

Plasticity in thermal hardening of the invasive Asian house gecko

Yingyod Lapwong (✉ yingyod.lapwong@student.uts.edu.au)

University of Technology Sydney <https://orcid.org/0000-0003-0699-4627>

Ariya Dejtaradol

Prince of Songkla University

Jonathan K. Webb

University of Technology Sydney

Research Article

Keywords: Thermal hardening, Thermal stress, Adaptation, Invasive species

Posted Date: February 23rd, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-240623/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

The Asian house gecko (*Hemidactylus frenatus*) is a tropical invasive species that has established and spread throughout several temperate regions around the world. In some invasive species, rapid thermal acclimation (thermal hardening) may contribute to their success in occupying a wide range of climates. In this study, we investigated whether invasive house geckos from southeastern Australia show differing thermal hardening responses than individuals from the native range in Thailand. In the laboratory, we measured the basal heat tolerance (CT_{max}) of the geckos and their heat hardening response after being subjected to the second thermal stress after 1, 3, 5, 7, 9, or 11 hours. When geckos had recovered, we measured their basal cold tolerance (CT_{min}) and cold hardening response over the same time intervals. We then explored whether hardening responses differed between populations or among time intervals. We found that basal heat tolerances did not differ between populations, but geckos from Australia had lower cold tolerance than geckos from Thailand. The magnitude of the heat hardening was similar between populations, but the introduced geckos had a higher magnitude of cold hardening. The native geckos could maximize their cold tolerance capacity for only 0.6 °C, comparing to 0.9 °C of the introduced geckos. Also, geckos from Australia exhibited faster responses to thermal stress than did geckos from Thailand. Maximum thermal tolerances as a result of hardening responses peaked within three hours after thermal stress in Australian geckos (adjusted means = 44.0 °C for CT_{max} and 9.9 °C for CT_{min}) and at five hours after thermal stress in Thai geckos (adjusted means = 44.2 °C and 10.2 °C, respectively). The plasticity in the thermal hardening of the invasive gecko should enable it to survive rapid temperature fluctuations, especially cold snap, that occasionally occur in temperate regions.

Introduction

Invasive species are a global environmental problem due to their ability to disrupt native ecosystems and cause declines or extinctions of native species (Lockwood et al. 2013). In recent decades, research has focused on accurately predicting the spread of invaders in their non-native ranges. Species distribution models (SDMs) have been widely used to predict the distribution limit of invasive species (Jiménez-Valverde et al. 2011; Rödder et al. 2008); nonetheless, many invasive species have surpassed that limit, and have spread further in non-native ranges than initially predicted (Kolbe et al. 2012; Leal and Gunderson 2012; McCann et al. 2014; Vimercati et al. 2018). In some cases, thermal plasticity may be a contributing factor for these unexpected range expansions (Kelley 2014). Several studies on invasive species have shown that individuals from non-native ranges have displayed rapid shifts in thermal biology, allowing them to function over a wide range of temperatures (Braby and Somero 2006; McCann et al. 2014; Zerebecki and Sorte 2011).

Thermal hardening is a rapid thermal acclimation within minutes or hours after a brief exposure to extreme temperature (Angilletta 2009). The exposure to high temperatures can facilitate the upregulation of heat-shock proteins (HSPs), which allow the organisms to increase their heat tolerance and survival at higher temperatures (Sørensen et al. 2003). Likewise, the exposure to cold temperatures can generate the

upregulation of cold-shock proteins (CSP) (Ritossa 1962; Seebacher 2005; Thieringer et al. 1998) or induce metabolic adjustments without additional protein syntheses (Lee et al. 1987; Teets and Denlinger 2013; Teets et al. 2020), which allow organisms to survive exposure to colder temperatures. These rapid responses to thermal stresses should facilitate the survival of introduced species during the transport and early introduction phases of the invasion when they encounter unfamiliar climates (Chown et al. 2007; Nyamukondiwa et al. 2010). To date, most studies investigating the thermal hardening responses have focused on dipteran insects (Chown et al. 2007; Hu et al. 2014; Nyamukondiwa et al. 2010).

The Asian house gecko (*Hemidactylus frenatus*) is one of the most successful species of tropical invasive reptiles that has spread throughout tropical and temperate regions worldwide (Carranza and Arnold 2006). As a tropical species, the gecko should be vulnerable to thermal extremes since it has evolved in a relatively thermal invariant climate (Ghalambor et al. 2006; Janzen 1967). Despite this, the gecko has established populations in temperate regions of Mexico, Australia, and East Asia (Farr 2011; Hoskin 2011; Kurita 2013), where ambient temperatures fluctuate widely daily, and thermal extremes (both heat and cold) are greater than those experienced in its native range. In southeastern Australia, the New South Wales (NSW) population of *H. frenatus* is the most southern population of the species (Hoskin 2011). This part of Australia has a greater thermal fluctuation than in southern Thailand (Fig. 1). Southeastern Australia also experiences frequently prolonged heatwaves (Cowan et al. 2014); therefore, we predicted that this introduced NSW population of *H. frenatus* should exhibit higher heat hardening ability than native conspecifics. The geckos in southeastern Australia should also experience colder temperatures in winter than those experienced in the tropics; therefore, we expected to see more significant cold hardening in the introduced population. Furthermore, based on previous studies on insects, we predicted that the time course of hardening responses would differ between geckos from the introduced population and the native range. To test these predictions, we collected geckos from a native population in Thailand and an introduced population in southeastern Australia and measured their thermal hardening capacity in the laboratory.

Materials And Methods

Study populations

In this study, we chose a population from southern Thailand to represent the native population because it is located at the center of the native distribution (Ota and Whitaker 2010). For the introduced population, we chose NSW since it is the southernmost population of this species (Hoskin 2011). Although the Asian house geckos have been introduced to Australia since the 1960s, they have reached NSW in the 2000s, giving the population approximately 20 years old (Hoskin 2011). We collected 60 *H. frenatus* from southern Thailand (Hat Yai; 7.006278, 100.498871, and Satun; 6.831708, 99.5363708) from November 2018 – January 2019 to represent the native population. We collected 60 geckos from New South Wales (NSW), southeastern Australia (Yamba; -29.436890, 153.357986, and Coffs Harbour; -30.292685, 153.119707) in February 2019 to serve the introduced population. Between 19 h – 21 h, we walked around buildings and caught the geckos by hand, with the help of a laser pointer to attract them to

reachable heights (Cole 2004). Geckos from Thailand were transported to Prince of Songkla University (PSU), while geckos from NSW were transported to the University of Technology Sydney (UTS). We measured SVLs of all geckos to 0.01 mm using a vernier caliper. We started the experiments the next day right after the arrival to minimize the effect of acclimatization. While being captive, we kept a single gecko in a 2L ventilated plastic cage (200 × 150 × 60 mm, Sistema®, New Zealand) containing a tissue paper, a water dish, and a cardboard tube (as a shelter). In Thailand, we put the cages in a room with ambient temperatures and glass windows to provide natural light. In Australia, since we transferred the geckos to a further south location, we set up the environments to resemble those in northern NSW. We put the cages on a shelf with heated cable (32°C) in a temperature-controlled room (23°C) to allow the geckos to thermoregulate. This thermal gradient (23-32°C) covers the thermal preferences of the Asian house gecko in northern New South Wales, which is approximately 29°C ($T_{\text{set}} = 26\text{-}32^{\circ}\text{C}$) (Lapwong et al. 2020). We set the light cycle at 12h:12 h. We fed each gecko with five crickets every third day at 17 h-19 h. After the experiment, we euthanased the geckos from NSW due to their invasive status, using MS222 (Conroy et al. 2009), and released the geckos from Thailand to where they were captured.

Thermal hardening measurement

We applied the heat hardening measurement method developed by (Phillips et al. 2016). Firstly, we put a single gecko into a cylindrical plastic tube with a plastic cap and acclimate it at 23°C for 10 minutes. Then we changed the cap with another one with a thermocouple already inserted before partially submerged the tube into a water bath to moderate the temperature in the tube. The thermocouple was connected to an electric thermometer (OMEGA® Thermistor thermometer- 450 ATH, accuracy $\pm 0.1^{\circ}\text{C}$) for real-time temperature measurements. We used the same tubing in both heat and cold tolerance measurements. We used a water heater (Anova Precision Cooker 2.0 – Bluetooth, China) to increase, or ice to decrease water temperatures. We controlled the change of the temperature in the tube at the rate of 1°C per minute. We regularly rolled the tube to check the gecko's righting reflex, i.e., the ability to rotate itself after being turnover. When the gecko lost the reflex, we stopped the experiment and recorded the last temperatures that the gecko still be able to right itself as CT_{max} or CT_{min} . To determine thermal hardening, we measured the critical thermal limitations of the same animal twice, assigned as the basal and the final CTs. We varied interval periods between each measurement as 1, 3, 5, 7, 9, and 11 hours. Each animal was measured only twice to avoid the carry-over effect. All the measurements were conducted solely by Lapwong.

Data analyses

In the analyses, we aimed to determine the effects of locations (Thailand vs. Australia) and time intervals between two thermal shocks as treatment groups on the basal CTs, final CTs and shifted CTs. While the basal CTs indicate the initial thermal tolerances of the animals, the final CTs show the maximized thermal tolerances as a result of hardening responses. Besides, the shifted CTs reveal the thermal hardening capacities of the animals. We used the general linear model to determine the effects of locations and time intervals on the basal CTs, final CTs, and shifted CTs, with SVLs as a covariate. Also,

since the basal CTs could influence the final CTs and shifted CTs, we included the basal CTs as another covariate to the analyses. We used a t-test to determine the difference in SVLs between native and introduced geckos. Besides, we used the Pearson correlation coefficient to evaluate the correlation between SVLs and shifted CTs, and between basal CTs and shifted CTs. Before the analyses, we used the Kolmogorov-Smirnov test to check the normality of basal CTs and the residuals of the CTs. We found that 95% of our data sets were normally distributed ($P > 0.05$). The Levene's test of equality of variances also confirmed the homogeneity of variances ($P > 0.05$). We performed all statistical analyses using IBM® SPSS® Statistics Version 24.

Results

The introduced geckos were significantly larger than the native geckos (52.33 ± 0.52 vs. 48.97 ± 0.46 mm, $t_{118} = -4.824$, $P < 0.05$). The size of the geckos did not directly correlate with heat hardening ($r = -0.031$, $P = 0.74$) or cold hardening capacity ($r = 0.078$, $P = 0.40$)

Heat tolerance

The general linear model revealed no effect of locations ($F_{1,107} = 2.321$, $P = 0.13$), treatment groups ($F_{1,107} = 0.938$, $P = 0.46$), and interaction between locations and groups ($F_{1,107} = 0.191$, $P = 0.97$), on the basal CT_{max} . SVLs did not have a significant effect as a covariate ($F_{1,107} = 3.809$, $P = 0.05$). The mean adjusted basal CT_{max} were 43.5 °C and 43.7 °C for native and introduced geckos, respectively. There was a significant negative correlation between basal CT_{max} and the change in CT_{max} (ΔCT_{max} ; $r = -0.474$, $P < 0.05$). The model revealed no effect of locations ($F_{1,106} = 0.305$, $P = 0.58$), but a significant effect of time interval ($F_{5,106} = 2.178$, $P < 0.05$), and a significant interaction between time and location ($F_{5,106} = 3.776$, $P < 0.05$) on final CT_{max} . That is, the time course of heat resistance differed between locations (Fig. 2a). Between two covariates, only the basal CT_{max} had a significant effect on final CT_{max} ($F_{5,106} = 53.012$, $P < 0.05$), but not SVLs ($F_{5,106} = 1.344$, $P = 0.25$). There was also no effect of locations ($F_{1,106} = 0.265$, $P = 0.61$), but a significant effect of time interval ($F_{5,106} = 2.933$, $P < 0.05$), and a significant interaction between time and location ($F_{5,106} = 5.140$, $P < 0.05$) on shifted CT_{max} . That is, the time course of heat hardening differed between locations (Fig. 3a). Between two covariates, only the basal CT_{max} had a significant effect on shifted CT_{max} ($F_{5,106} = 32.562$, $P < 0.05$), but not SVLs ($F_{5,106} = 0.573$, $P = 0.45$). For instance, the Thailand geckos had the highest final CT_{max} at the 5-hour interval (adjusted $CT_{max} = 44.2$ °C, adjusted $\Delta CT_{max} = 0.6$ °C), whereas the NSW geckos had the highest final CT_{max} at the 1-hour interval (adjusted $CT_{max} = 44.0$ °C, adjusted $\Delta CT_{max} = 0.4$ °C).

Cold tolerance

The general linear model revealed a significant effect of location on the basal CT_{min} ($F_{1,107} = 27.384$, $P < 0.05$), and there was no effect of treatment group ($F_{1,107} = 1.017$, $P = 0.41$) or the interaction between location and group ($F_{1,107} = 0.270$, $P = 0.93$). SVLs did not have a significant effect as a covariate ($F_{1,107}$

= 2.753, $P = 0.10$). The mean basal CT_{\min} were 11.2 °C for Thai geckos and 10.4 °C for Australian geckos. There was a significant positive correlation between basal CT_{\min} and the change in CT_{\min} (ΔCT_{\min} ; $r = 0.554$, $P < 0.05$). The model also showed significant effects of locations ($F_{1,106} = 5.905$, $P < 0.05$), time intervals between cold shocks ($F_{5,106} = 2.513$, $P < 0.05$), and interaction between time intervals and locations ($F_{5,106} = 5.583$, $P < 0.05$) on final CT_{\min} . That is, the time course for cold hardening differed between native and introduced geckos (Fig. 2b). Between two covariates, only the basal CT_{\min} had a significant effect on final CT_{\min} ($F_{5,106} = 14.243$, $P < 0.05$), but not SVLs ($F_{5,106} = 2.131$, $P = 0.18$). There were also effects of locations ($F_{1,106} = 5.905$, $P < 0.05$), time intervals between cold shocks ($F_{5,106} = 2.513$, $P < 0.05$), and interaction between time intervals and locations ($F_{5,106} = 5.583$, $P < 0.05$) on shifted CT_{\min} . That is, the time course of cold hardening differed between locations (Fig. 3a). Between two covariates, only the basal CT_{\min} had a significant effect on shifted CT_{\min} ($F_{5,106} = 68.539$, $P < 0.05$), but not SVLs ($F_{5,106} = 2.131$, $P = 0.18$). For instance, while the native geckos had the lowest final CT_{\min} at the 5-hour interval (adjusted $CT_{\min} = 10.2$ °C, adjusted $\Delta CT_{\min} = -0.6$ °C), the introduced geckos had the lowest CT_{\min} at the 3-hour interval (adjusted $CT_{\min} = 9.9$ °C, adjusted $\Delta CT_{\min} = -0.9$ °C).

Discussion

The Asian house geckos have established in the temperate region of southeastern Australia for more than 20 years (Hoskin 2011), so we expected them to have more substantial thermal hardening capacity, especially cold hardening, than their native conspecifics. As predicted, we found a greater degree of cold hardening, but not heat hardening, of the introduced populations. For cold tolerance, geckos from NSW had lower basal CT_{\min} and final CT_{\min} than geckos from Thailand. The analysis confirmed that the lower final CT_{\min} was beyond the effect of the lower basal CT_{\min} . The geckos from NSW could shift their cold tolerance to a greater degree than the geckos from Thailand. Our findings for both basal cold tolerance and cold hardening agree with the results reported for other species of invasive lizards that have shifted cold tolerance downwards following successful spread to colder regions (Angetter et al. 2011; Kolbe et al. 2012; Leal and Gunderson 2012). The ability to withstand low temperatures of this invasive geckos also suggests that they do not always rely on the warm climate inside the buildings and can spread into natural habitats.

For heat tolerance, basal CT_{\max} and ΔCT_{\max} were similar in geckos from Thailand and NSW. These results contrast with those from a study on another tropical reptile, *Lampropholis coggeri*, which found an interpopulation divergence in heat hardening (Phillips et al. 2016). In that study, the magnitude of heat hardening diverged among populations and was higher for skinks from localities with higher seasonal variation in daily maximum under-canopy temperatures. By contrast, we found little interpopulation variation in either basal heat tolerance or the magnitude of heat hardening. This finding could be due to the already high initial heat tolerance, so there is no evolutionary reason for the geckos to uplift their heat tolerance. Interestingly, while the magnitude of the hardening response (around 0.7 °C) is similar to that reported for other geckos (e.g., *Amalosia lesueurii*, Abayarathna et al. (2019)), the basal CT_{\max} of *H.*

frenatus (43.6 °C) is much higher than that reported for most other gekkonids (i.e., mean of 40.8 °C, (Clusella-Trullas and Chown 2014)). Alternatively, perhaps the CT_{max} of geckos may have already reached an upward limit, such that there is little opportunity for further upward shifts. In support of this idea, there was a negative correlation between the basal CT_{max} and ΔCT_{max} , a finding that was also reported for tropical skinks (Phillips et al. 2016). That is, individuals with low basal CT_{max} showed higher hardening responses and *vice versa*. This pattern mirrors finding in other taxa, such as *Drosophila*, and suggests that there is a hard upper limit to shift thermal tolerance upwards (Hoffmann et al. 2003; van Heerwaarden et al. 2016).

Besides the magnitude of the hardening response, we documented apparent differences in the time courses of plastic responses to thermal tolerance. Interestingly, geckos from NSW responded faster to both heat shocks and cold shocks than did geckos from Thailand. This result mirrors findings from comparative studies on invasive insects and their congeneric species with limited distributions. For example, the cosmopolitan Mediterranean fruit fly, *Ceratitis capitata*, responded to the thermal stresses faster than the less successful invasive congener, *C. rosa* (Nyamukondiwa et al. 2010). In another study on fruit flies, 3rd instar larvae of the widespread invasive *Bactrocera dorsalis* and more geographically restricted *B. correcta* were allocated to groups subjected to exposure to different temperatures (25, 30, 35, 37, 39, 41 °C) followed by exposure to 45 °C. Interestingly, larvae of the invasive fly had higher survival after exposure to milder temperatures (35 °C and upwards). In contrast, the non-invasive *B. correcta* only showed a heat shock response after exposure to temperatures of 39 °C and above (Hu et al. 2014). While these results document clear differences in the plasticity of thermal hardening responses between invasive and non-invasive species, as far as we are aware, few studies have compared hardening responses in the introduced populations to the native ones. Thus, it is possible that invasive flies may develop those thermal sensitivities as the post-invasion response to novel climates.

In the current study, we suggest that plasticity in thermal hardening in house geckos has arisen in response to the colder climate and the strong predictability in thermal extremes in southeastern Australia. Even in temperate NSW, thermal fluctuations can range from 12.9–43.3 °C during summer (Fig. 1b). In the native range, geckos are rarely exposed to critical temperatures (annual thermal fluctuation ranges from 18.2–39.2 °C, Fig. 1a), so there may be little benefit to shifting down their cold tolerance or reacting quickly to exposure to thermal stress. On the other hand, there is a higher chance for the introduced geckos to experience critical or near-critical temperatures, so faster physiological responses should enhance their survival. It is also possible that plasticity for thermal hardening occurred during the transport phase of the invasion. For example, a study on marine bivalves found that exposure to high thermal stress during simulated transported promoted strong selection for enhanced survival upon exposure to the second thermal stress (Lenz et al. 2018). Irrespective of when the shift in plasticity in hardening occurred in *H. frenatus*, it is likely that invasive geckos would benefit from rapid hardening responses during regular heatwaves or cold snaps, both of which frequently occur in southeastern Australia. However, without further molecular studies, we retained to conclude that these shifts in thermal

hardening responses of the Asian house geckos in NSW were a result of natural selection or just non-inherited plasticity (i.e., epigenetic).

In summary, we found that *H. frenatus* from NSW could tolerate colder and responded faster to both heat and cold stresses than did geckos from Thailand. Such plasticity to thermal stress is likely to influence the survival of individuals and should facilitate their further invasion, especially to the temperate zone. However, since this study included only two populations, additional studies of *H. frenatus* from different geographic ranges are preferred to solidify our conclusion.

Declarations

Acknowledgments

We thank Dr. Sansareeya Wangulangkul, Hattaya Jaroensap, Phruetthiphong Phetchuay, Wanitchaya Tirakunpisut, and Wisanu Promnin for their help with gecko collection and husbandry. We thank Gemma Armstrong and Theja Abayarathna for assistance with laboratory setting, and Alyssa Trotter for guidance and advice about obtaining biosecurity clearance. The University of Technology Sydney financially supported this project.

Compliance with ethical standards

Conflict of interest: The authors declare no conflicts of interest.

Ethical statement: This research followed the protocols approved by of the University of Technology Sydney Animal Care and Ethics Committee (UTS ACEC ETH17-1588). In New South Wales, DPI has granted a permit to Lapwong for working with the introduced *Hemidactylus frenatus* under NSW Biosecurity Act 2015 (Reference number V18/3468). In Thailand, Dejtardol was granted a permit to conduct research involving animals (U1-02470-2559) by the Institute for Animals for Scientific Purpose Development (IAD).

References

Abayarathna T, Murray BR, Webb JK (2019) Higher incubation temperatures produce long-lasting upward shifts in cold tolerance, but not heat tolerance, of hatchling geckos. *Biology Open* 8:bio042564. <https://doi.org/10.1242/bio.042564>

Angetter L-S, LÖTters S, RÖDder D (2011) Climate niche shift in invasive species: the case of the brown anole. *Biological Journal of the Linnean Society* 104:943-954. <https://doi.org/10.1111/j.1095-8312.2011.01780.x>

Angilletta MJ (2009) *Thermal Adaptation : a Theoretical and Empirical Synthesis*. Thermal Acclimation. Oxford University Press USA - OSO, Oxford, United Kindom

- Braby CE, Somero GN (2006) Ecological gradients and relative abundance of native (*Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) blue mussels in the California hybrid zone. *Marine Biology* 148:1249-1262. <https://doi.org/10.1007/s00227-005-0177-0>
- Bureau of Meteorology (2020) Climate statistics for Australian locations. <http://www.bom.gov.au/climate/data/>. Accessed 22/05/2020
- Carranza S, Arnold EN (2006) Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 38:531-545. <https://doi.org/10.1016/j.ympev.2005.07.012>
- Chown SL, Slabber S, McGeoch MA, Janion C, Leinaas HP (2007) Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society B: Biological Sciences* 274:2531-2537. <https://doi.org/10.1098/rspb.2007.0772>
- Clusella-Trullas S, Chown S (2014) Lizard thermal trait variation at multiple scales: A review. *Journal of Comparative Physiology B* 184:5 - 21. <https://doi.org/10.1007/s00360-013-0776-x>
- Cole NC (2004) A novel technique for capturing arboreal geckos. *Herpetological Review* 35:358-359
- Conroy CJ, Papenfuss T, Parker J, Hahn NE (2009) Use of tricaine methanesulfonate (MS222) for euthanasia of reptiles. *Journal of the American Association for Laboratory Animal Science* 48:28-32
- Cowan T, Purich A, Perkins S, Pezza A, Boschhat G, Sadler K (2014) More frequent, longer, and hotter heat waves for Australia in the twenty-first century. *Journal of Climate* 27:5851-5871. <https://doi.org/10.1175/jcli-d-14-00092.1>
- Farr WL (2011) Distribution of *Hemidactylus frenatus* in Mexico. *The Southwestern Naturalist* 56:265-273
- Ghalambor CK, Huey RB, Martin PR, Tewksbury JJ, Wang G (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and comparative biology* 46:5-17. <https://doi.org/10.1093/icb/icj003>
- Hoffmann A, Sørensen J, Loeschcke V (2003) Adaptation of *Drosophila* to temperature extremes: Bringing together quantitative and molecular approaches. *Journal of Thermal Biology* 28:175-216. [https://doi.org/10.1016/S0306-4565\(02\)00057-8](https://doi.org/10.1016/S0306-4565(02)00057-8)
- Hoskin CJ (2011) The invasion and potential impact of the Asian house gecko (*Hemidactylus frenatus*) in Australia. *Austral Ecology* 36:240-251. <https://doi.org/10.1111/j.1442-9993.2010.02143.x>
- Hu J-t, Chen B, Li Z-h (2014) Thermal plasticity is related to the hardening response of heat shock protein expression in two *Bactrocera* fruit flies. *Journal of Insect Physiology* 67:105-113. <https://doi.org/10.1016/j.jinsphys.2014.06.009>

- Janzen DH (1967) Why mountain passes are higher in the tropics. *The American Naturalist* 101:233-249. <https://doi.org/10.1086/282487>
- Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. *Biological Invasions* 13:2785-2797. <https://doi.org/10.1007/s10530-011-9963-4>
- Kelley AL (2014) The role thermal physiology plays in species invasion. *Conservation Physiology* 2:1. <https://doi.org/10.1093/conphys/cou045>
- Kolbe JJ, VanMiddlesworth PS, Losin N, Dappen N, Losos JB (2012) Climatic niche shift predicts thermal trait response in one but not both introductions of the Puerto Rican lizard *Anolis cristatellus* to Miami, Florida, USA. *Ecology and Evolution* 2:1503-1516. <https://doi.org/10.1002/ece3.263>
- Kurita T (2013) Current status of the introduced common house gecko, *Hemidactylus frenatus* (Squamata: Gekkonidae), on Amamioshima Island of the Ryukyu Archipelago, Japan. *Current Herpetology* 32:50-60. <https://doi.org/10.5358/hsj.32.50>
- Lapwong Y, Dejtaradol A, Webb JK (2020) Shifts in thermal preference of introduced Asian house geckos (*Hemidactylus frenatus*) in temperate regions of southeastern Australia. *Journal of Thermal Biology* 91. <https://doi.org/10.1016/j.jtherbio.2020.102625>
- Leal M, Gunderson AR (2012) Rapid change in the thermal tolerance of a tropical lizard. *American Naturalist* 180:815-822. <https://doi.org/10.1086/668077>
- Lee RE, Jr., Chen CP, Denlinger DL (1987) A rapid cold-hardening process in insects. *Science* 238:1415-1417. <https://doi.org/10.1126/science.238.4832.1415>
- Lenz M et al. (2018) Heat challenges can enhance population tolerance to thermal stress in mussels: a potential mechanism by which ship transport can increase species invasiveness. *Biological Invasions* 20:3107-3122. [10.1007/s10530-018-1762-8](https://doi.org/10.1007/s10530-018-1762-8)
- Lockwood JL, Hoopes MF, Marchetti MP (2013) *Invasion Ecology*. 2nd edn. John Wiley and Sons Ltd, Chicester
- McCann S, Greenlees MJ, Newell D, Shine R (2014) Rapid acclimation to cold allows the cane toad to invade montane areas within its Australian range. *Functional Ecology* 28:1166-1174. <https://doi.org/10.1111/1365-2435.12255>
- Nyamukondiwa C, Kleynhans E, Terblanche JS (2010) Phenotypic plasticity of thermal tolerance contributes to the invasion potential of Mediterranean fruit flies (*Ceratitidis capitata*). *Ecological Entomology* 35:565-575. <https://doi.org/10.1111/j.1365-2311.2010.01215.x>

Hemidactylus frenatus. The IUCN Red List of Threatened Species 2010: e.T176130A7184890 (2010). Accessed 12 April 2017

Phillips BL, Muñoz MM, Hatcher A, Macdonald SL, Llewelyn J, Lucy V, Moritz C (2016) Heat hardening in a tropical lizard: geographic variation explained by the predictability and variance in environmental temperatures. *Functional Ecology* 30:1161-1168. <https://doi.org/10.1111/1365-2435.12609>

Ritossa F (1962) A new puffing pattern induced by temperature shock and DNP in drosophila. *Experientia* 18:571-573. <https://doi.org/10.1007/BF02172188>

Rödger D, Solé M, Böhme W (2008) Predict the potential distributions of two alien invasive Housegeckoes (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). *North-Western Journal of Zoology* 4:236-246

Seebacher F (2005) A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? *Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology* 175:453-461. <http://dx.doi.org/10.1007/s00360-005-0010-6>

Sørensen JG, Kristensen TN, Loeschcke V (2003) The evolutionary and ecological role of heat shock proteins. *Ecology Letters* 6:1025-1037. <https://doi.org/10.1046/j.1461-0248.2003.00528.x>

Teets NM, Denlinger DL (2013) Physiological mechanisms of seasonal and rapid cold-hardening in insects. *Physiological Entomology* 38:105-116. <https://doi.org/10.1111/phen.12019>

Teets NM, Gantz JD, Kawarasaki Y (2020) Rapid cold hardening: ecological relevance, physiological mechanisms and new perspectives. *The Journal of Experimental Biology* 223:jeb203448. <https://doi.org/10.1242/jeb.203448>

Thai Meteorological Department (2020) Climatological Data for the Period 1981–2010.

Thieringer HA, Jones PG, Inouye M (1998) Cold shock and adaptation. *BioEssays* 20:49-57. [https://doi.org/10.1002/\(SICI\)1521-1878\(199801\)20:1<49::AID-BIES8>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1521-1878(199801)20:1<49::AID-BIES8>3.0.CO;2-N)

van Heerwaarden B, Kellermann V, Sgrò CM (2016) Limited scope for plasticity to increase upper thermal limits. *Functional Ecology* 30:1947-1956. <https://doi.org/10.1111/1365-2435.12687>

Vimercati G, Davies S, Measey J (2018) Rapid adaptive response to a Mediterranean environment reduces phenotypic mismatch in a recent amphibian invader. *The Journal of Experimental Biology* 221:jeb.174797. <https://doi.org/10.1242/jeb.174797>

Zerebecki RA, Sorte CJB (2011) Temperature tolerance and stress proteins as mechanisms of invasive species success. *PloS one* 6:e14806-e14806. <https://doi.org/10.1371/journal.pone.0014806>

Figures

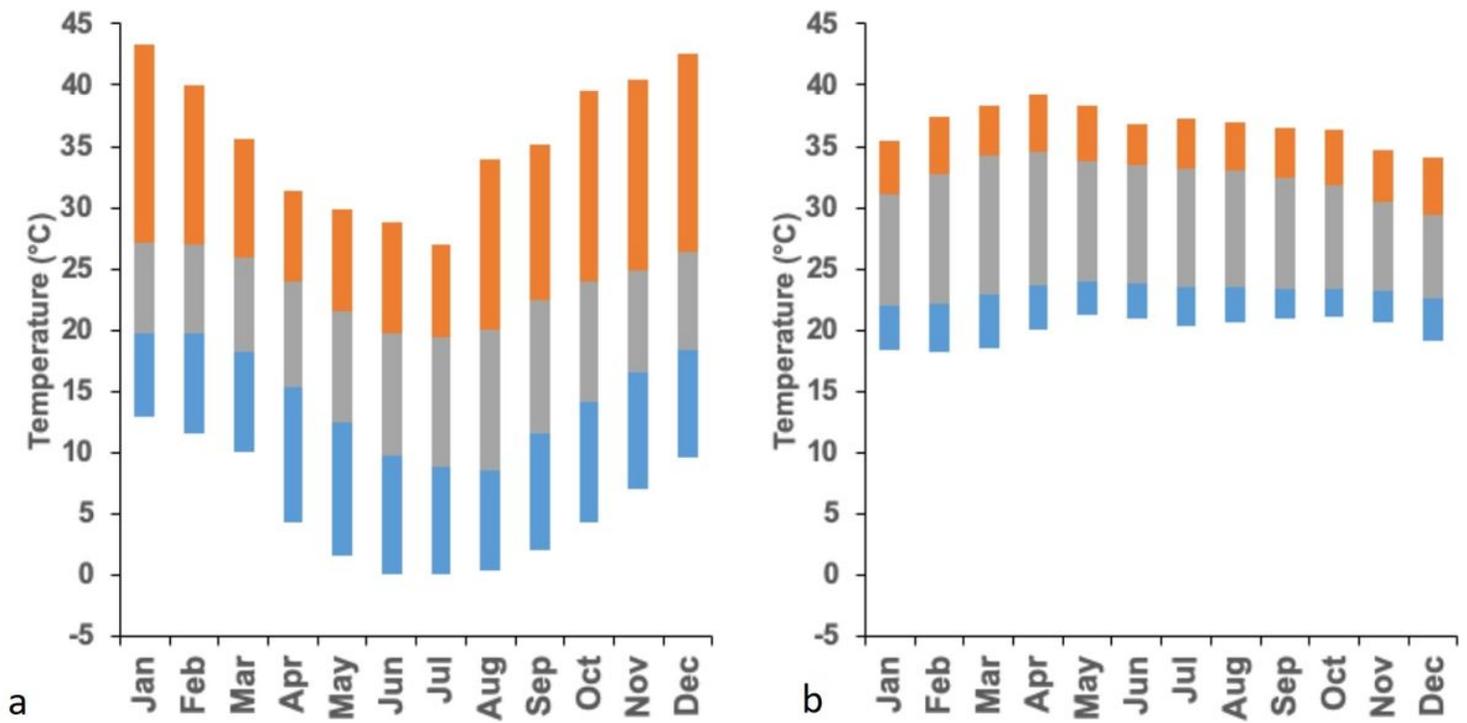


Figure 1

Temperature profiles of (a) Coffs Harbour, southeastern Australia, and (b) Hat Yai, southern Thailand; blue bars represent extreme low-temperature ranges, grey bars represent average-temperature ranges, and orange bars represent extreme high-temperature ranges.

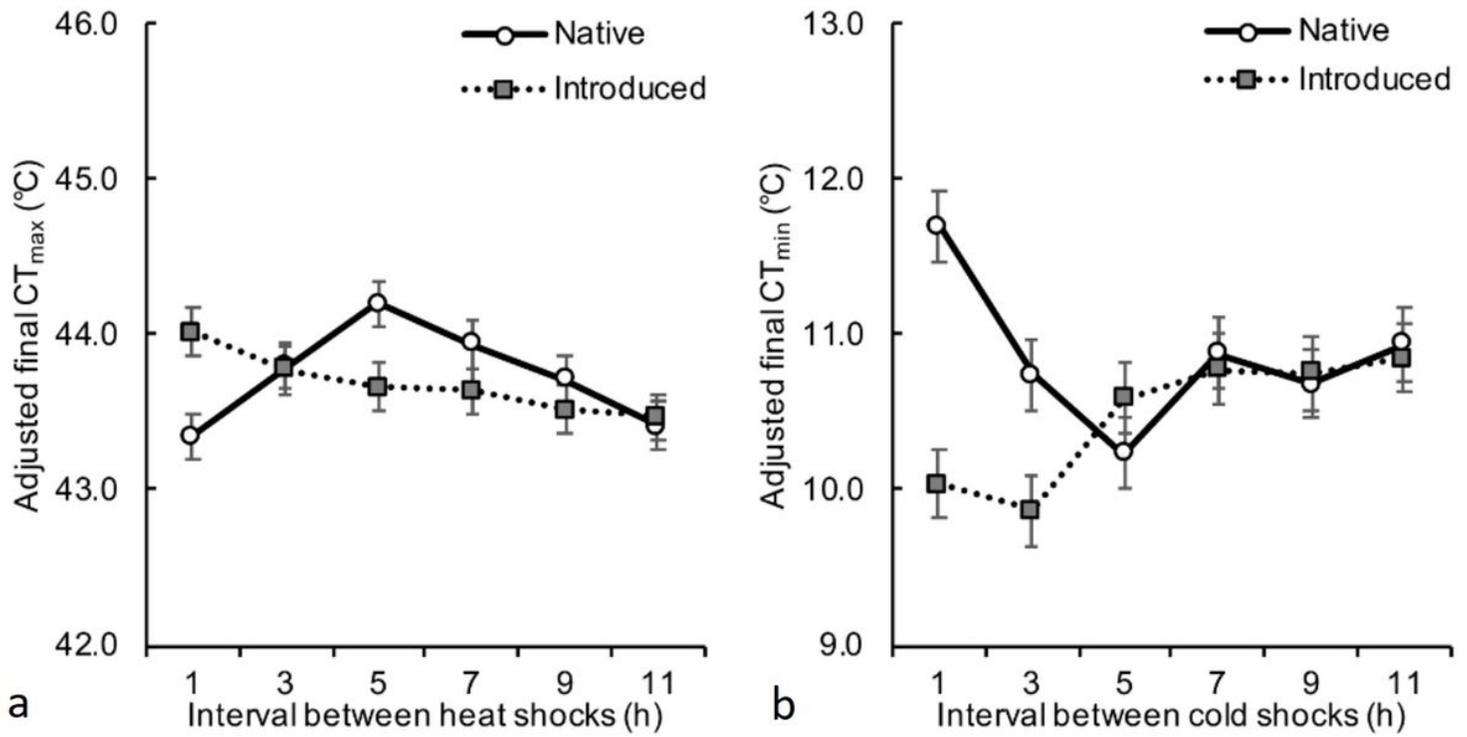


Figure 2

(a) Mean (\pm SE) adjusted final CT_{max} and (b) mean (\pm SE) adjusted final CT_{min} of native and introduced geckos at different intervals between thermal shocks.

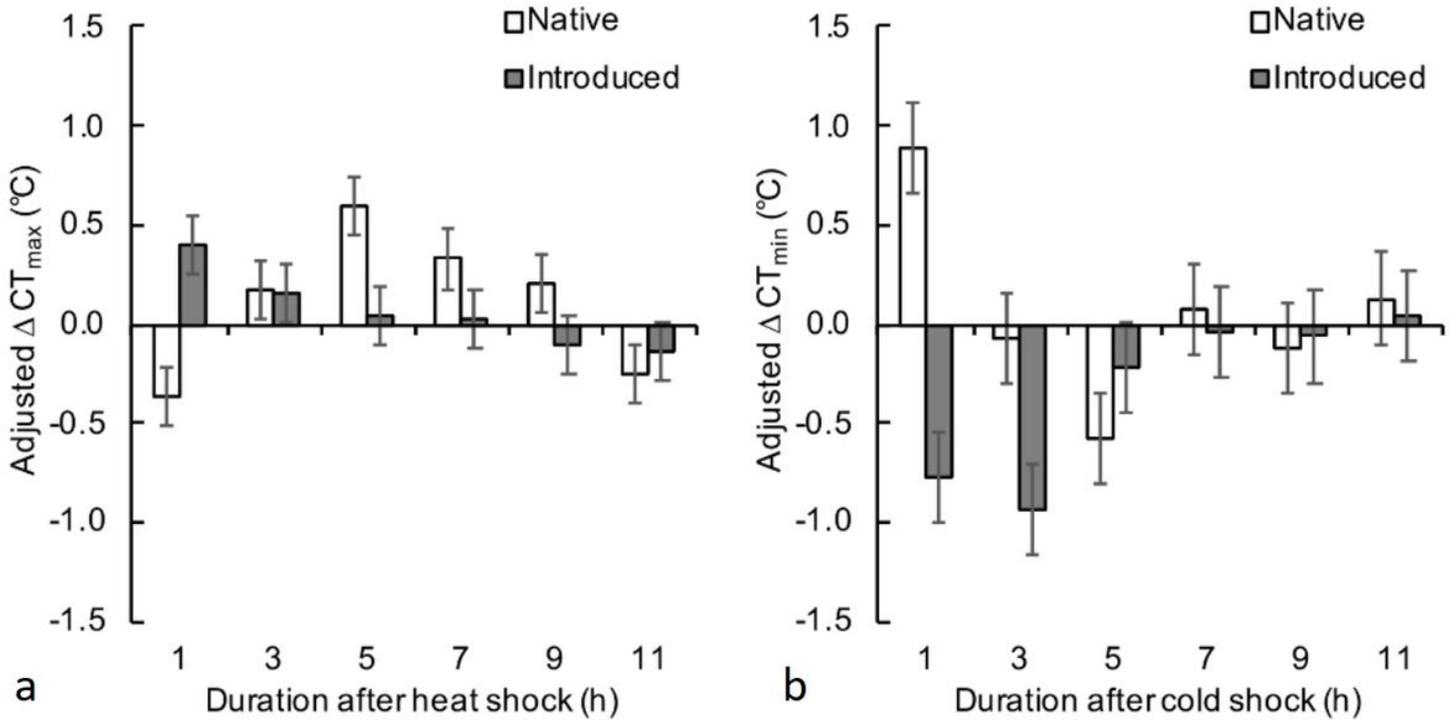


Figure 3

(a) Time interval between heat shocks versus Δ CT_{max} and (b) time interval between cold shocks versus Δ CT_{min}. The figure shows population means and associated standard errors.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Thermalhardeninganalysis.xlsx](#)