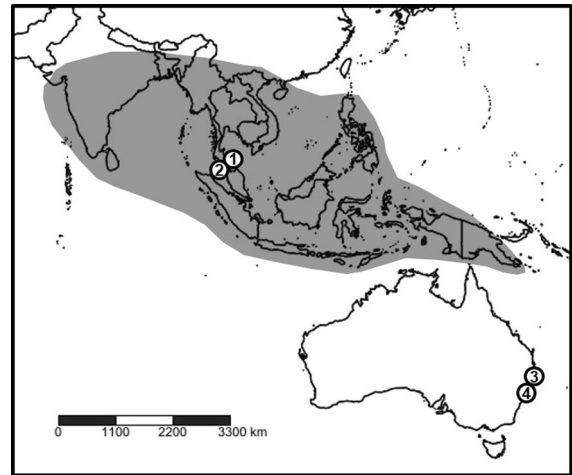
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spread, we need to understand the factors that promote or limit the distribution of the invader (Lockwood et al. 2013). One common approach for predicting the spread of invaders is to use ecological niche models that incorporate the climatic distribution of the species in its native range to predict its future range (Jiménez-Valverde et al. 2011; Peterson 2003; Rödder et al. 2008). For ectotherms, physiological traits can be incorporated into mechanistic models to predict future geographic ranges (Kearney et al. 2008). However, both of these modeling approaches may yield inaccurate predictions if species display niche shifts in newly invaded areas (due to release from competitors or predators), or if their thermal traits have changed over time due to adaptive plasticity or evolution (Jeschke and Strayer 2008). For example, populations of some invasive species have displayed rapid divergence in thermal traits, which has allowed them to spread beyond their predicted ranges (Kolbe et al. 2012; Leal and Gunderson 2012; McCann et al. 2014; Vimercati et al. 2018). To date, most studies have compared the thermal physiology of invasive species and native species (Kelley 2014), and less is known about how the thermal physiology of invasive species can change during the invasion processes.

The Asian house gecko (*Hemidactylus frenatus*) is one of the most widespread and successful invasive reptiles, and it occurs in all tropical regions around the world (Carranza and Arnold 2006). The gecko is native to South and Southeast Asia, and its natural geographic range encompasses India, Sri Lanka, Bangladesh, southern China, Thailand, Malaysia, Indonesia, and the Philippines (Fig. 1) (Bansal and Karanth 2010; Carranza and Arnold 2006; Case et al. 1994; Lever 2006; Ota and Whitaker 2010). The house geckos established populations in tropical Australia in the 1960s, and since 2000s the species has established populations in colder subtropical regions of eastern Australia (Hoskin 2011). The study by Gill et al. (2001) found that most introduced *H. frenatus* entering New Zealand came from ship trade originating from tropical Asia, including Thailand, Singapore, Malaysia, Indonesia, Vietnam, the Philippines, and Papua New Guinea. Therefore, we assumed that the established population in Australia originated from similar trade involving coastal tropical populations. Although *H. frenatus* could spread into areas with low and fluctuating temperatures, the introduced populations should have a slower evolution rate due to their limited



**Fig. 1** Locations of study populations of *H. frenatus* in Thailand [Hat Yai (1) and Satun (2)] and Australia [Yamba (3) and Coffs Harbour (4)]. Study populations in each country were 100 km apart. Grey shading indicates the native distribution of *H. frenatus* (Bansal and Karanth 2010; Carranza and Arnold 2006; Case et al. 1994; Ota and Whitaker 2010)

propagules, genetic diversity, and gene flow (Allendorf and Lundquist 2003; Sakai et al. 2001). Accordingly, the species' ability to expand into cold climates within a short period is unexpected because tropical ectotherms have narrower thermal tolerance limits than temperate organisms (Addo-Bediako et al. 2000; Kingsolver 2009), which is predicted to make it more difficult for such species to survive in colder environments (Ghalambor et al. 2006; Janzen 1967). Moreover, in tropical lizards, thermoregulation is thought to buffer thermal physiology from selection (Bogert 1949; Huey et al. 2003). Nonetheless, the house gecko's ability to establish populations in colder regions suggests that cold tolerance may be labile and may have diverged between native and introduced populations. For example, a recent study showed that an introduced population of the tropical lizard *Anolis cristatellus* from Miami tolerated colder temperatures than a source population in Puerto Rico (Leal and Gunderson 2012). This shift in cold tolerance occurred in < 35 years, suggesting that rapid shifts in thermal tolerance are possible. Likewise, a study on the invasive brown anole *A. sagrei* along a latitudinal cline in the southeastern United States found that cold tolerance was lowest in the most northerly population (Kolbe et al. 2014). Interestingly, anoles also shifted their cold tolerance downward after 18 weeks of

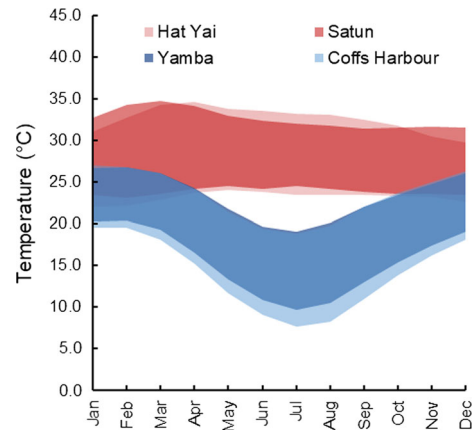
exposure to cold temperatures in the lab, but northern populations still tolerated colder temperatures than southerly populations (Kolbe et al. 2014). Although the exact mechanism responsible for this difference in cold tolerance was unclear, adaptive plasticity can set the stage for longer-term evolutionary shifts in thermal traits (Ghalambor et al. 2007).

Here we investigate whether the thermal traits of the invasive house gecko have changed during its invasion of Australia. The gecko occurs mostly inside human-made buildings, which may provide a thermal buffer against high and low temperatures. Thus, geckos may display similar traits in their native and invaded range (niche conservatism). Alternatively, if geckos routinely experience cold temperatures in their introduced range, we would predict that geckos from Australian populations would have lower cold tolerance than geckos from likely source populations in Thailand. We also explored whether geckos from Australia showed seasonal acclimation, as occurs in some tropical lizards (e.g., *A. sagrei*) that have successfully colonized colder environments (Kolbe et al. 2014). To answer these questions, we measured heat tolerance and cold tolerance of geckos from native populations in Thailand and introduced populations in southeastern Australia.

## Methodology

### Study sites and collection of geckos

We collected *H. frenatus* from two native populations in Thailand and two introduced populations in eastern Australia. In each country, we chose populations that were 100 km apart. We chose two populations in the Thai-Malay Peninsula, namely Hat Yai (7.006278, 100.498871) and Satun (6.831708, 99.5363708) to represent the likely source of the introduced population in Australia (Fig. 1). Hat Yai is an urban area, whereas Satun (Bulon Le Island) is a rural area. At both sites, temperatures are high and invariant throughout the year (Fig. 2). We collected 36 geckos from Hat Yai and 21 from Satun during December 2018. In Australia, we chose two populations on the east coast where geckos have recently invaded. We collected geckos from Yamba (− 29.436890, 153.357986) and Coffs Harbour (− 30.292685, 153.119707) in a subtropical region of New South Wales (NSW), where



**Fig. 2** Monthly average temperature ranges in Hat Yai, Satun, Yamba, and Coffs Harbour. Data for Yamba and Coffs Harbour were collected from 1977 to 2019 (Bureau of Meteorology 2019). Data of Hat Yai and Satun were collected during 1981–2010 (Thai Meteorological Department 2019)

temperatures drop markedly during winter (Fig. 2). To determine whether geckos in Australia showed seasonal variation in thermal tolerance, we collected 20 geckos from Yamba and 13 from Coffs Harbour during August 2018 (winter), and 30 geckos from each location during February 2019 (summer).

We transported geckos collected in NSW to the University of Technology Sydney, while geckos collected in Thailand were transported to the Prince of Songkla University. In the laboratory, we recorded the snout-vent length (SVL, with a ruler, to nearest mm) and mass (nearest 0.01 g) of all geckos. Mean SVLs and mass of geckos were as follows: Hat Yai, SVL = 50 mm (range 43–59 mm), mass = 3.10 g (range 1.64–4.90 g); Satun, SVL = 48 mm (range 40–55 mm), mass = 2.48 g (range 1.63–4.22 g); Yamba, SVL = 52 mm (range 44–62 mm), mass = 3.27 g (range 1.88–7.49 g); Coffs Harbour, SVL = 52 mm (range 45–63 mm), mass = 3.35 g (range 1.73–5.69 g).

### Husbandry of geckos in captivity

Each gecko was housed individually in a 2L ventilated plastic cage (200 × 150 × 60 mm). Each cage contained a paper substrate, a cardboard tube as a shelter, and a small water dish. In Thailand, the geckos were kept in a room with ambient temperatures ranging from 23 °C at night to 32 °C by day and relative humidity ranging from 60 to 80%. In NSW, geckos

were kept in a temperature-controlled room (23 °C); we placed cages on a heating rack to provide a thermal gradient (23–32 °C) within each cage. We used a humidifier to maintain the relative humidity at 60%, while the lighting was set to 12:12 light to dark cycle. We fed geckos live crickets or mealworms every third day between 1700 and 1900 h. Geckos were kept in captivity for no more than 10 days and were then released to their sites of capture (Thailand) or were euthanized (Australia).

### Estimating thermal tolerance

To determine the critical thermal minimum ( $CT_{\min}$ ) and critical thermal maximum ( $CT_{\max}$ ), we used the righting response test of Phillips et al. (2016). To do this, we placed each gecko in a 100 ml plastic tube (150 mm long, 40 mm in diameter) with a plastic cap, and maintained the temperature at 23 °C for 10 min to establish a consistent baseline body temperature. Before measurements, we replaced the cap with a modified plastic cap containing a thermistor probe attached to an electronic thermometer (OMEGA® Thermistor thermometer-450 ATH, accuracy  $\pm 0.1$  °C). To commence the test, we submerged the tube containing the lizard in a water bath. For  $CT_{\min}$ , we lowered the temperature at a rate of 1 °C per minute by adding ice, while for  $CT_{\max}$ , we raised the temperature at the same rate by using a heater (Anova Precision Cooker 2.0—Bluetooth, China). We rotated the tube every 10 s to check the righting reflex of the gecko. When the gecko lost its righting reflex, we stopped and recorded the temperature and removed the gecko to let its body temperature return to ambient. The measurements of  $CT_{\min}$  and  $CT_{\max}$  were separated by 5 days so the geckos could fully recover from thermal shocks.

### Statistical analyses

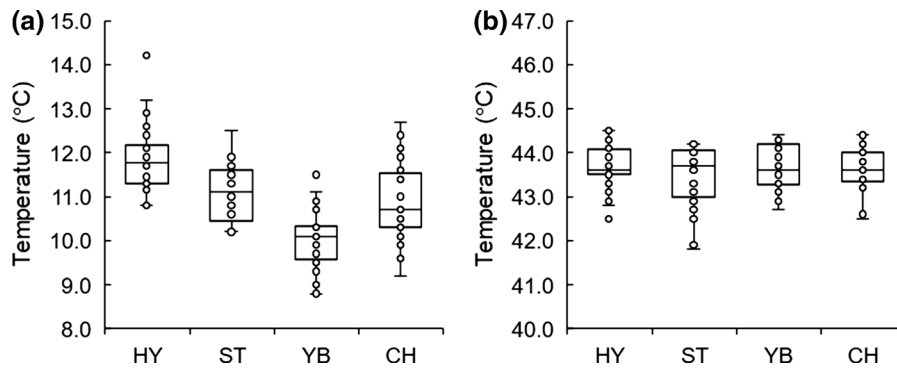
Our a priori hypothesis was that geckos from Australia would have lower cold tolerance than geckos from Thailand, whereas heat tolerance would be similar. Therefore, we used one-factor ANOVAs with planned comparison (Australia versus Thailand) to test our hypothesis (Day and Quinn 1989). In this analysis, we compared data from native and introduced geckos captured in the summer since they have experienced climate that overlapping in time. We used the same

statistical method to compare thermal tolerances of introduced geckos captured in summer and winter to investigate seasonal acclimation in Australia. Prior to statistical analyses, we plotted the data (normal Q–Q plots) and carried out Kolmogorov–Smirnov tests to check whether data were normally distributed. We plotted data (means and SE) and used Levene’s tests to assess whether variances were homogeneous. Data for  $CT_{\min}$  met the assumptions of the ANOVA (K-S tests, all  $P > 0.05$ , Levene’s tests all  $P > 0.05$ ). Data for  $CT_{\max}$  met the assumptions of homogeneity of variances (Levene’s test statistic = 2.285,  $P = 0.08$ ), and, except for one location (Coffs Harbour), data were normally distributed (K-S tests,  $P > 0.05$ ). Because ANOVA is robust to minor departures from normality, we elected not to transform data for  $CT_{\max}$  (Quinn and Keough 2002).

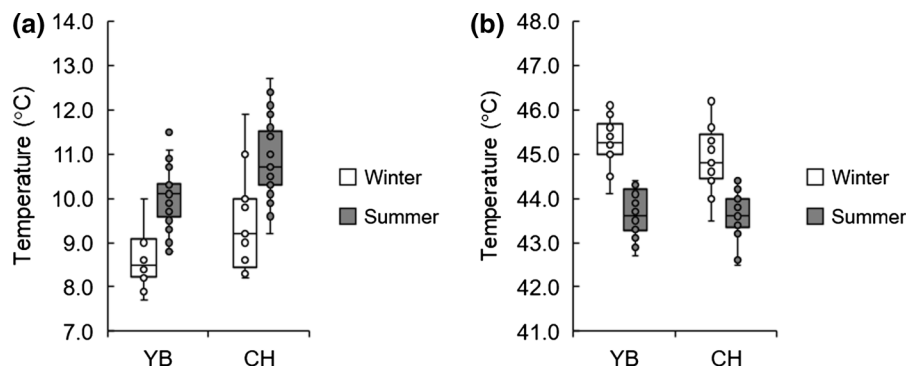
## Results

By comparing native and introduced geckos captured in summer, cold tolerance of *H. frenatus* differed among populations (ANOVA  $F_{3,113} = 36.93$ ,  $P = 0.001$ ). A planned comparison showed that  $CT_{\min}$  of geckos was higher in populations from Thailand (mean = 11.6 °C) than populations from Australia (mean = 10.4 °C; contrast  $t = 7.71$ ,  $P = 0.001$ , Fig. 3). By contrast,  $CT_{\max}$  did not differ among populations (means = 43.6 °C for HY, 43.4 °C for ST, 43.7 °C for YB, and 43.6 °C for CH; ANOVA  $F_{3,113} = 0.90$ ,  $P = 0.45$ , Fig. 3).

We carried out a two-factor ANOVA to determine whether Australian populations showed seasonal differences in thermal tolerance. For  $CT_{\min}$ , there was a significant effect of season ( $F_{1,89} = 72.25$ ,  $P = 0.001$ ), population ( $F_{1,89} = 24.19$ ,  $P = 0.001$ ) but no significant interaction ( $F_{1,89} = 0.01$ ,  $P = 0.91$ ). That is, geckos from Yamba and Coffs Harbor both had lower  $CT_{\min}$  in winter compared to summer (Fig. 4). For  $CT_{\max}$ , there was a significant effect of season ( $F_{1,89} = 132.91$ ,  $P = 0.001$ ), but no difference between populations ( $F_{1,89} = 2.72$ ,  $P = 0.10$ ) and no interaction ( $F_{1,89} = 0.87$ ,  $P = 0.35$ ). Thus, geckos had higher  $CT_{\max}$  in winter than in summer (Fig. 4).



**Fig. 3** Thermal tolerances of *H. frenatus* from Thailand [Hat Yai (HY) and Satun (ST)], and southeastern Australia [Yamba (YB) and Coffs Harbour (CH)]. **a** CT<sub>min</sub> was significantly lower in the Australian populations, whereas **b** CT<sub>max</sub> did not differ among populations



**Fig. 4** Thermal tolerances of *H. frenatus* from Yamba (YB), and Coffs Harbour (CH) populations in winter and; while **a** CT<sub>min</sub> were significantly higher in summer, **b** CT<sub>max</sub> were significantly lower in summer in both populations

## Discussion

We discovered population differences in the cold tolerance of invasive house geckos. Populations from southeastern Australia had lower cold tolerance than populations from Thailand (Fig. 3), suggesting that geckos have shifted their cold tolerance downwards in response to lower environmental temperatures in the invaded range relative to the likely source range. Such shifts have been documented in other tropical invasive lizards. For example, the cold tolerance of crested anoles (*Anolis cristatellus*) was 3 °C lower in an introduced population (Miami) compared to a native population in Puerto Rico (Leal and Gunderson 2012). Although the mechanisms responsible for the downward shift in cold tolerance in house geckos are unclear, we found evidence that Australian populations showed seasonal acclimation; cold tolerance was ~ 1.5 °C lower in winter than in summer, and this pattern was consistent in both east coast

populations (Fig. 4). Likewise, a study on invasive *Anolis sagrei* also detected seasonal acclimation in thermal tolerance in introduced populations, but northern populations showed greater cold tolerance after acclimation than southern populations (Kolbe et al. 2014). Thus, both acclimation and genetic effects (and possibly, developmental plasticity) may contribute to greater cold tolerance in invasive species in non-native ranges (Urban et al. 2014).

We also found that the heat tolerance of *H. frenatus* did not differ between likely source populations in Thailand and its invasive range in southeastern Australia. This pattern is not surprising since maximum air temperatures in temperate regions are similar to those experienced in the tropics. In diverse groups of lizards, low variation in heat tolerance and high variation in cold tolerance have been observed (Clusella-Trullas and Chown 2014). The CT<sub>max</sub> of *H. frenatus* (~ 43.6 °C) was almost 3 °C higher than the mean of 40.8 °C reported for 14 other gecko

species (Clusella-Trullas and Chown 2014). The high  $CT_{max}$  of *H. frenatus* may have contributed to its invasion success worldwide, as it would confer a survival advantage during transportation. In a comparative study between native and invasive species, Kelley (2014) suggested that invasive species usually have broader ranges of functional temperatures, as well as higher thermal tolerances. Animals with higher heat tolerance may have a survival advantage during transportation and spread phases of the invasion pathway.

Our most unexpected finding was that the seasonal shifts in cold tolerance in the NSW populations were accompanied by an increase in heat tolerance (Fig. 4b). Repeated cold shocks (i.e., cold hardening) have been reported to trigger higher heat tolerance in species of bacteria and insects by inducing heat shock proteins (García et al. 2001; Sejerkilde et al. 2003). In most species, this cross-protection effect was a rapid response that lasted hours (Hutchison and Maness 1979). Potentially, this physiological mechanism might explain the upward shift in heat tolerance of geckos collected during winter, but further research is necessary to explore this in more detail. Another possible explanation for the pattern of heat and cold tolerance is that geckos might experience both low and high temperatures in winter in urban areas. For example, an inter-population study of a tropical lizard (*Lampropholis coggeri*) by Llewelyn et al. (2016), found that lizards from colder environments had higher heat tolerance, and tended to select hotter microhabitats for thermoregulation. During our winter field trip, we typically found Asian house geckos around heated microhabitats, such as next to spotlights, electronic devices, or behind refrigerators. Therefore, these urban geckos may experience not only low but also high  $T_b$  during winter, which lead to acclimation to a broader range of temperatures.

In conclusion, our study supports the growing body of literature that shows that tropical vertebrate ectotherms can display shifts in cold tolerance and develop seasonal acclimation (Kolbe et al. 2012; Leal and Gunderson 2012; McCann et al. 2014). Our best estimates suggest that *H. frenatus* has been established in NSW for 20 years (Hoskin 2011), so these shifts have occurred in 20 generations. Given that rapid shifts in cold adaptation can facilitate the spread of invaders in incipient ranges, models that seek to

predict spread will need to account for evolutionary changes in thermal traits in invasive species.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** In Australia, all procedures were performed following an ethical standard under the approval of the University of Technology Sydney Animal Care and Ethics Committee (UTS ACEC ETH17-1588). Lapwong was granted permission to deal with the introduced *Hemidactylus frenatus* under NSW Biosecurity Act 2015 (Reference number V18/3468). In Thailand, Dejaradol was granted permission to conduct research involving animals (U1-02470-2559) by the Institute for Animals for Scientific Purpose Development (IAD).

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