Thermal and Behavioral Adaptations of the Invasive Asian House Geckos (*Hemidactylus frenatus*)

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Certificate of Original Authorship

I, Yingyod Lapwong, declare that this thesis, is submitted in fulfillment of the requirements for the award of Doctor of Philosophy, in the School of Life Science, Facility of Science, at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

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Acknowledgments

My Ph.D. has not begun from the day I enrolled and finished on the day I graduate; it is a life-long journey. As far as I remember, I started to have an interest in science even before my kindergarten. Growing up in the countryside, I had been very close to nature, and that makes me care so much about saving it. I thank my parents for raising me in a perfect environment. My grandparents are also big influencers. My grandmum, Yai Yom, is my idol scientist. She worked in a kitchen like a chemist despite her limited school education. My childhood with fraternal grandparents on an island even opened me up for a broader view of nature. Throughout 36 years of my life, my family has always been a great support. I thank my family for shaping me up for who I am today with all the love and care.

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Dejtaradol, who has been granted permission to conduct research involving animals (U1-02470-2559) by the Institute for Animals for Scientific Purpose Development (IAD).

My sincere apologies if I have missed anyone.

Preface

The main body of this thesis comprises seven chapters, including five data chapters that I have submitted to journals. Therefore, I have formatted each chapter following the guidelines of each particular journal. This circumstance creates some minor differences in format among chapters and some unavoidable repetition in the introduction and methods.

At the beginning of each chapter, I have stated the contributions of all authors involved as per submitted manuscripts. In all of the chapters, I am the first author and the corresponding author since I primarily conceived, designed, and implemented the research, and written the manuscripts.

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Abstract

The Asian house gecko (*Hemidactylus frenatus*) is one of the most widespread invasive species in the world; however, little is known about the factors that facilitated the success of this invasive gecko. Despite the tropical origin, the gecko has established populations in temperate regions of southeastern Australia. Therefore, I investigated thermal tolerance, thermal hardening, and thermal preference of the introduced geckos in New South Wales (NSW), in comparison with their native populations in Thailand. I found that house geckos from NSW could tolerate colder temperatures, responded to thermal stresses faster, and selected lower body temperatures than geckos from Thailand. The introduced geckos also showed an ability to acclimate seasonally and thermoregulate after feeding (post-feeding thermophily). These thermal adaptions would enable the geckos to survive and perform well in the cold climate of temperate regions, and conserve energy during the winter when food is limited.

Previous studies suggested that successful invasive species have a suite of correlated behaviors that facilitate the invasion. However, since the benefits of each behavior could vary among situations, the ability to adjust behaviors should be necessary for invasive species. Therefore, I investigated the behaviors of the Asian house geckos from different populations to determine the effects of community composition on the expressions. For exploratory behavior, I found that the geckos from core communities tended to hide more and explore less. This behavioral type ensures their safety, as well as increases their chance of getting introduced. In contrast, the geckos from edge populations tended to hide less and explore more, so they should extend their range quickly. For agonistic behavior, I found that the geckos from a competitor-rich community were more aggressive than conspecifics from a competitor-released community. I suggest that the geckos adjust their behavior to balance the trade-off between access to resources and energy consumption.

My study has demonstrated the ability of the Asian house gecko to adjust both thermal biology and behavior in responding to different ecological contexts. Therefore, the gecko is likely to expand its range further, and cause problems beyond those predicted by static models. More screening of entry points, and community-based citizen science projects whereby people identify house geckos and their locations, may help to control and prevent future spread. Future studies of the molecular pathways underpinning shifts in thermal biology, along with studies of aggressive behaviors in other communities, would be useful for evaluating the generality of my results.

Chapter 1

Introduction

1.1. Biological invasion

1.1.1. Definition of biological invasion

In nature, species rarely disperse across natural barriers, which initially limited their distributions. While species have been accidentally carried across barriers by natural phenomena, such as storms, floods, or ocean currents, members of genus *Homo*, especially *H. sapiens*, have invented technologies to help them overcome those obstacles. Our ancestors migrated across the African desert and the Red Sea to reach Eurasia around 50,000 – 60,000 or 100,000 – 130,000 years ago (López et al. 2015). While roaming, humans brought other species with them, which allowed those species to cross their natural distribution ranges (Lockwood et al. 2013). After being introduced, some species caused impacts on the incipient ecosystems, ranging from mild to severe. One of the earliest examples of a high impact invasion event is the introduction of dingoes. Dingoes were brought from Asia by the pre-historic (possibly Neolithic) people that migrated to Australia around 4,600 – 18,300 years ago (Oskarsson et al. 2011). The dingoes competed with native predators, such as thylacines and Tasmanian devils, and were responsible for the declines of those native predators in mainland Australia (Johnson and Wroe 2003). In summary, biological invasions occur when species have been introduced to non-native ranges, established, spread, and in many cases, have changed the local ecosystems substantially. Humans may transport species for a variety of reasons, but a more significant number of species have been accidentally introduced in recent times due to the high volume of transport and trade (Hulme 2009).

1.1.2. Impacts of biological invasion

Invasive species have become a significant concern in recent decades because they have caused ecological and economic impacts worldwide (McNeely et al. 2001, Lockwood et al. 2013). For instance, upon introduction to an ecological community, introduced species compete with native species and, over time, may lead to the decline and extinction of native species. In predator-prey interactions, introduced species can severely influence native species due to the lack of coevolution. In Australia, toxic cane toads are responsible for the catastrophic decline of several native predators (Burnett 1997, Fukuda et al. 2016). Because native predators have not coevolved with anurans containing bufotoxins, therefore, they do not have physiological resistance to toad toxins. The introduction of diseases, parasites, or their vectors can also directly impact native species. For example, many native bird species of Hawaii are suffering from the infections of introduced avian malaria (*Plasmodium relictum*), of which the vector is the introduced southern house mosquito (*Culex quiquefasciatus*) (Lowe et al. 2000).

In some cases, introduced species directly facilitate native species or increase species diversity in recipient landscapes by reshaping habitats (Bruno et al. 2005). However, this should not be interpreted as a benefit of introduced species because the net impact should be evaluated from the whole system, not from a *per species* perspective. In an equilibrium system, a demographic change of a species might affect others around them. For example, in coastal areas of the Northern Pacific ocean, the introduced green crab *Carcinus maenas* was assumed to facilitate small crustaceans and polychaetes by consuming their natural competitors (Cohen et al. 1995, Grosholz et al. 2000). This alteration in the benthic community could interrupt microbial, planktonic, and pelagic community structures, but those domino effects have rarely been investigated. Some introduced species are responsible for landscape modification, creating more or less favorable habitats for native and other introduced species. For example, the common carp (*Cyprinus carpio*) has an extreme feeding behavior that can uproot aquatic plants and make water turbid (Lougheed et al. 1998, Badiou and Goldsborough 2015). The introduction of the carp might favor other sessile plants or animals by opening spaces but, at the same time, disfavor small submerged plants and phytoplankton by reducing light intensity in the water column. In summary, invasive species can cause negative ecological impacts by 1) directly interacting with native species, 2) reshaping community structures and trophic cascades, and 3) modifying habitat. In the long run, biological invasions are considered a significant cause of biodiversity loss (Reddy 2008).

Many introduced species have become pests, causing substantial economic loss worldwide (Pimentel et al. 2000, McLeod 2004). A large number of invasive species, such as zebra mussels, golden apple snails, rabbits, fruit flies and many species of weed, are responsible for lower yields in agriculture and fisheries (Vitousek et al. 1997). Human health can be severely affected by introduced venomous or poisonous species (e.g., ants, bees, spiders, snakes, and toxic plants), pathogenic species (e.g., viruses and bacteria), pathogen vector species (e.g., mosquitos), or allergenic species (e.g., pollens of some plants) (Neill and Arim 2011, Mazza et al. 2014). Some species could cause environmental problems by changing the incipient environments. For example, water hyacinths (*Eichhornia crassipes* (Mart.) Solms) are capable of blocking transportation routes and decreasing dissolved oxygen in water (Patel 2012). In Australia, European rabbits (*Oryctolagus cuniculus*) have overgrazed vegetation, contributing to soil erosion (Lowe et al. 2003). Therefore, economic impacts from invasive non-native species include: 1) the loss of resources, 2) costs associated with control, and 3) costs associated with ecosystem restoration. The annual cost associated with non-native species was estimated to be \$137 billion USD in the USA (Pimentel et al. 2000) and \$720 million AUD in Australia for invasive animals (McLeod 2004).

1.1.3. Invasion pathways

A biological invasion is not a single event but rather a continuous process. Generally, an invasion consists of several stages, namely transport, introduction, establishment, spread, and impact (Lockwood et al. 2013). Failing in one step could mean overall failure. For example, many species have been transported to new habitats, but not all of them survived or bred in new environments after arrival (Bomford et al. 2008). Although they have established populations, the introduced species might fail to spread further (e.g., flat-tailed house gecko (*Hemidactylus platyurus*) in Florida (Meshaka and Lewis 1994)). Even if they have extended their range, the introduced species might not cause adverse impacts to native economies or environments (e.g., banteng (*Bos javanicus*) in Australia (Bowman and Panton 1991)).

By entering new ecosystems, species need to adapt to unfamiliar resources and environments as soon as possible to survive. However, too much plasticity can reduce fitness due to energy loss. Accordingly, introduced species with pre-adaptations tend to become more successful. Firstly, introduced species likely invade habitats with similar climates (Rödder et al. 2008, Tingley et al. 2017). This ecological match allows their physiological metabolisms to function without the energetic cost. Apart from climate similarity, biological niche homology also secures their survival. For example, closely related species usually require resembling niches; therefore, the introduced species can spread fast after being introduced to habitats with a high number of congener species (Liu et al. 2014). Also, species with convergent evolution would fit in non-native environments effortlessly. In Australia, several introduced non-marsupial mammals, such as dingoes and rabbits, have successfully replaced their native counterparts, thylacines, and bilbies, respectively, despite their separate evolutionary histories (Johnson and Wroe 2003, McLeod 2004).

Successful biological invasions are usually attributable to intrinsic traits of species and propagule pressure (i.e., size of the introduced population). Early studies in this field often focused on life history, generalism, and morphological features as invasion-facilitating factors. However, later studies have shown inconsistencies and exceptions of those characteristics as invasion advantages (Ricklefs 2005, Colautti et al. 2006, Chapple et al. 2012). Concerning the discussion by Ricklefs (2005), biological characteristics are an essential factor but might have been overrated. Another key to success is propagule pressure or introduction attempt (Colautti et al. 2006). The more individuals introduced should lead to a higher number of survivors and thus a better chance to establish a population. Many studies also revealed that propagule pressures could be helpful in both pre- and post-establishment stages (Colautti et al. 2006, Drake and Lodge 2006, Wilson et al. 2009, Barnett et al. 2017). On top of that, humans have strong influences on invasion success. Typically, the species that associate with humans tend to get introduced more than other species, both intentionally and accidentally (Liu et al. 2014). For example, dogs, cats, pigs, and goats that have been domesticated and deliberately brought by humans to other locations are now among the most successful invasive species in the world (Lowe et al. 2000). At the same time, although mice and rats are unwanted, they have spread all over the globe through maritime trading (Cucchi et al. 2005, Schmid et al. 2015). A study by Tingley et al. (2010) also confirmed that a majority of invasive amphibians have close relations with humans since ancient times.

Introduced species can form mutualisms with native species, facilitating them to overcome resistances (Simberloff and Von Holle 1999, Bruno et al. 2005, Lockwood et al. 2013). When entering a new ecosystem, an introduced species does not only exploit but also provides resources. One of the most conspicuous examples is the relationship between introduced pollinators and native plants, or *vice versa*. Additionally, non-native species can facilitate other non-native species in the same way (Lockwood et al. 2013).

1.1.4. Resistances to biological invasions

The primary factor that prevents an ecosystem from biological invasions is its physical characteristics. Climate patterns are the most significant resistance because it affects the physiological functions of every organism. As a result, climate data has become the primary variable for predicting the distribution of species (Rödder et al. 2008, Liu et al. 2014). However, behavioral adaptation can minimize the significance of climate (Werner 1990, Kowalczyk and Zalewski 2011, Lei and Booth 2014). Also, a previous study by Liu et al. (2014) found that topographic heterogeneity could lower post-establishment spread rates in amphibians and reptiles globally.

The introduced species may thrive in the non-native range due to the absence of natural enemies; however, this is not always true because the recipient ecosystems might have resisting mechanisms (Bruno et al. 2005). In the introduced range, the species might experience more significant ecological pressures, such as competition, predation, or disease, than in their native ranges (Bomford et al. 2008). Typically, an ecosystem with high biodiversity tends to have stronger resistance because most resources and spaces are already occupied (Ricklefs 2005, Stachowicz and Tilman 2005). In contrast, undisturbed or isolated ecosystems usually have weak resistances due to low pressures through evolutionary history. As a result, on a global scale, Europe, North America, Australia, and the Pacific Islands have suffered a larger number of invasive species compared to

Asia, Africa, and South America (Binggeli 1996, Ricklefs 2005, Richardson and Rejmánek 2011).

Theoretically, an introduced species with a small initial population is expected to suffer from genetic problems due to genetic drifts, bottleneck effects, founder effects, or Allee effects, especially in unintentional introductions (Taylor and Hasting 2005, Drake and Lodge 2006, Puillandre et al. 2007). However, due to the high volume of travel and trade movement, a species is likely to be repeatedly introduced from many source populations, creating genetic admixtures (Kolbe et al. 2008, Wilson et al. 2009). This mechanism allows introduced species even to have higher genetic diversity than any particular populations in the native range (Tonione et al. 2011, Lockwood et al. 2013). Moreover, some species can recover from those low genetic diversity problems quickly due to high growth, reproductions, and survival rates (Chapple et al. 2013, Detwiler and Criscione 2014).

1.1.5. Trends in biological invasion research

Currently, core knowledge of biological invasions has been widely established (i.e., books, publications, and databases). Early research on biological invasions had focused on dispersal pathways, impacts, and post-invasion management. Nevertheless, practical solutions for controlling invasions are still uncertain or ineffective in many cases due to unknown factors. For example, there have been debates on whether the release of *Myxoma* virus or the top-down predation by cats is more appropriate for rabbit control on Macquarie Island (Bergstrom et al. 2009b, a, Dowding et al. 2009). Accordingly, despite decade-long studies on biological invasion, there are still many knowledge gaps. In addition, as the world is changing rapidly, new invasive species and new invasion pathways will emerge in the future.

In a growing economy, high transport and trading volume would favor species to disperse away more often (Gill et al. 2001, Hulme 2009). Although quarantine or surveillance processes are becoming stricter, the larger propagule number should increase the possibilities of species to sneak through and eventually be introduced to new territories. Furthermore, subsequent introductions will increase the size and variation of propagules, allowing them to overcome genetic problems. With admixture, introduced species likely adapt to new environments better (Kolbe et al. 2008). Growing economies also disturb ecosystems by degrading or destroying natural habitats, resulting in weaker biotic resistance.

Freezing winters have prevented most parts of the world from invasions of tropical species (Gill et al. 2001). However, some introduced species may have adapted or evolved to survive in colder weather (Kowalczyk and Zalewski 2011, Leal and Gunderson 2012, McCann et al. 2014). The heat island effect and concrete surfaces in urban areas could also provide warm habitats for thermoregulation (Lei and Booth 2014, Mollov et al. 2015). Furthermore, climate change can also increase the complexity of biological invasions (Hellmann et al. 2008, Hulme 2016). As the climate is a primary parameter that indicates invasion risk, changing climates can alter the resistance of particular regions. With increasingly warmer weather in urban heat islands, tropical species should invade temperate regions more easily (Rödder et al. 2008).

Introduced species usually come to attention only when they have posed some threats to ecosystems or economies, so there are not many studies in the early stages of invasion (Puth and Post 2005). Furthermore, scientists have tended to ignore invasive species in their original native regions because of their abundance and harmlessness. As a result, knowledge of invasive species often comes from the later stages, in non-native ranges, which might not precisely reflect the invasion history of the species because introduced populations should have already adapted or evolved (Lockwood et al. 2013). For example, most of the early investigations on invasive brown tree snakes (*Boiga irregularis*) were from the island of Guam and occurred after the snake had already wiped out the island's avifauna. Later studies found that some morphological characters of the snake have drastically changed after years of naturalization (Whittier et al. 2000, Savidge et al. 2007, Trembath and Fearn 2008). Some characteristics that benefited in the early stages of invasion could have been minimized or lost through the process. Several studies on cane toads revealed that the toads have become less likely to disperse after the population has established for long periods (Lindström et al. 2013, Gruber et al. 2017), so the actual dispersal rate might be underestimated when considering only core populations alone. Accordingly, spatial or chronological comparative studies of invasive species would provide more precise and useful information for further management.

1.2. The thermal biology of invasive species

In recent decades, there have been intensive studies on the thermal biology of invasive species, aiming to predict their future distribution ranges (Peterson 2003, Rödder et al. 2008, Jimenez-Valverde et al. 2011). The expected thermal characteristics of invasive species include wide ranges of functional body temperature (i.e., eurythermy) and high thermal tolerance (Kelley 2014, Tepolt and Somero 2014). Also, previous studies on several geographically widespread invasive species found their ability to alter some thermal traits so that they could survive in a wide range of climates (Kolbe et al. 2012, Leal and Gunderson 2012, McCann et al. 2014, Kosmala et al. 2018). Therefore, the study on thermal biology should allow us to understand why some ectothermic species are successful invaders, whereas other species are not.

The broad range of functional body temperatures and high thermal tolerance should allow invasive species to survive through invasion processes, thrive in many different climates, and outcompete thermally-naïve native species (Kelley 2014). Therefore, many studies focused on thermal tolerances as a primary factor that promote the range expansions of invasive species (Zerebecki and Sorte 2011, Bates et al. 2013). In comparison with temperate species, tropical species tend to have narrower ranges of functional body temperature because they have evolved in a relatively stable climate (Janzen 1967, Ghalambor et al. 2006). Therefore, tropical species are unlikely to survive in the fluctuating climate of temperate regions. However, several studies on the tropical crested anole (*Anolis cristatellus*) found evidence of thermal adaptation during the expansion to the colder regions of Florida (Kolbe et al. 2012, Leal and Gunderson 2012). This phenomenon suggested that some tropical species might be capable of shifting their cold tolerance after being introduced to a colder region.

Thermal acclimation is another adaptation that allows animals to shift their thermal physiology to changing climate conditions so that it can function under the new thermal regime (Lagerspetz 2006). Physiologically, thermal acclimations involve regulation of metabolic enzymes and stress proteins, including heat shock proteins and cold shock proteins (Ritossa 1962, Thieringer et al. 1998, Seebacher et al. 2003, Seebacher 2005). This ability is adaptive and reversible, which means the animals can quickly change their functional temperatures according to climate conditions they have just experienced. For example, cane toads in Australia can shift their thermal tolerances downwards following 12-hour acclimatization to cold temperatures (McCann et al. 2014). Therefore, thermal acclimation is a rapid physiological response that can help an animal to expand its distribution range beyond its preferred climate. However, thermal acclimation can be limited since it is controlled by genetic factors (Somero 2010, Seebacher et al. 2012).

In cold climates, the ability to thermoregulate is crucial due to the limit of the natural heat sources (Davenport 1992). In this scenario, reptiles are more vulnerable than birds and mammals because they are unable to generate heat metabolically (Angilletta et al. 2002). In responding to this physiological imparity, reptiles instead exploit behaviors to attain preferred body temperatures. While diurnal reptiles mainly sunbathe, nocturnal reptiles depend on heat conductions with the substratum to warm up their bodies (Bustard 1967, Webb and Shine 1998, Kearney 2001). By thermoregulating, lizards can also avoid exceeding their critical body temperatures (Domínguez–Guerrero et al. 2019), thereby decoupling climate as a selective pressure (Bogert 1949, Méndez-Galeano et al. 2020).

1.3. The behavior of invasive species

While intrinsic characteristics and propagule pressures are important factors in determining the success of biological invasions, there are often inconsistencies between predictions and biological reality (Chapple et al. 2012). Many closely related species can exhibit stark differences in invasion success despite strong similarities in morphology and ecology (Meshaka and Lewis 1994, Chapple et al. 2011). For example, while the small skink *Lampropholis delicata* has become a successful invasive species, the sympatric congeners *L. guichenoti* failed to spread outside its native range. Several comparative studies pointed out that *L. delicata* has become more successful as an invasive species because of its prominent exploratory and antipredator behaviors (Chapple et al. 2011, Bezzina et al. 2014). Hence, besides the life history, the behavior should be another critical factor that assists a species to invade new ecosystems. Furthermore, many studies in a range of invasive species have found a set of correlated behaviors that is potentially responsible for their successes, including exploratory behavior, aggressiveness, and antipredator behavior (Evans et al. 2010, Chapple et al. 2012, Sih et al. 2014).

However, a fixed behavioral type might be beneficial in one situation but detrimental in many others; hence, successful invasive species should possess behavioral plasticity or adaptations in responding to different ecological contexts (Burton et al. 2010, Fogarty et al. 2011, Chapple et al. 2012, Liebl and Martin 2012, Lindström et al. 2013, Sih et al. 2014, Gruber et al. 2017). On a short temporal scale, a behavioral adaptation can assure the survival of the introduced population during a sudden change. A study on an invasive mosquitofish (*Gambusia affinis*) by Cote et al. (2013) found that the fish could quickly change its social behavior to avoid predation after exposure to predators. On the other hand, behavioral adaptations could occur on a spatial scale. For example, the introduced cane toads in Australia showed different behavioral types among geographically distinct populations. The toads from core populations were less likely to disperse in long distances than conspecifics from edge populations, possibly because the energy conservation has outweighed the benefit from exploration (Lindström et al. 2013, Gruber et al. 2017). Remarkably, the toad has also shifted its behavior, from being primarily nocturnal to being active throughout the day, to survive in dryer parts of Australia (Webb et al. 2014). Therefore, behavioral adaptations as a response to ecological context changes should be crucial during the invasion process of the non-native species.

1.4. Asian house gecko (*Hemidactylus frenatus*)

1.4.1. Biology and ecology

The Asian house gecko (*Hemidactylus frenatus*; family Gekkonidae) is native to South and Southeast Asia (Ota and Whitaker 2010). This medium-sized gecko (snout-vent length, henceforth SVL, 42 - 67 mm) is sexually dimorphic, with males attaining larger body sizes than females (Zug et al. 2007, Das 2010, Chan-ard et al. 2015). The gecko has distinctive spiny tubercles on its tail, giving it another common name, "spiny-tailed house gecko" (Chan-ard et al. 2015). The gecko has a slightly compressed body, relatively large head, a round tail that is typically longer than SVL. Toe-pads are present on every digit, making this species a fantastic climber. Its color ranges from pale brown to dark grey (Zug et al. 2007, Das 2010, Chan-ard et al. 2015). Similar to many Gekkonid lizards, geckos in this genus can change their skin color to attain excellent camouflage (Vroonen et al. 2012, Das et al. 2014, Fulgione et al. 2014).

The gecko is mainly insectivorous and prefers small soft-body insects, especially dipterans (Canyon and Hii 1997, Tkaczenko et al. 2014). However, this gecko is a generalist predator that feeds on various types of insects in different circumstances (Tkaczenko et al. 2014). Previous studies also reported that house geckos also feed on smaller lizards (Bolger and Case 1992, Alemán and Sunyer 2015). There have been confirmations of cannibalism in the Asian house gecko (Galina-Tessaro et al. 1999, Perez et al. 2012). In a sole report, the gecko was reported to feed on eggs of its species (Kusuminda et al. 2013). As a tropical reptile, the Asian house gecko needs a warm climate to be able to forage actively; it will stop feeding when the temperature is less than 17°C (Lei and Booth 2014).

In Southeast Asia, arboreal colubrid snakes and larger geckos have adapted to feed on the abundant house geckos (Bolger and Case 1992, Leong and Foo 2009, Das 2010, Sanchez 2010, Parves and Alam 2015). In addition to natural predators, the house geckos also suffer high predation pressure from domestic cats, dogs, and rats (Case et al. 1994, de Sliva 2006, Ditchkoff et al. 2006, Bucol 2019). Some birds and bats predate on geckos opportunistically (personal observation). Accordingly, in native habitats, this gecko lives in high predation-risk environments. As a non-native species, its role as prey in new food webs is less known. There were reports of several native birds feeding on this gecko, but its significance as a food source has not been evaluated (Barquero and Hilje 2005, Rojas-González and Wakida-Kusunoki 2012).

In its native tropical climate, the gecko breeds throughout the year, while some sub-tropical populations also breed seasonally (Ota 1994, Amey 2013). Exceptionally, female Asian house geckos can store sperms for an extended period after copulation (Yamamoto and Ota 2006). This feature allows the gecko to reproduce after a long journey from donor to recipient locations without additional matings. The gecko usually lays two hard-shelled eggs at a time. The incubation period varies, ranging from 53 to 88 days (McCoid 1994). The house gecko also displays communal oviposition behavior (McCoid 1994, Krysko et al. 2003), which could increase the survival rates of the eggs and the hatchlings (Doody et al. 2009). The gecko has a high fecundity rate, which contributes to a high population growth rate (Amey 2013, Nicholson et al. 2015)).

1.4.2. Behavior

The social behaviors of the house geckos consist of both acoustic and visual expressions. Reptiles in the family Gekkonidae are well-known for their distinctive ability to produce loud calls to communicate as a result of their nocturnal lifestyle. The studies on vocal communications of house geckos in the genus *Hemidactylus* found similar patterns among members (Marcellini 1974, 1977a, Petras 1995, Regalado 2003). A certain number of calling patterns were interpreted and classified, such as courtship calls, territorial calls, and stress call. In the Asian house gecko, at least five vocal arrangements were recognized, indicating its complex social behavior (Marcellini 1974, Marcellini 1977b). Additionally, the gecko uses visual signals for short-distance communication. Most geckos, including the Asian house gecko, use postures and tail movements during physical confrontations with conspecifics (Marcellini 1977a, Petras 1995). Social interactions with other sympatric species are complicated and poorly studied, especially in their native habitats.

1.4.3. Range expansion

The Asian house gecko is among the most successful invasive reptile species in the world (Case et al. 1994, Bomford et al. 2008, Hoskin 2011). The gecko probably spread from its native range as early as 4,000 years ago when Polynesian people migrated from Asia to the Pacific Islands (Case et al. 1994). Outside of its native distribution range in South and Southeast Asia, the geckos have become naturalized in the Ryukyu Islands, the Pacific Islands (including the Galápagos), Northern Australia, Northern Latin Americas, the Caribbean Islands, and Eastern Africa (including Madagascar and Mascarene Islands) (Carranza and Arnold 2006, Rödder et al. 2008, Kraus 2009, Ota and Whitaker 2010, Farr 2011, Hoskin 2011, Torres-Carvajal and Tapia 2011, Kurita 2013, Torres-Carvajal 2015, Bañuelos-Alamillo et al. 2016). Surprisingly, house geckoes in this genus, possibly including the Asian house gecko, have minimal self-dispersal abilities; they rely heavily on human-mediated dispersal (Klawinski 1991, Locey and Stone 2006, Short and Petren 2011). These geckoes spread worldwide through multiple long-distance introductions via human-mediated transportations (e.g., jumping dispersals), which is a lot faster and more complicated than a single deliberate introduction. This method of dispersal also induces genetic admixture, making populations more likely to establish in novel habitats (Tonione et al. 2011). In the future, the gecko is likely to expand faster and further through the assistance of the urban heat island effect and climate change (Rödder et al. 2008).

Asian house geckos usually get unintentionally transported and introduced to non-native ranges by human-associated vessels (Case et al. 1994, Carranza and Arnold 2006, Rödder et al. 2008). A study by Gill et al. (2001) found that the gecko was the most accidentally imported reptile to New Zealand between 1929 and 2000, especially after 1980. They hid in various types of cargo from at least 14 different regions. Fortunately, the cold climate of New Zealand has prevented the gecko from successfully establishing. In a shorter distance, the geckos (and their eggs) could travel together with people in small vehicles. In a specific report, a gecko had traveled for 50 km on top of the moving vehicle (Norval et al. 2012).

While the introduction pattern of the Asia house gecko is well pictured, the factors that help it to expand its range are still poorly known. A study by Barnett et al. (2017) suggested that propagule pressure and time of arrival were the main factors that determine range expansion. However, this study has only explained the situation after the species has already well-established. To fully understand how far this species can disperse in incipient ranges, we need more information on factors that facilitate survival and spread during the early stages of the invasion.

1.4.4. Impacts of the introduced Asian house gecko

The most notable impact of the Asia house gecko is its ability to outcompete native fauna. Many studies have reported population declines, or even local extinctions, of native geckos after the introductions of the Asian house gecko (Bolger and Case 1992, Petren et al. 1993, Case et al. 1994, Petren and Case 1996, Brown et al. 2002, Cole et al. 2005, Dame and Petren 2006, Cole and Harris 2011, Alemán and Sunyer 2015). According to the competitive exclusion principle, species with similar or highly overlapping niches will try to outcompete each other, causing the weaker species to decline or go extinct (Pocheville 2015). The proposed invasive mechanisms include direct agonistic interactions, predation, sexual interference, and competition for resources. However, some native species have shown strong resistance and did not receive direct impacts from the invasive house gecko (Yang et al. 2012, Nicholson et al. 2015, Cisterne et al. 2019). Previously, most attention has focused on the gecko's competitive efficiency; hence, the impacts on other communities, such as prey arthropods and predators, are poorly understood. Although the Asian house gecko is considered a generalist, it prefers some insects more than others (Tkaczenko et al. 2014). Thus, the composition of the insect community, especially in urban areas, could change, but the degree to which this has occurred is unknown.

Another potential threat of the introduced gecko is its capability to harbor diseases and parasites. The Asian house geckos could carry many parasites, which could infect native fauna (Matsuo and Oku 2002, Barton 2007, 2015, Barnett et al. 2018). For example, a Pentastomid parasite (*Raillietiella frenata*) commonly found in the Asian house gecko can switch to the new host, the Cane Toad (*Rhinella marina*), in both native range in Panama (Kelehear et al. 2015) and introduced range in Australia (Kelehear et al. 2013). Also, the gecko can be a vector of pathogenic bacteria *Salmonella* (Oboegbulem and Iseghohimhen 1985, Callaway et al. 2011, Jiménez et al. 2015). So far, the gecko is not responsible for any direct economic loss.

In the laboratory, the Asian house gecko often attacks other geckos (Bolger and Case 1992, Case et al. 1994, Cole et al. 2005). The gecko is territorial and uses aggressive behavior to prevent territory incursions and secure resources (Stamps 1977). Even without confrontation, smaller native geckos avoided staying close to the Asian house gecko (Petren et al. 1993, Cole et al. 2005). Sharing habitats with the exotic gecko, the native geckos tend to lose opportunities to feed and mate, and maybe more exposed to predators. Also, there are reports of the Asian house gecko trying to predate other geckos (Alemán and Sunyer 2015).

However, since direct interactions are rare *in situ*, exploitative competition could be another important displacement mechanism (Petren and Case 1996). House geckos are fast and furious hunters and can substantially reduce food levels in the system (Petren and Case 1996, Brown et al. 2002). As a result, the rival geckos may not have enough food to maintain healthy populations. In a case study by Cole and Harris (2011), Mauritius's endemic Ornate Day Gecko (*Phelsuma ornate*) had to change its foraging period to avoid competition with the introduced gecko, which might force them to encounter unfamiliar predators.

1.4.5. Status of the Asian house gecko in Australia

Hoskin (2011) documented the invasion history and the potential risks of the Asian house gecko in Australia. The geckos usually established in coastal cities first, indicating that maritime shipment was the primary intercontinental introduction pathway (Csurhes and Markula 2016). The Asian house gecko first arrived in Australia as early as the 1830s but failed to establish until the 1960s (Newbery and Jones 2007, Hoskin 2011). The successful establishment at a later time is possibly the result of frequently repeated introductions. The species then spread inland in cars, trucks or trains since they were usually found along transportation routes (Mckay et al. 2009). As a tropical species, the Asian house gecko is most abundant in the northern part of the country (Hoskin 2011). Despite unconfirmed establishments, the gecko has been reported from colder transportation hubs, including Canberra, Sydney, Melbourne, Perth, and Hobart (Welbourne 2012, Csurhes and Markula 2016).

According to Hoskin's review, impacts of the Asian house gecko on native Australian ecosystems were likely but not well studied (Hoskin 2011). Although Vanderduys and Kutt (2013) suggested that the gecko might be harmless to native ecosystems as its distribution is limited to urban habitats, a more recent study by Barnett et al. (2017) confirmed that the gecko could spread into bushland if the propagule pressure were large enough. There are limited empirical studies on the impacts of this gecko on the Australian ecosystem. Yang et al. (2012) revealed that the introduced gecko posed no threat to sympatric native species, *Gehyra australis*. However, they also revealed niche partitioning between both species. As a host of many parasites, the house gecko has the potential to transfer them to native fauna (Kelehear et al. 2013). A recent study also suggested that the Asian house gecko could be a competent spreader of native parasites due to their high abundances (Barnett et al. 2018).

1.5. Aims of the study

My study aimed to investigate the roles of thermal biology and behavior of the Asian house gecko during the invasion process. Since the gecko is a tropical species, it is thought to have a narrow range of functional body temperatures and a limited ability to tolerate cold temperatures (Janzen 1967). Therefore, the range expansion of the Asian house gecko into the temperate region of southeastern Australia is unexpected. Besides experiencing cold winters, this region also has frequent summer heatwaves. Therefore, to survive in southeastern Australia, house geckos could have either exploited the buffered climate of urban areas (by living inside insulated houses), or they may have shifted their thermal physiology. To investigate these alternative hypotheses, in the first part of my study, I carried out experiments to answer five broad questions:

1) Can introduced geckos tolerate colder and hotter temperatures?
2) Can introduced geckos shift their thermal tolerances after thermal shocks?
3) Do introduced geckos have a lower thermal preference?
4) Do introduced geckos acclimate seasonally?
5) Do introduced geckos increase body temperatures after feeding (post-feeding thermophily)?

In the second part of my study, I focused on two behaviors that could facilitate the invasion of the gecko, including exploratory behavior and agonistic behavior. However, instead of observing the behaviors of a single population of the Asian house gecko, I compared multiple populations from different environments, to investigate how ecological contexts affect the degree of behavioral flexibility. I carried out behavioral experiments to answer two questions:

1) Do Asian house geckos display variation in their aggressive and exploratory behaviors in response to different ecological contexts?
2) If yes, how do those behaviors facilitate the geckos during the invasion process?

1.6. Thesis structure

This thesis consists of a series of manuscripts that I have submitted or plan to submit to scientific journals. My thesis is composed of manuscripts that fall within two broad themes that focus on thermal biology and behavior. In the first part, I compared three thermal traits: thermal tolerance, thermal hardening, and thermal preference of native geckos from Thailand and introduced geckos from southeastern Australia. In the second part of my thesis, I explore how behaviors of geckos from different populations vary depending on the composition of the community. I explain those studies in more detail in each chapter.

Chapter 2 describes the divergence in thermal tolerance among four populations of the Asian house geckos, two from Thailand and two from NSW, Australia. This chapter also describes the patterns of seasonal acclimation in thermal tolerance of the introduced geckos from southeastern Australia.

Chapter 3 describes the divergence in thermal hardening between native house geckos from Thailand and introduced geckos from NSW.

Chapter 4 describes the divergence in thermal preference among four populations of the Asian house geckos, two native populations in Thailand, and two introduced populations in NSW. In this chapter, I describe patterns of thermoregulation, seasonal acclimation in thermal preferences, and post-feeding thermophily of the introduced geckos from southeastern Australia.

Chapter 5 describes the divergence in exploratory behavior among two core populations and three edge populations of the Asian house gecko, with an additional comparison with the flat-tailed house gecko. This chapter explains how interaction pressure can influence behaviors and how behavioral adaptation can facilitate the dispersal of the gecko.

Chapter 6 describes the divergence in agonistic behavior between geckos from a competitor-rich and a competitor-release community. This chapter explains the contradictory results of previous studies that documented the aggressiveness and lack of aggressiveness of the introduced geckos in different populations.

1.7. Ethics and permits

In Australia, all procedures were performed in accordance with ethical standards under the approval of the University of Technology Sydney Animal Care and Ethics Committee (UTS ACEC ETH17-1588). I was granted a biosecurity permit to capture and bring introduced *Hemidactylus frenatus* to the laboratory under NSW Biosecurity Act 2015 (Reference number V18/3468). In Thailand, I conducted experiments under the supervision of Ariya Dejtaradol. She has been granted permission to conduct research involving animals (U1-02470-2559) by the Institute for Animals for Scientific Purpose Development (IAD).

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Chapter 2

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

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CRediT authorship contribution statement

Yingyod Lapwong: Conceptualization, Methodology, Investigation, Data Curation, Writing - Original Draft. Ariya Dejtaradol: Methodology, Resources. Jonathan Webb: Supervisor, Conceptualization, Methodology, Writing - Review & Editing.

2.1. 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 south-east 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 from 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 between populations from Thailand and Australia (range = 43.6-43.7°C). By contrast, geckos from southeastern Australia had lower cold tolerance (CT_{min}) (mean = 10.4°C) than geckos from Thailand (mean = 11.6°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

2.2. Introduction

Invasive species cause ecological and economic impacts worldwide and have become a significant concern in recent decades (McNeely et al. 2001, Pimentel et al. 2005, Jardine and Sanchirico 2018). 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 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 (Peterson 2003, Rödder et al. 2008, Jiménez-Valverde et al. 2011). 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 species thermal traits change 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 southern India and Sri Lanka, Bangladesh, southern China, Thailand, Malaysia, Indonesia, and Philippines (Fig. 2-1.) (Case et al. 1994, Carranza and Arnold 2006, Lever 2006, Bansal and Karanth 2010, Ota and Whitaker 2010). House geckos established populations in tropical Australia in the 1960s, and since 2000 the species has established populations in colder subtropical regions of eastern Australia (Hoskin 2011). The species' ability to expand into cold climates 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 (Janzen 1967, Ghalambor et al. 2006). 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 highest in the most northerly population (Kolbe et al. 2014). Interestingly, anoles also shifted their cold tolerance downwards 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 mainly 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 incipient range (niche conservatism). Alternatively, if geckos routinely experience cold temperatures in their introduced range, we would predict that geckos from the temperate region of Australia would have lower cold tolerance than geckos from native 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 populations in their native range in Thailand, and introduced populations in southeastern Australia.

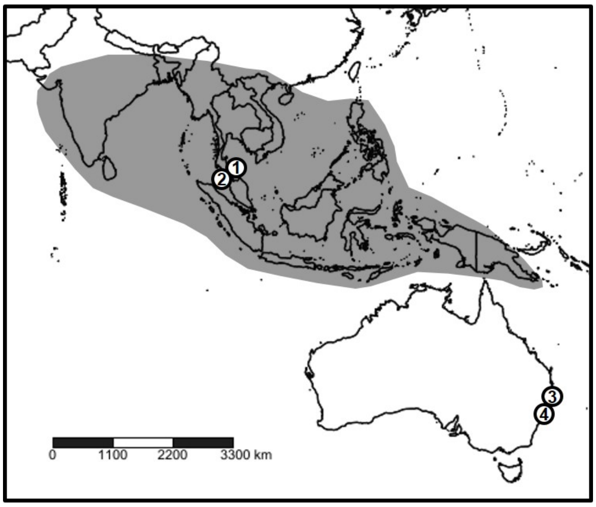

Figure 2-1 Locations of study populations of *H. frenatus* in Thailand [Hat Yai (1) and Satun (2)] and Australia [Yamba (3) and Coffs Harbour (4)]. Study populations in each country were 100 km apart. Grey shading indicates the native distribution of *H. frenatus*

(Case et al. 1994, Carranza and Arnold 2006, Bansal and Karanth 2010, Ota and Whitaker 2010).

2.3. Materials and methods

2.3.1. 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), because they are located in the center of the gecko's native distribution range (Fig. 2-1). 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. 2-2). 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, approximately since the 2000s (Hoskin 2011). We collected geckos from Yamba (-29.436890, 153.357986) and Coffs Harbour (-30.292685, 153.119707) in a subtropical region of New South Wales, where temperatures drop markedly during winter (Fig. 2-2). To determine whether geckos in Australia showed seasonal variation in thermal tolerance, we collected 20 geckos from Yamba and 13 from Coffs Harbour in 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 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 (1.88-7.49 g); Coffs Harbour, SVL = 52 mm (range 45–63 cm), mass = 3.35 g (1.73–5.69 g).

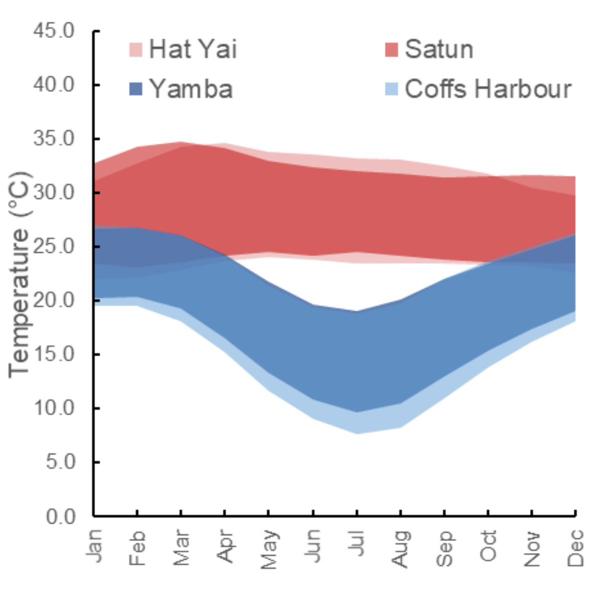

Figure 2-2 Monthly average temperature ranges in Hat Yai, Satun, Yamba, and Coffs Harbour. Data for Yamba and Coffs Harbour were collected from 1977 – 2019 (Bureau of Meteorology 2019). Data of Hat Yai and Satun were collected during 1981 – 2010 (Thai Meteorological Department 2019).

2.3.2. Husbandry of geckos in captivity

Each gecko was housed individually in a 2L ventilated plastic cage (200 x 150 x 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 – 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, dropping to room temperature at night. We used a humidifier to maintain the relative humidity at 60%, while the lighting was set to 12:12 light to dark circle. We fed geckos live crickets or mealworms every third day between 1700 – 1900h. Geckos were kept in captivity for no more than ten days and were then released to their site of capture (Thailand) or were euthanized (Australia).

2.3.3. Estimating thermal tolerance

The critical thermal maxima and minima are the upper and lower body temperatures, at which an animal's ability to move is impaired (Cowles and Bogert 1944). In lizards, the loss of righting reflex is often used to estimate critical thermal limits (Lutterschmidt and Hutchison 1997). This reflex describes the ability of an animal to right itself after being turned upside down. To determine the CT_{min} and 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 minutes 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 ± 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 seconds 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 temperature. The measurements of CT_{min} and CT_{max} were separated by five days so the geckos could fully recover from thermal shock.

2.3.4. 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). 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).

2.4. Results

2.4.1. Thermal tolerances of native and introduced populations of *H. frenatus*

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. 2-3a). By contrast, CT_{max} did not differ among populations (ANOVA $F_{3,113} = 0.90$, P = 0.45, Fig. 2-3b).

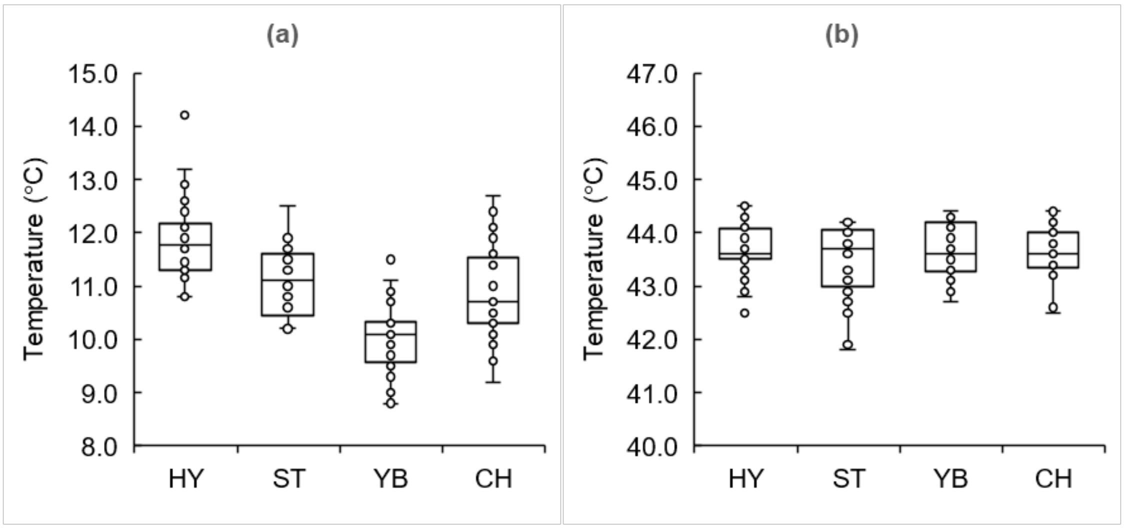

Figure 2-3 Thermal tolerances of *H. frenatus* from Thailand [Hat Yai (HY) and Satun (ST)], and southeastern Australia [Yamba (YB) and Coffs Harbour (CH)]. The open bars represent interquartile range (IQR), with the crosslines as medians. Open circles along the middle lines present the data distribution. (a) CT_{min} was significantly lower in Australian populations, whereas (b) CT_{max} did not differ among populations.

2.4.2. Seasonal variation in thermal tolerance of introduced populations of *H. frenatus*

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. 2-4a). 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 2-4b).

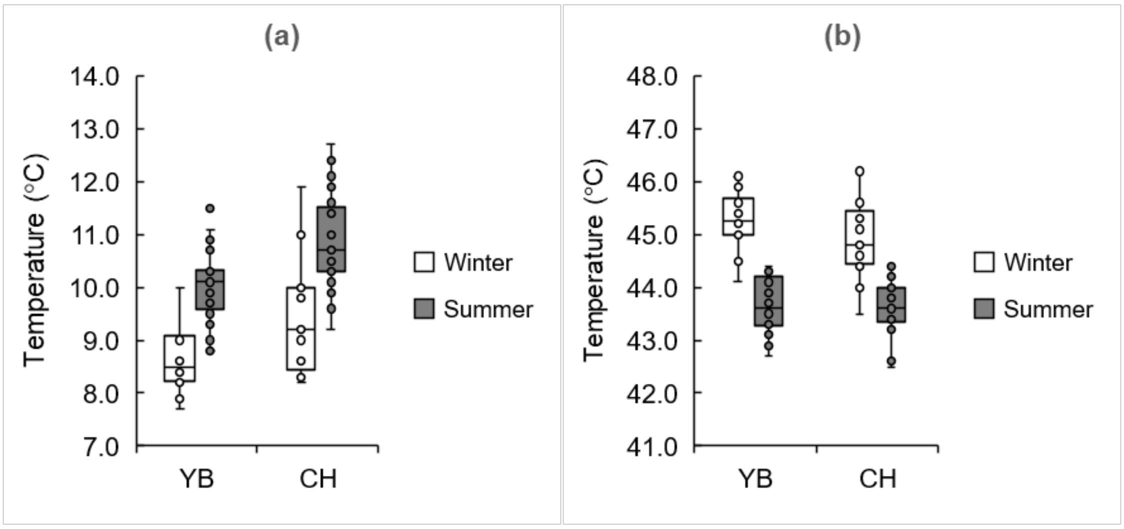

Figure 2-4 Thermal tolerances of *H. frenatus* from Yamba (YB), and Coffs Harbour (CH) populations in winter and; while (a) CT_{min} were significantly higher in summer, (b) CT_{max} were significantly lower in summer in both populations.

2.5. 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. 2-3), suggesting that geckos have shifted their cold tolerance downwards in response to lower environmental temperatures. 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. 2-4). 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 populations in its native range 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 frequently observed (Clusella-Trullas and Chown 2014). The CT_{max} 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. 2-4b). 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 temperature.

2.6. Conclusion

In conclusion, our study supports the growing body of literature that shows that tropical reptiles can display shifts in cold tolerance and develop seasonal acclimation (Kolbe et al. 2012, Leal and Gunderson 2012, McCann et al. 2014). A previous study suggested that *H. frenatus* has 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 seeking to predict spread will need to account for evolutionary changes in invasive species' thermal traits.

Compliance with ethical standards

Ethical approval

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

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Chapter 3

Rapid responses to thermal stresses of the invasive Asian House Gecko (*Hemidactylus frenatus*) in a temperate region of Australia

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CRediT authorship contribution statement

Yingyod Lapwong: Conceptualization, Methodology, Investigation, Data Curation, Writing - Original Draft. Ariya Dejtaradol: Methodology, Resources. Jonathan Webb: Supervisor, Conceptualization, Methodology, Writing - Review & Editing.

3.1. 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 compared to 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 responses over the same time intervals. We then explored whether hardening responses differed between populations or among time intervals. Basal heat tolerance did not differ between populations, but geckos from Australia had lower cold tolerance than geckos from Thailand. The magnitude of the heat hardening and cold hardening responses was similar among populations. However, 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). Faster responses to heat stress and cold stress may have allowed invasive geckos to survive rapid temperature fluctuations that occur in temperate regions.

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

3.2. 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 (Rödder et al. 2008, Jiménez-Valverde et al. 2011); 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, Zerebecki and Sorte 2011, McCann et al. 2014).

Thermal hardening is a rapid thermal acclimation that occurs within minutes or hours after a brief exposure to extreme temperature (Angilletta 2009). 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, Thieringer et al. 1998, Seebacher 2005) 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 of invaders have compared the responses of invaders with those of congeneric species in the native range (Hu et al. 2014). Most of these experimental studies have focused on arthropods, and have shown that invasive species can have increased plasticity for thermal tolerance, or may exhibit different time courses for plastic responses (Chown et al. 2007, Nyamukondiwa et al. 2010). For example, a study on the Mediterranean fruit fly *Ceratitis capitata* and the narrowly distributed congener *C. rosa* found that common-garden reared flies had similar levels of survival to high and low temperatures. However, while the range of temperatures that induced rapid cold hardening was similar for both species, at 5.5°C, the invasive *C. capitata* developed rapid cold hardening faster and maintained this ability for longer than did *C. rosa* (Nyamukondiwa et al. 2010). While studies on arthropods have increased our understanding of how thermal hardening can differ between invasive and native species, fewer studies have examined whether thermal hardening can change during the invasion (Lenz et al. 2018).

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 around the world (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 (Janzen 1967, Ghalambor et al. 2006). 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 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. 3-1). 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.

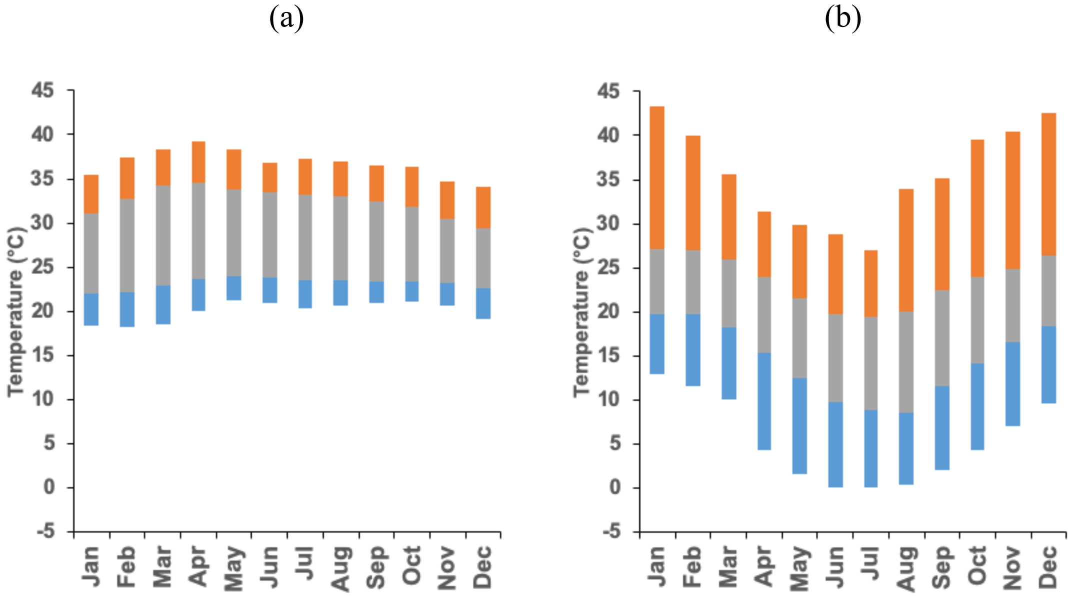

Figure 3-1 Temperature profiles of (a) Coffs Harbour, southeastern Australia, and (b) Hat Yai, southern Thailand; blue bars represent extreme low-temperature ranges, grey bars represent average-temperature ranges, and orange bars represent extreme high-

temperature ranges. Data from Hat Yai (Thai Meteorological Department 2020) and Coffs Harbour recorded (Bureau of Meteorology 2020) recorded between 1981-2010.

3.3. Materials and methods

3.3.1. Studied populations

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 additionally collected another 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. At the collection times, daily temperatures range between 23-32°C in southern Thailand and 20-30°C in northern NSW. 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 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 x 150 x 60 mm, Sistema®, New Zealand) containing a piece of tissue paper, a water dish, and a cardboard tube as a shelter, with 23-32°C ambient temperature, 12:12 light to dark circle. We fed with five crickets every third day at 17h-19h. 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 back to where they were captured.

3.3.2. 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 inserted and then 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 ± 0.1°C) for real-time temperature 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 carryover effect.

3.3.3. Data analyses

To analyze the data, we used a two-factor ANOVA to determine the effects of locations (Thailand vs. Australia) and time intervals as treatment groups on the basal CTs. We also performed two-factor ANCOVA to determine the effects of the locations and time intervals on the final CTs with the basal CTs as covariates. 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 ($P > 0.05$). We plotted graphs between the basal CTs and final CTs of each group, which revealed approximate linear relationships between them. The Levene's test of equality of variances also confirmed the homogeneity of variances ($P > 0.05$).

3.4. Results

3.4.1. Heat tolerance

The two-factor ANOVA revealed no effect of location ($F_{1,108} = 0.584$, $P = 0.45$), treatment group ($F_{1,108} = 1.078$, $P = 0.38$), and interaction between location and group ($F_{1,108} = 0.132$, $P = 0.99$), on the basal CT_{max}. The mean basal CT_{max} of both populations was 43.6°C. There was a significant negative correlation between basal CT_{max} and the change in CT_{max} (ΔCT_{max}; $r = - 0.474$, $P < 0.05$). A two-factor ANCOVA with basal CT_{max} as the covariate, and final CT_{max} as the dependent variable revealed no effect of location ($F_{1,107} = 1.378$, $P = 0.24$), but a significant effect of time interval ($F_{5,107} = 2.447$, $P < 0.05$), and a significant interaction between time and location ($F_{5,107} = 3.960$, $P < 0.05$). That is, the time course of heat resistance differed between locations (Fig. 3-2a & 3-3a). For instance, the Thailand geckos had the highest final CT_{max} at the 5-hour interval (adjusted mean = 44.2°C, $\Delta CT_{max} = 0.7$°C), whereas the NSW geckos had the highest final CT_{max} at the 1-hour interval (adjusted mean = 44.0°C, $\Delta CT_{max} = 0.4$°C)

3.4.2. Cold tolerance

A two-factor ANOVA showed a significant effect of location on the basal CT_{min} ($F_{1,108} = 24.589$, $P < 0.05$), and there was no effect of treatment group ($F_{1,108} = 1.069$, $P = 0.38$) or the interaction between location and group ($F_{1,108} = 0.221$, $P = 0.95$). 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}; $r = 0.554$, $P < 0.05$). A two-factor ANCOVA, with basal CT_{min} as the covariate, and final CT_{min} as the dependent variable, showed no effect of location ($F_{1,107} = 3.917$, $P = 0.05$), but a significant effect of the time intervals between cold shocks ($F_{5,107} = 2.405$, $P <$

0.05), and a significant interaction between time intervals and locations ($F_{5,107}$ = 5.901, $P < 0.05$). That is, the time course for cold hardening differed between native and introduced geckos (Fig. 3-2b & 3-3b). For instance, while the native geckos had the lowest final CT_{min} at the 5-hour interval (adjusted mean = 10.2°C, ΔCT_{min} = -0.9°C), the introduced geckos had the lowest CT_{min} at the 3-hour interval (adjusted CT_{min} = 9.9 °C, ΔCT_{min} = -0.5°C)

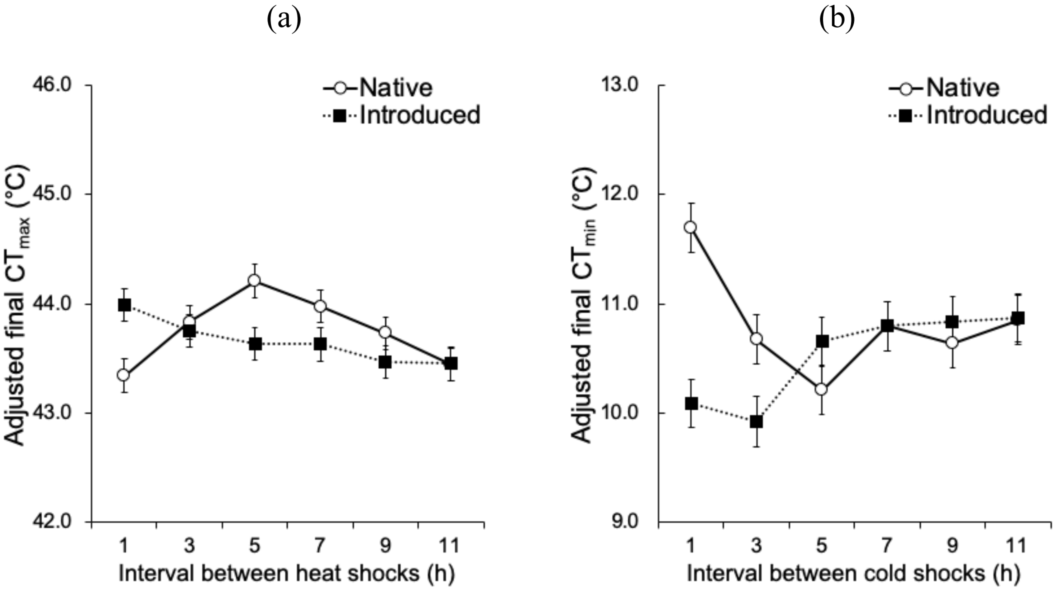

Figure 3-2 (a) Mean (±SE) final CT_{max} and (b) mean (±SE) final CT_{min} (after being adjusted by ANCOVA) of native and introduced geckos at different intervals between thermal shocks.

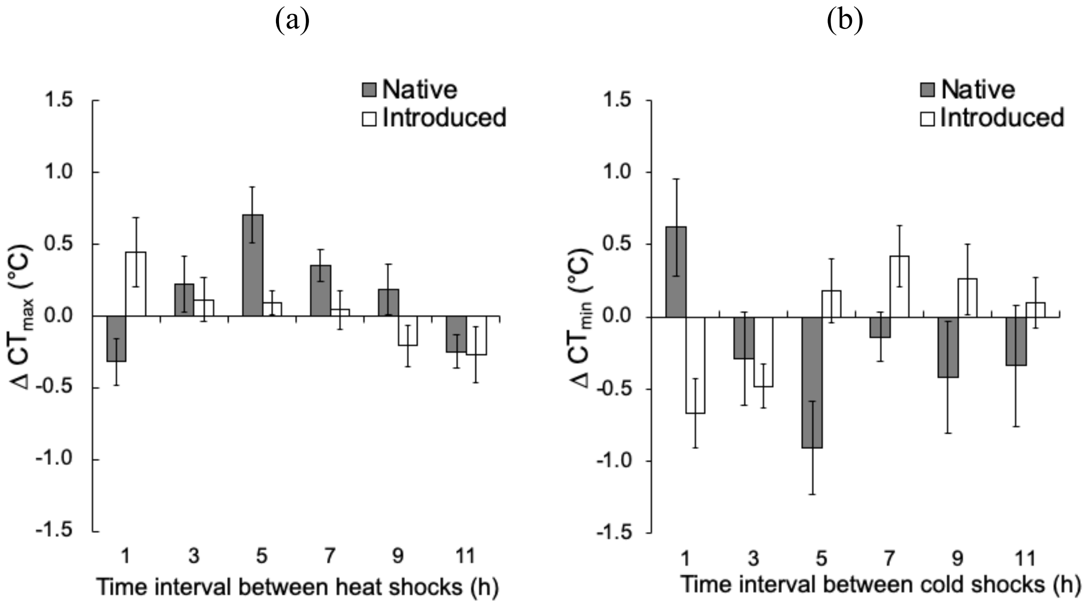

Figure 3-3 (a) Time interval between heat shocks versus ΔCT_{max} and (b) time interval between cold shocks and delta ΔCT_{min}. The figure shows population means and associated standard errors.

3.5. 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 than their native conspecifics. Surprisingly, we found no difference in the degree of thermal hardening between the introduced and the native populations of the geckos. For heat tolerance, basal CT_{max} and ΔCT_{max} was similar in geckos from Thailand and NSW. For cold tolerance, geckos from NSW had lower basal CT_{min} than geckos from Thailand, but ΔCT_{min} was similar. Our findings for basal cold tolerance 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). However, our results for heat hardening 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 gecko's tendency to occupy buildings that may be buffered from high temperatures. 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, Heerwaarden et al. 2016). 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)).

While we found no interpopulation differences in 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 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. 3-1b). In the native range, geckos are rarely exposed to critical temperatures (annual thermal fluctuation ranges from 18.2-39.2°C, Fig. 3-1a), so there may be little benefit to 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 chronic heatwaves or cold snaps, both of which frequently occur in southeastern Australia.

3.6. Conclusion

Despite its tropical origin, we found that *H. frenatus* from NSW responded faster to both heat and cold stresses than did geckos from Thailand. Such plasticity in the time course of responses to thermal stress is likely to influence the survival of individuals and should facilitate their further invasion, especially to the temperate zone.

3.7. Acknowledgments

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Chapter 4

Shifts in thermal preference of introduced Asian house geckos (*Hemidactylus frenatus*) in temperate regions of southeastern Australia

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CRediT authorship contribution statement

Yingyod Lapwong: Conceptualization, Methodology, Investigation, Data Curation, Writing - Original Draft. Ariya Dejtaradol: Methodology, Resources. Jonathan Webb: Supervisor, Conceptualization, Methodology, Writing - Review & Editing.

4.1. Abstract

Despite its tropical origin, the Asian house gecko (*Hemidactylus frenatus*) is currently invading higher latitudes around the world. In this study, we investigated whether the introduced geckos in the subtropical/temperate region of southeastern Australia have shifted their thermal biology to cope with colder temperatures. In the lab, we measured the body temperatures of geckos from Thailand and Australia in a cost-free thermal gradient. Native *H. frenatus* from Thailand displayed a diel pattern of thermoregulation. Geckos maintained higher body temperatures during mid-afternoon and at dusk but selected cooler temperatures during the night. Introduced geckos showed a similar pattern of thermoregulation, but selected lower body temperatures in summer (mean = 28.9°C) and winter (mean = 25.5°C) than native geckos (mean = 31.5°C). While the Asian house geckos from Thailand did not alter their body temperatures after feeding, their conspecifics from southeastern Australia selected body temperatures that were 1.6–3.1°C higher after feeding. In conclusion, our study shows that invasive house geckos in Australia have shifted their preferred body temperatures downwards relative to their native conspecifics in Thailand, presumably as a result of plasticity or natural selection. Our findings suggest that these tropical geckos have adapted to colder regions, and thus, they may spread much further than expected for a tropical ectotherm.

Keywords: invasive species, ectotherm, thermal biology, critical thermal, adaptation, acclimation

4.2. Introduction

The Asian house gecko (*Hemidactylus. frenatus*) is one of the most successful and widespread invasive gecko species (Carranza and Arnold 2006, Hoskin 2011). The gecko is a potential threat to native ecosystems because it can compete with native species, can prey on smaller lizards, and may act as a vector of diseases and parasites (Brown et al. 2002, Cole et al. 2005, Callaway et al. 2011, Cole and Harris 2011, Alemán and Sunyer 2015, Barton 2015, Jiménez et al. 2015, Kelehear et al. 2015, Barnett et al. 2018). Although the geckos have been introduced across the globe, and have been rapidly expanding their range since the 1980s, they were expected to be restricted to warm regions due to their tropical origin (Gill et al. 2001, Rödder et al. 2008). Tropical ectotherms tend to have narrower functional body temperatures because they have evolved in a relatively stable climate (Janzen 1967, Kingsolver 2009), so they are unlikely to survive in colder regions. However, the Asian house gecko has recently established populations in subtropical and temperate areas of Mexico, East Asia, and Australia (Marcellini 1976, Ota 1994, Hoskin 2011, Kurita 2013). Therefore, we aimed to investigate how this introduced gecko can successfully survive in colder regions.

The first hypothesis that could explain this phenomenon is that the introduced gecko might exploit the buffered climate of urban areas to thermoregulate and survive. It is well established that urban areas can provide warmer environments for animals due to the urban heat island effect, which could benefit ectotherms (Heisler and Brazel 2010). For example, there was a report of the unexpected activity of the Kotschy's Gecko (*Mediodactylus kotschyi*) during winter in some Bulgarian cities, which was suspected to be a result of the urban heat island effect (Mollov et al. 2015). In its native habitats, this gecko species typically stay inactive during the colder months of the year. Besides, humans usually heat their residences during colder weather, which potentially benefits house geckos. Even without central heating, lights and other electronic devices (e.g., fridges) can provide heated microhabitats that geckos may exploit.

Alternatively, house geckos may have shifted their thermal physiology to allow them to survive in colder environments. On the one hand, thermoregulation can enable species to function efficiently in novel habitats, thereby buffering physiological traits from selection, i.e., the Bogert effect (Bogert 1949, Angilletta 2009, Stellatelli et al. 2017). However, several introduced tropical species have displayed post-invasion shifts in thermal biology. For example, the introduced Crested Anole (*Anolis cristatellus*) in Florida could tolerate ~3°C colder temperatures than their conspecifics in their warmer native range (Leal and Gunderson 2012). In Australia, introduced cane toads have rapidly acclimated to colder temperatures; toads became more cold tolerant after being exposed to cold temperatures for 12h (McCann et al. 2014). Nevertheless, a recent study on *Anolis* by Muñoz and Bodensteiner (2019) suggested that, unlike the cold tolerance, the evolution of thermal preference might not be prominent and may occur slowly. While plasticity in thermal tolerance and thermal acclimation are two traits likely to facilitate the success of invasive species (Kelley 2014), few studies have examined whether tropical invaders display shifts in thermal preference.

In ectotherms, thermal preferences are correlated with the thermal sensitivity of performance curves and therefore reflect a behavioral effort to optimize the balance between performance efficiency and energy consumption (Angilletta 2009). If preferred temperatures influence fitness, we expect thermal adaptation (e.g., plasticity or evolution) to produce different thermal preferences between populations (Angilletta et al. 2010). For example, *Drosophila melanogaster* and *D. simulans* from hotter regions had higher preferred temperatures for egg-laying than did flies collected from cooler regions (Nevo et al. 1998). However, thermoregulation may also buffer organisms from environmental heterogeneity, such that thermal preferences may be similar among ectotherms from different populations or elevations (Muñoz and Bodensteiner 2019). Therefore, if invasive house geckos were able to thermoregulate in urban habitats in colder regions (i.e., dodging selection on thermal traits), we should see similar thermal preferences in native and non-native populations. However, if geckos can shift their performance curves downwards in novel habitats, then invasive geckos should prefer lower body temperatures in colder regions than conspecifics from native ranges (Angilletta et al. 2010). Such downward shifts could result from plasticity, seasonal acclimation, or selection of thermal traits. To test these predictions, we measured the pre-feeding and post-feeding body temperatures (T_b) of geckos from Thailand and Australia in a cost-free thermal gradient. We also compared T_b of geckos from Australia between winter and summer.

4.3. Materials and methods

4.3.1. Study populations

We studied four populations of *H. frenatus*: two native populations from southern Thailand and two introduced populations from southeastern Australia. In southern Thailand, the monthly average minimum temperatures are relatively consistent throughout the year and never drop below 20°C, while the monthly average minimum temperatures of southeastern Australia range from around 20°C in summer to below 10°C in winter (Fig. 4-1). We collected 21 native *H. frenatus* from Hat Yai (7.007535, 100.498533) in November 2018 and 19 from Satun (Bulon Le Island) (6.828929, 99.535595) in January 2019, and 17 introduced *H. frenatus* from Yamba (-29.436890, 153.357986) and 13 from Coffs Harbour (-30.292685, 153.119707) in August 2018 (winter) and another 20 from each site in February 2019 (summer) (Table 4-1). We measured the snout-to-vent length (SVL) and mass of all geckos.

Geckos from Hat Yai and Satun were transported to Prince of Songkla University (PSU), while geckos from Yamba and Coffs Harbour were transported to the University of Technology Sydney (UTS). While in captivity, each individual was kept in a 2L ventilated plastic container (200 x 150 x 60 mm, Sistema®, New Zealand). We placed a paper substrate, a cardboard shelter, and a small Petri dish filled with water in each container. In Thailand, we kept the geckos in a room with natural ambient temperatures ranging from 23°C at night and 32°C during the day. In Australia, we kept geckos under similar conditions by putting the containers on a heated wire to create a thermal gradient (23-32°C) for the geckos. We fed each gecko with five small crickets every third day. All geckos were acclimatized for two weeks before starting the experiment.

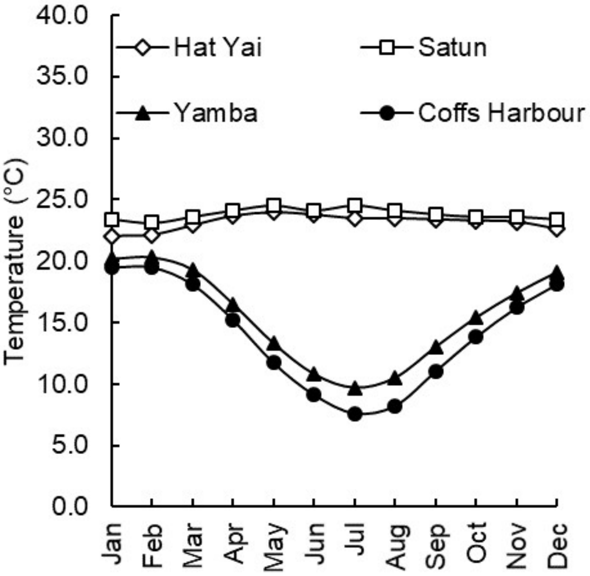

Figure 4-1 Monthly average minimum temperatures in Hat Yai, Satun, Yamba, and Coffs Harbour. Data of Yamba and Coffs Harbour were observed from 1877 – 2019

(Bureau of Meteorology 2019). Data of Hat Yai and Satun were observed from 1981 – 2010 (Thai Meteorological Department 2019).

4.3.2. Preferred body temperatures in a cost-free thermal gradient

Most nocturnal reptiles rarely bask and gain heat from substratum to warm up their bodies (Bustard 1967, Webb and Shine 1998, Kearney 2001). We estimated the preferred body temperatures of geckos by placing them in a cost-free thermal gradient. The gradient consisted of eight 1 m long iron pipes (square cross-section 40 x10 cm) strapped to a wooden board. Each tube had a circular hole (diameter 10 mm) spaced at 10 cm intervals to allow air to ventilate and light to shine through. Twelve rows of heating cable (HabiStat®, UK) were placed at one end of the board, while another twelve rows of a plastic tube connected to a water cooling system (Julabo® F10-UC, Germany) were placed at the other end. This apparatus created a temperature gradient ranging from 15°C at the cold end to 40°C at the hot end. Room temperature was set to 23°C and light period was set to 12:12 light to dark circle. To measure body temperatures of geckos, we fitted them with modified miniature data loggers (Thermochron® iButton® DS1921G). We modified the data logger by taking out the aluminum and plastic cases, which reduced the mass from 3.0 g to 1.0 g. Then, we programmed the data logger to continuously record the temperature every 10 minutes before attaching it to the dorsal surface of the gecko with masking tape. In a pilot study, we left the data loggers on eight geckos for 48 hours and fed them with crickets after the first 24 hours to ensure that the data logger did not affect the gecko's movements or feeding. Since the geckos fed regularly and moved around unhindered, we assumed that the data logger had minimal effects on the geckos during this short period. To commence the experiment, we put a single gecko (fasted for two days) with a data logger on its back into each pipe at 17:00 h. The geckos were given one hour to acclimate and explore the gradient, so the actual start time of measurement was at 18:00 h. After 24 hours (18:00 h the next day), we fed three crickets to each gecko by putting them in a hole in the middle of the gradient. In our preliminary study, all geckos finished feeding within one minute. The experiment ended after 48 hours, at 18:00 h on the second day. We removed the data logger from each gecko and returned them to their cages. After completing all the experiments, we released native geckos to their sites of capture, but due to biosecurity laws, we euthanased the house geckos in Australia via lethal injection of tricaine methanesulfonate (MS222) (Conroy et al. 2009).

4.3.3. Data analysis

After finishing the experiment, we downloaded the data loggers. All temperatures recorded from 18:10h of the first day until 18:00h of the third day were used (288 records in total). We calculated hourly mean T_b from six records within a particular hour. For example, the hourly mean T_b at 19h derived from six records within 18:10h – 19:00h. As a result, we obtained 48 hourly T_b of each individual. Since we collected data from the same individuals repeatedly, we used repeated measures ANOVA to determine the effects of location, sex, and season on T_b of the gecko. Within each population, we also include the time of the day and feeding condition as a within-subject effect. We compared two native populations to two summer-captured introduced populations to determine the impact of location on T_b of the geckos in the thermal gradients. Then, we compared T_b of the introduced geckos between seasons. Prior to statistical analyses, we carried out Kolmogorov-Smirnov tests to check whether the data were normally distributed. Although there were some skewness, most of the data (75%) were normally distributed ($P > 0.05$). Additionally, we obtained the set point temperatures (T_{set}) from the central 50% of T_b to determine the preferred ranges of functional body temperatures of the geckos.

4.4. Results

We first examined variation in size of geckos between the four locations (pooled data, $n = 108$). Two factor ANOVAs, with sex and location as factors, and SVL and mass as dependent variables, showed that geckos from Australia were larger (location: $F_{3,100} = 8.66$, $P < 0.01$) and heavier (location: $F_{3,100} = 4.71$, $P < 0.01$) than geckos from Thailand (Table 4-1). The LSD post hoc tests confirmed that geckos from Coffs Harbour and Yamba were larger and heavier than geckos from Hat Yai and Satun. Male geckos were significantly larger ($F_{1,100} = 32.72$, $P < 0.01$) and heavier ($F_{1,100} = 35.94$, $P < 0.01$) than females. The interaction between location and sex was not significant for SVL ($F_{3,100} = 0.02$, $P = 1.00$) or mass ($F_{3,100} = 0.09$, $P = 0.97$), confirming that the pattern was consistent across locations (Table 4-1). In Australia, there was no seasonal variation in SVL ($F_{1,64} = 0.45$, $P = 0.50$) or mass ($F_{1,64} = 0.10$, $P = 0.75$) of the introduced geckos.

Table 4-1 Mean (±SE) for snout-vent-length (SVL) and mass of geckos used in the thermal gradient experiments.

Population	Male			Female		
	n	SVL (mm)	Mass (g)	*n*	SVL (mm)	Mass (g)
Hat Yai	10	51.11±0.73	3.34±0.16	11	47.01±0.81	2.18±0.12
Satun	9	50.96±1.37	3.17±0.24	10	47.24±0.73	2.27±0.09
Yamba (Winter)	9	55.14±1.36	4.01±0.59	8	50.76±0.78	2.99±0.31

Yamba (Summer)	10	53.69±1.05	3.78±0.30	10	50.35±1.01	2.77±0.14
Coffs Harbour (Winter)	8	52.86±1.31	3.41±0.23	3	47.13±0.63	2.49±0.23
Coffs Harbour (Summer)	10	55.61±1.52	4.18±0.34	10	51.76±0.81	3.00±0.17

All four populations of *H. frenatus* showed a similar pattern of diel thermoregulation. They selected higher T_b in the thermal gradient from the morning toward the evening and then selected lower temperatures overnight until the morning (Fig. 4-2). The repeated measures ANOVA confirmed a significant effect of the time of the day on selected T_b of the geckos ($F_{5.062,\ 364.449} = 2.32$, $P = 0.04$). However, the introduced geckos chose colder temperatures than the native ones (Table 4-2). Before feeding, the mean T_b of introduced geckos captured in summer was significantly lower than the native geckos (means = 28.9±0.3°C vs. 31.5±0.3°C respectively; $F_{3,\ 72} = 13.37$, $P < 0.01$). Tukey's HSD post hoc test showed no difference in pre-feeding T_b within two native and two introduced populations. After feeding, introduced geckos captured in summer selected higher T_b, but mean T_b were still lower than those of geckos from the native range (means = 30.5±0.2°C vs. 31.5±0.2°C respectively; $F_{3,\ 72} = 5.555$, $P < 0.01$). Similarly, Tukey's HSD post hoc test showed no difference in post-feeding T_b within two native and two introduced populations.

Within introduced populations, the mean T_b of geckos captured in winter were lower than those of geckos captured in summer. Before feeding, the mean T_b was 3.4°C lower in winter than in summer (means = 25.5±0.8°C vs. 28.9±0.3°C respectively; $F_{1,\ 64} = 17.27$, $P < 0.01$). There was no effect of the interaction between location and season on the pre-feeding Tb ($F_{1,\ 64} = 1.27$, $P = 0.27$), so the effect of season was consistent between locations. After feeding, the mean T_b was 1.9°C lower in winter than in summer (means = 28.6±0.9°C vs. 30.5±0.2°C respectively; $F_{1, 64} = 6.323$, $P = 0.01$). Similarly, there was no effect of the interaction between location and season on the pre-feeding Tb ($F_{1, 64} = 3.66$, $P = 0.06$), so the effect of season was consistent between locations.

Feeding did not affect the T_b of native geckos ($F_{1, 36} = 0.06$, $P = 0.81$), whereas the T_b of summer-captured introduced geckos was 1.6°C higher after feeding ($F_{1, 36} = 31.77$, $P < 0.01$). The repeated measures ANOVA revealed no effect of location ($F_{1, 36} = 0.34$, $P = 0.56$,) and sex ($F_{1, 36} = 0.45$, $P = 0.51$) on T_b of the native geckos. Similarly, there was no effect of location ($F_{1, 36} = 2.46$, $P = 0.13$) and sex ($F_{1, 36} = 1.93$, $P = 0.17$) on T_b of the introduced geckos captured in summer. Furthermore, the winter-captured geckos from introduced ranges increased their T_b for 3.1°C after feeding ($F_{1, 24} = 31.87$, $P < 0.01$). There was also no effect of location ($F_{1, 24} = 0.46$, $P = 0.50$) and sex ($F_{1, 24} = 1.51$, $P = 0.23$) on the T_b of introduced geckos captured in winter.

Table 4-2 Mean T_b and T_{set} of the geckos in different populations

Population	Pre-feeding		Post-feeding	
	Mean T_b	T_{set}	Mean T_b	T_{set}
Hat Yai	31.7±0.3°C	30.2±0.6 – 33.7±0.3°C	31.5±0.2°C	30.3±0.4 – 33.0±0.3°C
Satun	31.2±0.3°C	29.7±0.5 – 33.0±0.4°C	31.5±0.2°C	30.1±0.5 – 33.0±0.4°C
Yamba (winter)	24.9±0.4°C	21.7±1.0 – 27.2±1.4°C	27.9±0.2°C	26.5±1.1 – 29.2±1.4°C
Yamba (summer)	29.0±0.3°C	26.3±0.7 – 31.8±0.4°C	31.0±0.2°C	29.8±0.3 – 32.6±0.2°C

Coffs Harbour (winter)	26.3±0.5°C	23.0±0.5 – 33.0±0.4°C	29.5±0.4°C	27.5±1.5 – 31.8±1.1°C
Coffs Harbour (summer)	28.7±0.4°C	25.9±0.7 – 31.7±0.4°C	30.0±0.2°C	28.6±0.4 – 31.8±0.2°C

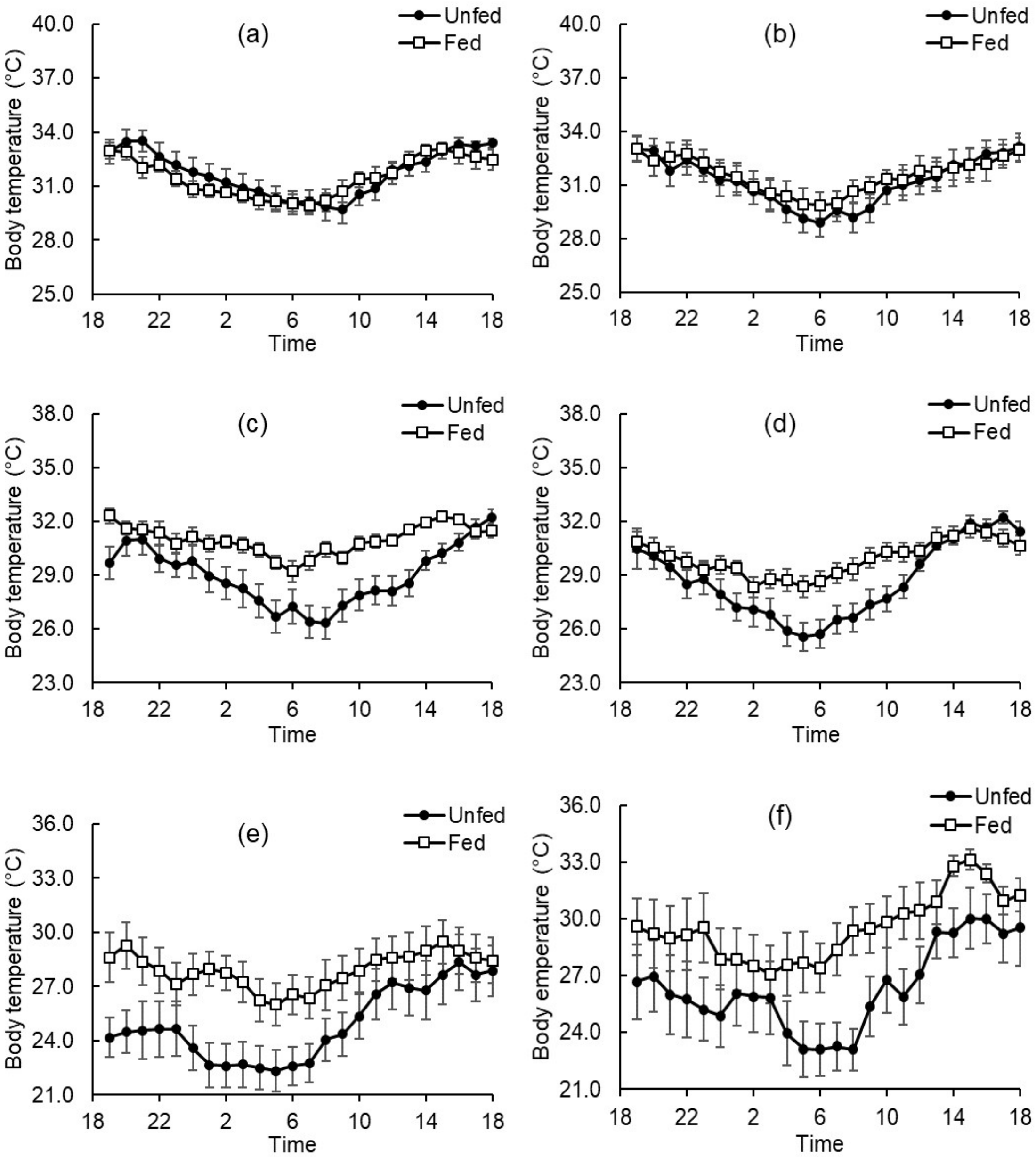

Figure 4-2 Hourly mean (±SE) T_b of *H. frenatus* from (a) Hat Yai, (b) Satun, (c) Yamba in summer, (d) Coffs Harbour in summer, (e) Yamba in winter, and (f) Coffs Harbour in winter.

4.5. Discussion

4.5.1. A shift in thermal preference

According to the "Bogert effect," thermoregulation should buffer ectotherms from the effects of selection so that thermal physiology should be consistent across geographical ranges (Bogert 1949, Huey et al. 2013). In this study, the house geckos in Australia selected lower T_b (mean pre-feeding T_b = 25.5-28.9°C) than their native counterparts (mean pre-feeding T_b = 31.5°C). This finding is similar to the pattern of thermoregulation in a non-invasive but widespread iguanid lizard, *Liolaemus multimaculatus*, from Argentina. In that species, individuals maintained similar field T_b across their geographic range. Still, lizards from the two southernmost populations selected lower T_b in a thermal gradient than lizards from northern latitudes (Stellatelli et al. 2020). In invasive house geckos, the downward shift in thermal preference should allow these ectotherms to function better in lower ambient temperatures. A recent study on the thermal sensitivity of *H. frenatus* along the latitudinal cline of Australia revealed that the geckos from higher latitudes (Brisbane) were more active than the gecko from lower latitudes (Cairns and Rockhampton) when the temperatures were low (15-20°C) (Cameron et al. 2018). Our results confirm that an invasive gecko species that resides inside houses have shifted their thermal preferences downwards, presumably because they are not entirely buffered from colder temperatures in colder regions.

The downwards shift in thermal preference of the introduced house gecko is likely an energy conservation mechanism that could enhance their invasion potential. In colder climates, a gecko with a lower thermal preference would not need to expend time and energy searching for warmer microhabitats. Lower thermal preference also decreases energy consumption because metabolic rates are directly thermal dependent (Thabethe et al. 2013). Some species of vertebrates trade-off their physiological performances for energy conservation by lowering their T_b when food sources became scarce (Christian et al. 1983, Thabethe et al. 2013). In southeastern Australia, a dry season significantly deteriorates abundance of insects – the primary food sources of the geckos (Lowman 1982); hence, energy conservation could be vital for their survival.

4.5.2. Post-feeding thermophily

The increase of T_b after feeding occurs in many species of reptiles and is known to enhance enzyme production during digestion (Regal 1966, Touzeau and Sievert 1993, Sievert and Andreadis 1999, Blouin-Demers and Weatherhead 2001). However, there was no difference between pre-feeding and post-feeding T_b of native geckos, probably because they already had high T_b. On the other hand, the introduced geckos with initially low pre-feeding T_b sought for higher temperatures after feeding in both seasons. A study on *H. frenatus* from Brisbane by Lei and Booth (2014) confirmed that the introduced gecko could digest quicker when its T_b was high. Therefore, we suggested that although the introduced gecko could survive in the cold climate of novel habitats, they still need heated microhabitats to stimulate digestive function. As a result, the need for high post-feeding T_b could restrict the introduced geckos to urban areas, at least in winter.

4.5.3. Diel variation of thermal preference

Regardless of its thermoregulation efficiency, *H. frenatus* actively adjusted their T_b. This ability enables the gecko to moderate energy consumption effectively. In the early evening, high T_b stimulated physiological performances, especially locomotion, so the geckos could efficiently forage, defense territories, and mate. After peak hours when those activities were not required anymore, and the maintaining of high T_b could lead to energy loss, hence the geckos translocate to cooler microhabitats to slow down their metabolism rates. While some species of gecko maintain consistent T_b throughout the day (Angilletta and Werner 1998, Tan and Schwanz 2015), other species showed a similar diel variation in thermal preference (Gil et al. 1994, Angilletta et al. 1999). The divergence of thermal preference dynamic in geckos and probably other reptiles is still understudied. We could only hypothesize that it should relate to the evolutionary history of each species or even differences in methodology used to investigate. A field study by Marcellini (1976) found that *H. frenatus* in San Luis Potosi, Mexico, maintained high T_b during the evening. He suggested that the house geckos behaviorally selected diurnal retreats to gain heat and then tried to keep high T_b throughout the night, which would allow them to achieve an optimal T_b for foraging, territory defensing, or mating. Our study partially supported this idea, which was that the geckos gradually increased their T_b during the day and maintained the highest T_b at dusk. On the other hand, instead of trying to keep high T_b throughout the night, we found that the gecko gradually decreased its T_b by moving toward the chilled ends of the thermal gradients until dawn. This different result was probably because Marcellini (1976) collected and measured T_b within just a few hours following sunset, so he might not be able to detect the dynamic.

4.5.4. Seasonal variation in thermal preference

In the Yamba and Coffs Harbour populations, the diel patterns of thermal preference were similar between seasons, but with an upward shift in T_b during summer. Since we measured the same populations in different seasons, this shift in thermal preference should be reversible or represent plasticity. This pattern of seasonal change has been reported in the field body temperatures of the Galapagos land iguanas (Christian et al. 1983). The authors suggested that those reptiles intentionally preferred lower body temperatures in winter to decrease their metabolism rate, so they could conserve energy when food sources and heat sources were limited. Although the geckos from different seasons were acclimatized in the same condition for two weeks, summer-captured geckos still have higher thermal preference than winter-captured geckos. The result suggested that *H. frenatus* in southeastern Australia need longer than two weeks to complete acclimation. Remarkably, geckos from both seasons showed similar cycles of thermoregulation despite different seasonal daylight periods. This result suggested that apart of heat, light is also another main trigger of thermoregulation behavior, which corresponded to previous studies in other species of geckos (Sievert and Hutchison 1988, Craioveanu et al. 2017).

4.6. Conclusion

Although the invasive house geckos may have exploited buffered climates in urban areas to survive during the early stages of invasion, our study confirmed that they have rapidly shifted their thermal biology through plasticity or evolution to withstand coldness. This phenomenon may have been facilitated by the geckos' fast maturation and high fecundity (Ota 1994, Hoskin 2011, Nicholson et al. 2015). In addition, we also found that the Asian house geckos possessed some thermoregulation behaviors that enhance energy conservation, which could be significantly beneficial during the invasion processes. While invasion syndrome (e.g., boldness, aggressiveness, exploratory behavior, etc.) has been considered as the most significant factor that promotes the global invasion of the house gecko (Petren et al. 1993, Case et al. 1994, Hoskin 2011), we propose that its capacity for physiological plasticity or evolution, and the energy conservation strategy may be additional critical factors that have helped this introduced species to establish and spread, especially in colder regions.

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Chapter 5

The exploratory behavior of the invasive Asian house gecko (*Hemidactylus frenatus*) and its potential contribution to range expansion

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5.1. Abstract

The Asian house gecko (*Hemidactylus frenatus*) is one of the most widespread reptile species in the world. To determine whether this species possesses behavioral traits that may facilitate transport, establishment, and spread, we measured the exploratory behavior and tendency to hide of *H. frenatus* from two core and three edge populations. We also observed the behavior of its sympatric non-invasive congener, *H. platyurus*, for comparison. We found no difference in the neophobia and the ability to find shelter among all geckos. However, *H. frenatus* showed divergence in exploration efficiency and the tendency to hide among populations, possibly as a result of different competition and predation stresses. The geckos from core populations tended to explore less and hide more than the conspecifics from edge populations. The shy personality of the core populations – the primary source of long-distance human-mediated dispersal – should facilitate their likelihood of being trapped in cargo, being transported, and evading detection. On the other hand, the more active exploratory behavior of individuals from the edge populations should promote their horizontal dispersal. Interestingly, the sympatric congener, *H. platyurus*, from the core community, were less likely to hide, which might be the reason underlying its unsuccessful intercontinental invasion status.

Keywords: Exploratory behavior, Behavioral divergence, Invasive species

5.2. Introduction

The introduction of non-native species has become a concerning problem globally due to their potential to cause negative impacts on the economy and ecosystems (Pimentel et al. 2000, McNeely et al. 2001, Lockwood et al. 2013). In the past two decades, the growing volume of global trading has increased the frequency of the unintentional introduction of alien species (Gill et al. 2001, Hulme 2009, Toy and Newfield 2010). However, only a minority of the introduced species have established populations and spread successfully (Bomford et al. 2008, Suarez and Tsutsui 2008). The resistances of the recipient ecosystems toward the incoming intruders include climate (Bomford et al. 2008), geography (Liu et al. 2014), and local biodiversity (Ricklefs 2005, Stachowicz and Tilman 2005). Also, the introduced population itself tends to suffer from the genetic bottleneck and Allee effects (Taylor and Hasting 2005, Drake and Lodge 2006, Puillandre et al. 2007, Tobin et al. 2011, Murakami et al. 2015). Nevertheless, many invasive species have managed to overcome those obstacles and continue to spread. One of the significant traits facilitating their successful invasions is the invasion syndrome; a set of correlated behaviors of the animal than enhances its chances to pass through the invasion barriers (Chapple et al. 2012).

Exploratory behavior usually has a positive correlation with dispersal efficiency (Krackow 2003, Cote et al. 2010, van Overveld et al. 2014). A review by Chapple et al. (2012) suggested that exploratory behavior was one of the notable traits that facilitate biological invasions. This behavior can play different roles in each stage of the invasion. At the early stage, explorative animals tend to encounter more diverse habitats, so they have a higher chance of getting transported via human-associated vessels (Chapple et al. 2012). With the multiple numbers of passengers and introductions, the species would have a better probability to establish, as well as overcoming the genetic bottleneck effect

(Colautti et al. 2006, Kolbe et al. 2008, Tonione et al. 2011). Later, exploratory behavior allows an animal to gather information from the surrounding environment so that it could evaluate opportunities and risks (Renner 1990). Therefore, after the introduction, the animals with intense exploratory behavior could quickly locate necessary resources, as well as identify threats, such as competitors, predators, or toxicity, ensuring their survival and establishment of a permanent population (Chapple et al. 2011, Liebl and Martin 2012). By contrast, exploratory behavior can increase predation risk and energy expenses, which might reduce the fitness of recently introduced populations (Burns et al. 2016). For example, the newly introduced brown rats (*Rattus norvegicus*) decreased their exploratory activities after several weeks following the introduction when the benefits from over-exploration were outweighed by energy consumption (Russell et al. 2010). Besides, if individuals are highly explorative, they might wander in a long-distance, causing them to have fewer chances to mate or form collaborations (Taylor and Hasting 2005, Tobin et al. 2011). Accordingly, species with flexible or diverse exploratory behavior should gain the optimum advantage from this behavior.

The Asian house gecko (*Hemidactylus frenatus*) is one of the most widespread species of reptile globally. The gecko is native to South and Southeast Asia but has been accidentally introduced via human-associated pathways and has become naturalized in the Ryukyu Islands, Pacific Islands, northern Latin America, and northeastern Australia (Carranza and Arnold 2006, Kraus 2009, Ota and Whitaker 2010, Farr 2011, Hoskin 2011, Torres-Carvajal and Tapia 2011, Kurita 2013, Torres-Carvajal 2015, Bañuelos-Alamillo et al. 2016). Previous studies on related invasive congeners, *H. mabouia*, and *H. turcicus*, suggested that the successful invasive house geckos relied mainly on the multiple human-mediated introductions, being known as jumping dispersals, to occupy vast geographic ranges (Locey and Stone 2006, Short and Petren 2011). However, those studies also revealed a limited horizontal dispersal of both species (e.g., 20 m/yr in *H. turcicus* (Locey and Stone 2006)). By contrast, some introduced populations of *H. frenatus* in northeastern Australia could diffusely disperse at a drastically faster rate (i.e., >80 m/yr) (Barnett et al. 2017). Therefore, as both a good jumper and a good runner, *H. frenatus* probably possess multiple modes of dispersal-related exploratory behavior.

In this study, we observed the exploratory behavior and the tendency to hide of *H. frenatus* from different populations to detect behavioral divergence and to analyze its benefits during the invasion process. We compared geckos from two core populations and another three edge populations. In this study, we defined the core population as a long-term established population with high density and high interaction pressures, either competition or predation. Previous studies revealed that the competition level in the core community of house geckos was high because of the aggregation of food around light sources (Petren and Case 1996, Petren and Case 1998). Although many studies revealed the decline in predation risk along with the rural-to-urban gradient (Rebolo-Ifrán et al. 2017, Eötvös et al. 2018, Eötvös et al. 2020), the situation seems to be reversed in the case of house gecko community. In this system, many species of predators have adapted to urban areas to exploit abundant house geckos as food sources. Those urban-adapted house gecko hunters include many colubrid snakes, larger lizards, and even larger congeners (Bolger and Case 1992, Leong and Foo 2009, Das 2010, Sanchez 2010, Parves and Alam 2015). There were also reports of cannibalism in house geckos (Galina-Tessaro et al. 1999, Perez et al. 2012). In addition to natural predators, the urban house geckos could suffer severe predation pressure from domestic cats, dogs, and rats (Case et al. 1994, de Sliva 2006, Ditchkoff et al. 2006, Bucol 2019). The more open habitats in urban areas also increase the chance of the geckos to get exposed to predators (McGregor et al. 2015, Dornburg et al. 2016). Accordingly, we assumed that the core community of house gecko should possess higher predator pressure than the edge community. Notably, the core populations are usually located in urban areas with connected transportation routes, making them potential propagule sources of human-mediated introduction. At the same time, the edge population had the opposite characteristics. We also added its non-invasive congener, *H. platyurus*, to the comparison to investigate behavioral divergence between these two related species.

5.3. Materials and methods

5.3.1. Study populations

We studied four populations of *H. frenatus* in Thailand; Hat Yai (7.007535, 100.498533; HY), Chiang Mai (18.797727, 98.952540; CM), Mook Island (7.373533, 99.308304; MK), and Bulon Island (6.828929, 99.535595; BL), and another population in southeastern Australia; Coffs Harbour (-30.292685, 153.119707; CH). We also collected sympatric congeners, *H. platyurus*, from Hat Yai for interspecific comparison. The house gecko communities in HY and CM represented the core community in an urban area. At the same time, the communities in MK and BL exemplified the edge populations where the geckos just recently established. Those villages on the islands emerged not long ago, in particular just after WWII in Bulon Le Island (Wongbusarakum 2007). Presumably, the migrations of people at that time were the introduction vectors of the house geckos to the islands. In addition to native populations, we added CH to the comparison as another edge population but from the introduced range. Coffs Harbour is a loose urban area located close to the invasion-front of *H. frenatus* in southeastern Australia (Hoskin 2011), so the competition and predation intensities should be mild.

5.3.2. Community surveys and specimen collections

We collected the geckos and conducted the experiments in Australia in February 2018 and Thailand during September – November 2018. Before the nights of capturing, we walked around the areas between 19h – 21h to observe house gecko community structures. We identified and counted every gecko we saw to calculate the percentage of each species relative to the total number of geckos observed. We collected 20 *H. frenatus* from each location in Thailand and another eight geckos from Coffs Harbour. We additionally collected 20 *H. platyurus* from Hat Yai. We measured the SVL and weight of all geckos. After the collection, we transferred the geckos from HY, MK, and BL to a laboratory in Prince of Songkla University and conducted the trials there. In different circumstances, we transferred the geckos from CM and CH to our residences and experimented there. During the experiments, we kept each gecko in a 2L container with a plate filled with water, a piece of tissue paper, and a paper tube as shelter, and placed them in an open-air room. If we kept the geckos for more than three days, we fed five crickets or mealworms every third day. After the experiment, we released the geckos back to their capture points.

5.3.3. Behavioral observations

To observe the exploratory behaviors of an arboreal gecko, we designed a vertical maze arena. The arena was a 30x30x5 cm white acrylic box with a clear front to enable the observation. Within the arena, small white acrylic plates were attached to create 16 cells. Each cell has a right triangle-shaped floor with openings connected to other cells at each corner. The cells on the top left and bottom right were covered with pieces of paper to create shelters (Fig. 5-1). To commence the trial, we transferred a 1-day fasted gecko in a paper tube made of A4 paper, closed both ends with rolled tissue papers, and left it for five minutes. We then took out the tissue paper clog, put one end to the opened hole at the center of the arena, and then gently used a paintbrush to poke the gecko to move inside one of the cells in the arena. This method would decrease the disturbing effect of direct handling on exploratory behavior. We videotaped four arenas at the same time for 30 minutes while no one was in the room. After finishing the trial, we removed the geckos and put them back into their cages. We cleaned and wiped the arenas with 70% ethanol to eliminate any secretions from the experimented geckos. We observed the gecko within the 9 h – 15 h period to avoid other confounding behaviors, including mating and foraging behaviors, which could occur during the late afternoon until early morning. We then observed and measured six variables, namely, (1) the time spent in the start cell, (2) the time spent to find a shelter, (3) the total time spent in shelters, (4) the average time spent in an open-cell (excluding the start cell), (5) the number of cell entries, and (6) the number of explored cells.

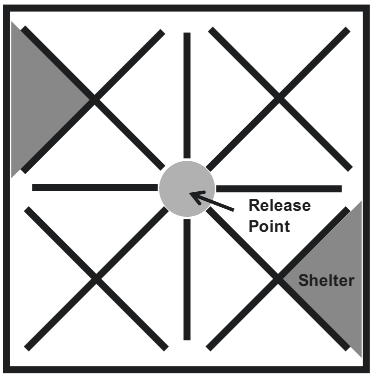


Figure 5-1 The maze arena used to observe the exploratory behavior of the gecko.

5.3.4. Data analysis

For the SVLs and weights of the gecko, we used two-way ANOVA with LSD post hoc test to determine the differences among populations and between sexes of geckos because our data approximately fitted the assumptions of the parametric analysis. Kolmogorov-Smirnov test showed that all, except only for the weights of female *H. frenatus* from

Bulon Le Island, were normally distributed (*P* > 0.05). Levene's test also confirmed the homogeneity of variances of our data sets (*P* > 0.05). After the trials, we removed several geckos from the analysis as outliners since they were inactive (i.e., stayed in an open cell for more than 10 minutes) or over-anxious (i.e., kept moving and spent less time in a shelter than in another open cell). In particular, we excluded data of 12 geckos from CM that were inactive during the trials on a rainy day. In the end, the numbers of geckos included in the analysis were 15 for *H. platyurus* and 61 for *H. frenatus* (HY = 17, CM = 7, MK = 14, BL = 17, and CH = 6). Prior to the statistical analysis, we used the Kolmogorov-Smirnov test to check the normality and Levene's test to illustrate the homogeneity of variances of our observed data. We found that only the times spent in shelters were normally distributed (*P* > 0.05) with equal variances (*P* > 0.05) so that we decided to use one-way ANOVA with LSD post hoc to determine the differences in this variable among populations. For the other observed variables, we used a non-parametric Kruskal-Wallis test with Dunn-Bonferroni post hoc to determine the differences among populations. We also used a non-parametric Wilcoxon signed-ranks test to determine whether the times spent in the start cell were longer than the average times spent in an open cell to detect neophobia. We performed all statistical analyses using SPSS®.

5.4. Results

5.4.1. House geckos communities

The percentage of occurrence of *H. frenatus* was lowest in HY (19%), followed by CM (35%), MK (53%), BL (92%), and CH (100%), respectively. In HY, the number of *H. frenatus* observed was less than half of *H. platyurus* (58%) (Fig. 5-2). Unfortunately, we could not precisely measure the density of geckos in the community because of the different distribution patterns. We could only assume from previous studies that the urban community should have a higher density of geckos due to the clumped distribution of insects around artificial light (Petren and Case 1996, Petren and Case 1998, Perry et al. 2008).

Two-way ANOVA showed that *H. platyurus* was significantly larger ($F_{5,96} = 3.16$, $P < 0.05$) and heavier ($F_{5,96} = 8.28$, $P < 0.05$) than most of *H. frenatus*, except for the introduced population in Coffs Harbour. Male geckos were larger ($F_{1,96} = 10.96$, $P < 0.05$) and heavier ($F_{1,96} = 5.85$, $P < 0.05$) than females. There was no effect of interaction between population and sex on SVL ($F_{5,96} = 0.58$, $P = 0.72$) or weight ($F_{5,96} = 0.48$, $P = 0.79$). That is, the differences between sexes were consistent across populations (Table 5-1).

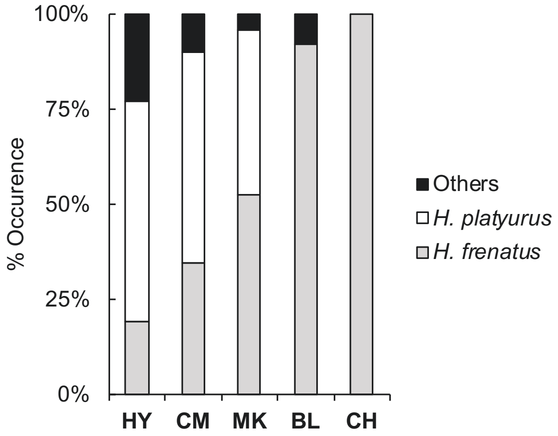


Figure 5-2 Percentages of occurrence of *H. frenatus*, *H. platyurus*, and other geckos in four locations; Hat Yai, (HY), Chiang Mai (CM), Mook Island (MK), Bulon Le Island (BL), and Coffs Harbour (CH).

Table 5-1 Means±SE of SVL and weight of *H. platyurus* from Hat Yai, and *H. frenatus* from five different populations.

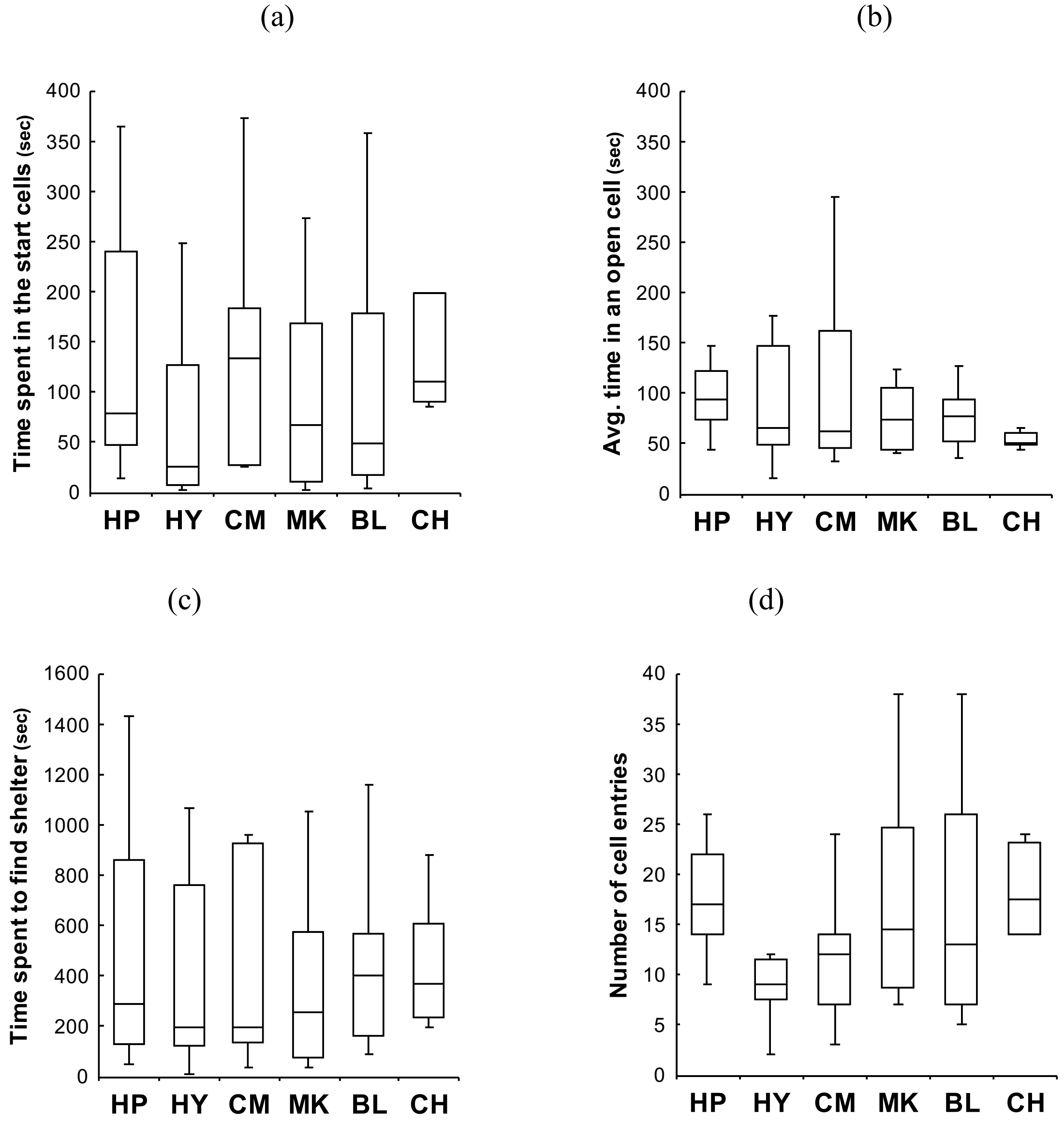
Species	Location	Male		Female	
		SVL	weight	SVL	weight
H. platyurus	Hat Yai	53.2±1.5	3.33±0.27	51.1±0.7	3.15±0.11
H. frenatus	Hat Yai	51.7±1.0	2.64±0.16	47.4±1.4	2.37±0.26
	Chiang Mai	50.6±1.2	2.84±0.21	48.8±1.0	2.51±0.17
	Mook Island	50.1±1.4	2.35±0.20	47.9±0.7	2.14±0.11
	Bulon Le Island	50.6±1.2	2.73±0.25	46.2±0.8	2.00±0.10
	Coffs Harbour	53.4±1.3	3.52±0.38	52.4±1.0	3.25±0.26

5.4.2. Behavioral observations

Among populations of the geckos, there was no difference in either the time spent in the start cell (mean = 112 seconds, $\chi^2_5 = 7.76$, $P = 0.17$) and the average time spent in an open cell (mean = 87 seconds, $\chi^2_5 = 6.92$, $P = 0.23$) (Fig. 5-3a – 5-3b). A Wilcoxon signed-ranks test revealed that the time spent in the start cell was not significantly different from the average time spent in an open ($Z = -0.63$, $P = 0.53$); therefore, geckos in this study showed no neophobia at all. The times spent to find shelter were not different among populations (mean = 470 seconds, $\chi^2_5 = 2.45$, $P = 0.78$) (Fig. 5-3c). The variation of the times spent to find shelter was high in every population (SD ranged from 248 to 442 seconds). However, 70% of the geckos found shelters before 10 minutes (Fig. 5-4).

The Kruskal-Wallis tests revealed that the number of cell entries and the number of explored cells were significantly different among populations ($\chi^2_5 = 13.57$, $P < 0.05$, and $\chi^2_5 = 12.25$, $P < 0.05$, respectively). While the Dunn-Bonferroni test failed to show any significant pair-wise differences in the number of cell entries, the analysis revealed a difference in the number of explored cells between *H. platyurus* and *H. frenatus* from Hat Yai (medians = 9 vs. 5, respectively, $P < 0.05$) (Fig. 5-3d – 5-3e).

The one-way ANOVA found a significant difference in the time spent in shelters among populations of geckos ($F_{5,75} = 6.91$, $P < 0.05$). The congeners, *H. platyurus*, spent less time in the shelters (mean = 383 seconds), which was closer to *H. frenatus* from the edge populations (means = 737 seconds for MK, 656 seconds for BL, and 717 seconds for CH). At the same time, *H. frenatus* from core populations spent much more time in shelters (means = 1,059 seconds for HY, and 997 seconds for CM) (Fig. 5-3f).


(a)
(b)
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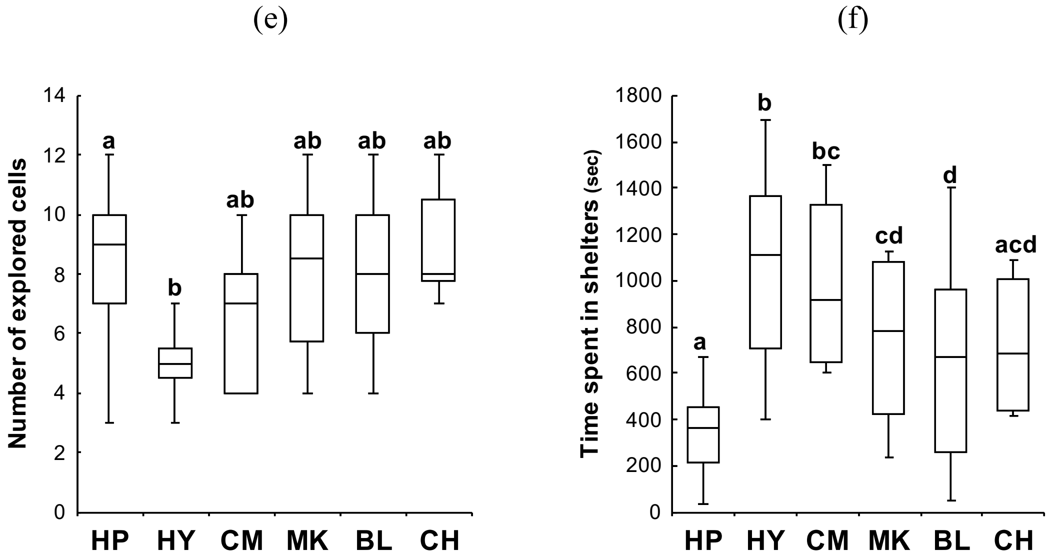

Figure 5-3 Six observed behavioral variables of *H. platyurus* from Hat Yai (HP), and *H. frenatus* from Hat Yai (HY), Chiang Mai (CM), Mook Island (MK), Bulon Le Island (BL), and Coffs Harbour (CH); (a) the time spent in the first cell, (b) the average time in an open cell, (c) the time spent to find shelter, (d) the number of cell entries, (e) the number of explored cells, and (f) the time spent in shelters. The letters above the bars represent grouping following post hoc tests ($P < 0.05$). Notably, the Kruskal-Wallis test found evidence of a difference in (d) number of cell entries, but the Dunn-Bonferroni test failed to show any significant pair-wise differences.

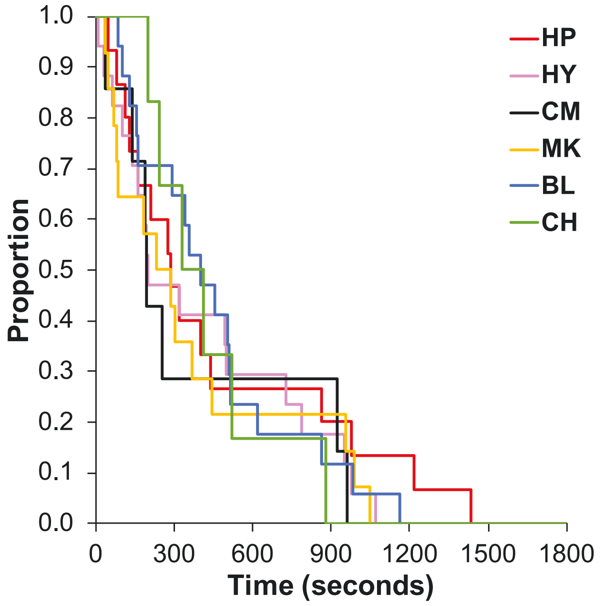

Figure 5-4 The times spent to find shelter of *H. platyurus* from Hat Yai (HP), and *H. frenatus* from Hat Yai (HY), Chiang Mai (CM), Mook Island (MK), Bulon Le Island (BL), and Coffs Harbour (CH).

5.5. Discussion

5.5.1. Exploratory behavior of *H. frenatus* and tendency to hide

Studies on a number of species have found that compared to conspecifics from rural areas, animals from urban areas tend to be bolder and less likely to hide because of the enemy-released environment and their habituation toward human activities (Ditchkoff et al. 2006, McCleery 2009, Aviles-Rodriguez 2015, Samia et al. 2017, Breck et al. 2019). By contrast, we found that *H. frenatus* from core populations explored less and hid more than the conspecifics from edge populations. We suggest that the intense interactions within the core community, including competition and predation, have posed a strong selection on *H. frenatus*, making them more likely to hide in closed refugee sites. In the edge community where stresses from competition and predation were released, individuals were less wary. While the slight degree of fear encourages the animal to explore, the extreme level forces it to hide (Lester 1969). In several studies on the landscape of fear, even without physical contact, subdominant individuals tended to avoid the bolder or larger sympatric hostiles (Petren et al. 1993, Cole et al. 2005, Lisičić et al. 2012). In our case, *H. frenatus* from core communities co-occurred with competent enemies (e.g., *H. platyurus*, *H. murrayi*, and *Gekko gecko*), which should favor selection for cautious behaviors. However, observations of direct interspecific interactions are needed to test this assumption.

Interestingly, although the timidity of *H. frenatus* from core populations might decrease their opportunity to explore, it could also increase their success during the introduction process. Its propensity to hide should enhance the chance of the gecko to get trapped, transported, and evade detection. This assumption was supported by empirical evidence reported by Gill et al. (2001). The researchers found that *H. frenatus* was the most accidentally introduced reptile species in New Zealand during the 1980s – 1990s. In contrast, the more explorative personality of the edge populations could promote horizontal dispersal. Several studies on invasive cane toads (*Rhinella marina*) in Australia found that the toads from the invasion-front dispersed faster than the core population, and one of the potential explanations was that the toads shifted its exploratory behavior as an enemy-released response (Urban et al. 2007, Gruber et al. 2017). In conclusion, we suggest that the spatiotemporal divergence in the exploratory behavior of *H. frenatus* should support dual modes of dispersal, i.e., jumping, and diffusing, which aided the gecko to spread at one of the fastest rates among other invasive reptiles.

5.5.2. Exploratory behavior of *H. platyurus* and tendency to hide

We also found a behavioral difference in the non-invasive congener, *H. platyurus.* Unlike the sympatric *H. frenatus*, this larger relative spent a considering amount of time in the open cells. Remarkably, both species of *Hemidactylus* first reached shelter in a similar amount of time, but *H. platyurus* spent less time in the shelter and continue to explore. By being larger, *H. platyurus* should not suffer from the interspecific interactions as the smaller *H. frenatus* did, so they become bolder. Although this boldness benefited *H. platyurus* in accessing necessary resources, it might limit the gecko from being human-mediated introduced. While Gill et al. (2001) recorded 17 of *H. frenatus* introduced from native Southeast Asia to New Zealand, they found only two of *H. platyurus* imported from the sympatric ranges. Also, another study in Florida reported a limited expansion of a long-time established population of *H. platyurus* (Meshaka and Lewis 1994). Those geckos were still localized even after a decade after the introduction. Interestingly, a comparative study by Chapple et al. (2011) also found that a higher tendency to hide of the invasive skink, *Lampropholis delicata*, was probably one of the traits helping it to become more successful than the non-invasive congener, *L. guichenoti*. Therefore, we argue that the unlikeliness to hide was one of the reasons underlying the unsuccessful intercontinental invasion of *H. platyurus*.

5.5.3. Exploration neophobia of the house geckos

Previous studies in the house sparrows (*Passer domesticus*) and the cane toads (*Rhinella marina*) found that the animals from edge populations had a lower degree of neophobia than the core population (Martin and Fitzgerald 2005, Candler and Bernal 2014). By contrast, there was no difference in neophobia toward novel habitats among populations or even between two species of house geckos in our study. More precisely, the house geckos did not show any latencies to explore at all. The disappearance of neophobia in house geckos probably evolved through their historical adaptation to disturbances within human settlements. Correspondingly, the experiments on related species of parrots revealed that the species inhabiting forest edges had the shortest latencies to explore, probably due to their evolution within a frequently disturbed environment (Mettke-Hofmann et al. 2002). Besides, unlike other species, these geckos still closely associated with humans even in rural areas; therefore, they have not lost this habituation.

5.6. Conclusion

Our results revealed strong interpopulation divergence in exploratory behavior in *H. frenatus*. Although the geckos from core populations were warier and less explorative, possibly because of the intense stresses in their communities, they exhibited behaviors that would make them more likely to get trapped, transported, and introduced to non-native ranges. On the other hand, the explorative personality of the geckos from edge populations should facilitate their ability to disperse horizontally. These differences in behaviors in different ecological contexts are likely to have contributed to the geckos' successful range expansion across the globe.

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Chapter 6

Interpopulation divergence in the aggressiveness of the Asian house gecko (*Hemidactylus frenatus*) driven by contrasting interaction pressures

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6.1. Abstract

Previous studies in the Pacific islands suggested that the aggressiveness of *H. frenatus* was a factor underlying its success as an invasive species. However, recent studies in Australia found that *H. frenatus* was not as aggressive as predicted. Therefore, we hypothesized that the aggressiveness of *H. frenatus* was not a fixed intrinsic trait, but rather adaptive regarding competition intensity in the community. We collected *H. frenatus* from a competitor-rich community in Hat Yai, and a competitor-released community in Bulon Le Island, both in Thailand, for trials. We paired those *H. frenatus* with their sympatric conspecifics in open arenas to observed four agonistic interactions, including arch-back, tail-wave, approach, and flight, for 30 min. We also paired the geckos from both populations to the larger *H. platyurus* to observed intraspecific interactions. We found that *H. frenatus* from the competitor-rich community was more aggressive against the competitor than the gecko from the competitor-released community. Accordingly, we concluded that after the introduction to the low competition intensity community, like Australia, *H. frenatus* might have lost its aggressiveness and receive a trade-off as the energy conservation and high population density. This behavioral flexibility should enable *H. frenatus* to thrive in different ecological contexts.

Keywords: Aggression, Agonistic behavior, Competition, Invasive species, House geckos

6.2. Introduction

In recent decades, the increasing numbers of invasive species have become a concerning problem due to their potential to deteriorate global biodiversity (Lockwood et al. 2013). One of the most crucial traits of invasive species is their ability to compete successfully with native species. Because all individuals need to acquire resources to survive, grow, and reproduce, competition is an important trait that can influence the dynamics of ecological communities (Ruscoe et al. 2011, Mittelbach 2012). When two species compete for a shared limited resource, exploitation of that resource by one species will deplete the resource for the other species. Some species may gather resources without physical confrontations (i.e., exploitative competition), whereas other species use agonistic behaviors to exclude competitors (i.e., interference competition) (Mittelbach 2012, Lang and Benbow 2013). The behavioral syndrome theory has described aggressiveness as a trait that usually positively correlates with boldness, exploratory, and other extrovert behaviors (Sih et al. 2014, Michelangeli et al. 2017). This repertoire of behavioral traits is beneficial, especially during the invasion process (Chapple et al. 2012). However, aggressiveness could be costly because it requires much energy, resulting in lower fitness when the animals were over-aggressive (Marler et al. 1995, Vøllestad and Quinn 2003).

Numerous studies in invasion biology have observed a high level of aggressiveness in the invasive species, which in turn, led to negative impacts on the native fauna (Chapple et al. 2012, Sih et al. 2014). Although the effects of competition by introduced species were less significant than predation, behavioral aggressiveness could still cause native species to decline or become extinct (i.e., competitive displacement) (Losos et al. 1993, Petren et al. 1993, Cole et al. 2005, Sanches et al. 2012). For example, a study in the Mascarene Islands suggested that several species of night gecko in genus

Nactus once existed on the islands of Réunion, Rodrigues, and mainland Mauritius, but later went extinct after the introduction of the Asian house geckos (*Hemidactylus frenatus*) (Arnold and Jones 1994). A later investigation by Cole et al. (2005) suggested that the competition for space by *H. frenatus* potentially has created the landscape of fear, forcing the native geckos to stay away from refugia, which exposed them to predators. Eventually, the presence of *H. frenatus* has caused population fragmentation and driven them to extinction.

Despite being one of the smallest members of its genus, the Asian house gecko (*Hemidactylus frenatus*) is the most widespread gecko species in the world (Carranza and Arnold 2006). The gecko is native to South and Southeast Asia but has established populations in other tropical regions of Asia, the Pacific islands, Australia, and Central America. Previous studies in the Pacific Islands suggested that the introduced *H. frenatus* were very aggressive towards native gecko species and were responsible for the decline of those species (Bolger and Case 1992, Case et al. 1994, Dame and Petren 2006). Those studies also suggested that male *H. frenatus* were more aggressive than females because they defend territories from rival males. However, a recent study in Australia concluded that *H. frenatus* tended to avoid the native *Gehyra australis* (Yang et al. 2012). A similar observation by Cisterne et al. (2018) also found that male *H. frenatus* were less aggressive than male *Gehyra dubia*. These contrasting findings raise several questions. First, why does aggressiveness in male *H. frenatus* appear to vary geographically? Second, what influences the aggression levels in this species? We hypothesized that the different levels of interaction pressures among gecko communities might be the reason behind that divergence in aggressiveness. Many studies in diverse groups of animals have found that the intense interaction pressures, which arise from interspecific competition, could drive individuals to become more aggressive, both intraspecifically and interspecifically (Reichert and Gerhardt 2014, Briffa et al. 2015, Kilgour et al. 2019). In this study, we observed and compared the agonistic behavior of *H. frenatus* from a competitor-rich community with another competitor-released community. We also assayed the behavior of a non-invasive congener, *H. platyurus*, for interspecific comparison.

6.3. Materials and methods

6.3.1. Study communities

We selected two house gecko communities to study; one competitor-rich and another competitor-released. We chose a gecko community at the Faculty of Science, Prince of Songkla University, Hat Yai, Thailand (7.007658°N; 100.498051°E) to serve as a competitor-rich community. In this site, there were three species of *Hemidactylus* sharing the habitat, including *H. frenatus*, *H. platyurus*, and *H. murrayi.* We mentioned this population of *H. frenatus* as the "mainland" for the rest of this paper. For the competitor-released community, we chose a rural and isolated Bulon Le Island, Satun, Thailand (6.832023°N; 99.536687°E) to study. As a highly human-associated species, we assumed that the gecko has arrived on the island following the settlement of Urak Lawoi people in the 1910s (Wongbusarakum 2007). Unlike the mainland community, there was no record of any other species of *Hemidactylus* on this island; therefore, *H. frenatus* solely dominated the community (Lapwong and Juthong 2018). Previous studies on lizard ecology also suggested that the insular community usually has a lower level of competition than the mainland (Lister 1976, Buckley and Jetz 2007). We mentioned this population of *H. frenatus* as the "island" for the rest of this paper. To confirm our assumption about the competition intensity of each community, we surveyed the community structure in both sites in December 2018. In each location, for two nights from 19h to 21h, an investigator walked around the buildings and counted every gecko he saw and identified them to species. Later, we caught the geckos and measured their SVLs and weights. We also observed whether the geckos had lost their tails or not. In total, we caught and measured 52 *H. frenatus* from the mainland and another 31 from the island. We additionally captured and measured 35 *H. platyurus* from the mainland.

After that, we collected 20 male *H. frenatus* from both sites and 40 male *H. platyurus* from the mainland and transferred them to a laboratory in Prince of Songkla University in December 2018. We only used male geckos in this study due to their prominent aggression and territory defense behavior (Bolger and Case 1992, Case et al. 1994, Dame and Petren 2006). In the laboratory, we kept each gecko in a 2L ventilated plastic container (10x10x20 cm) with a small Petri dish filled with water, a paper towel, and a paper tube as shelter. We placed all containers on shelves in an open-air room with natural light, of which ambient temperatures ranged from 23 – 32 °C. We fed each gecko with three mealworms every third day.

6.3.2. Agonistic behavioral trials

We used a 30x30x20 cm acrylic arena to observed the behaviors of the geckos. All sides of the arena were opaque except for the front side (30x20 cm), which was clear. On each of the left and right sides of the box, we created a 1-cm width retreat site with a 20x10 cm white foam board (Fig. 6-1). To commence the trial, we placed two geckos in the box and videotaped them for an hour. We conducted the trials between 17h to 22h when the geckos were highly active. The geckos were unfed for at least 24 hours to eliminate the effect of digestive activity. The intraspecific contests contained three groups, including mainland *H. frenatus*, island *H. frenatus*, and *H. platyurus*. We allocated 16 individuals of each group into eight pairs. From the videos, none of the geckoes was bitten, so we used the same individuals for the interspecific contests. To avoid any carry-on effects from the previous pairings, we rested the geckos for at least five days before starting the interspecific trials. We matched the same 32 *H. frenatus* (16 from the mainland and 16 from the island) site with 32 *H. platyurus*. The sizes of geckos in each pair were randomized because *H. platyurus* is generally larger than *H. frenatus*. The average SVL of *H. platyurus* was 52.6±0.6 mm (range = 46.9–58.9 mm), which was 3.0 mm larger than the mainland *H. frenatus* (average = 49.6±0.7 mm, range = 46.0–55.7 mm) and 2.8 mm larger than the island *H. frenatus* (average = 49.8±0.9 mm, range = 45.1–54.9 mm).

Although the repertoire of agonistic behaviors comprised various types of displays and expressions, we selected four that could be obviously and frequently observed, namely arch-back, tail-wave, approach, and flight. First, many geckos species usually arch their backs to visually intimidate competitors (Marcellini 1977, Regalado 2003, Briggs 2012) (Fig. 6-2a). In particular, a previous study on the social behavior of *H. frenatus* found a positive correlation between the frequencies of arch-back and attack (Dame and Petren 2006). On the other hand, geckos display tail-waves in multiple contexts (Fig. 6-2b), including when they sense their predators (Dial et al. 1989, Webb et al. 2009, Webb et al. 2010, Landová et al. 2016) or competitors (Rodríguez et al. 2011, Briggs 2012). Additionally, a study on another species of lizard (*Bassiana duperreyi*) revealed that the frequency of tail-waves negatively correlated with the body conditions; hence, a primary function of tail-waves should be to deflect attacks towards the tail, which can be autotomized (Telemeco et al. 2011). Accordingly, we categorized tail-waves as defensive behavior, which negatively correlated with aggressiveness. The approach behavior involved a male moving towards another male. In such situations, the subdominant individual would typically move away, an action we classified as flight so that physical contacts rarely occurred during the contest (Petren et al. 1993, Regalado 2003, Briggs 2012). In each pair, we counted those four expressions in both geckos.

6.3.3. Data analyses

The Kolmogorov-Smirnov test showed that all data, except the weights of mainland *H. frenatus*, were normally distributed ($P > 0.05$). Levene's test showed that only SVLs, but not weights, have homogeneous variances among groups ($P > 0.05$). The violated homogeneity of variances of weight was probably a consequence of different tail-loss rates. Although our data do not perfectly fit the assumptions to use two-factor ANOVA, we decided to cautiously continue with the analysis to determine whether SVLs and weights of the geckos were affected by gecko groups (mainland *H. frenatus*, island *H. frenatus*, and mainland *H. platyurus*) and sexes. However, to compensate for those assumptions' violations, we compared the *P-value* with 0.01 instead of 0.05. We used the binomial logistic regression to see if the tail-loss rates are different among groups and between sexes. Then, we used the log-linear model with the Poisson distribution (Poisson regression) to determine the effects of groups and competitor species on the expressions of *H. frenatus* because they were counting values. We also used the same analysis to determine the effect of competitor species on the expressions of *H. platyurus* for comparison.

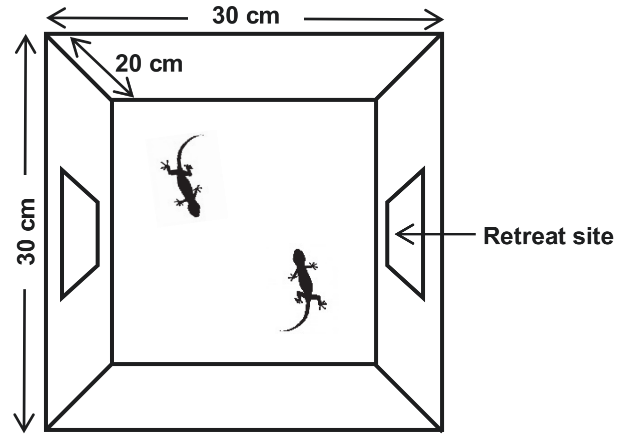

Figure 6-1 An arena used for observing agonistic behaviors of the geckos.

Figure 6-2 Two precautionary postures of the gecko; (a) arch-back and (b) tail-wave.

6.4. Results

6.4.1. Community structure and tail-loss rate

The mainland house gecko community comprised five species, namely *H. platyurus*, *H. murrayi*, *H. frenatus*, *Gehyra mutilata*, and *Gekko gecko*, while the island house gecko community comprised four species, namely *H. frenatus, G. mutilata*, *Gekko cf. tokehos*, and *Lepidodactylus lugubris*. The geckos in the genus *Hemidactylus* dominated both communities, with more than 85% of individuals belonging to this genus. In the mainland, *H. platyurus* had the highest observation rate (33 individuals/hour), following by *H. murrayi* (13 individuals/hour), and *H. frenatus* (13 individuals/hour). In contrast, the island was dominated by *H. frenatus* (36 individuals/hour) (Fig. 6-3). The overall observation rates of all geckos were 60 individuals/hour at the mainland and 39 individuals/hour at the island.

Two-factor ANOVAs revealed that the geckos from three groups had different SVLs ($F_{2,112} = 9.52$, $P < 0.01$) and weights ($F_{2,112} = 13.41$, $P < 0.01$). The Scheffé post hoc tests showed that, while *H. frenatus* from the mainland and the island populations did not have different SVLs and weights, *H. platyurus* were significantly larger and heavier. The geckos showed sexual dimorphisms in SVLs ($F_{1,112} = 14.15$, $P < 0.01$) and weights ($F_{1,112} = 9.83$, $P < 0.01$), with larger and heavier males. There was no effect of the interaction between group and sex on SVLs ($F_{2,112} = 1.53$, $P = 0.22$) and weights ($F_{2,112} = 1.96$, $P = 0.15$). That is, the effect of sex was consistent throughout every group. Binomial logistic regression suggested that tail-loss rates were different among the groups of geckos (Wald $\chi^2_2 = 7.08$, < 0.05) but not between sexes (Wald $\chi^2_1 = 0.02$, $P = 0.89$). The island *H. frenatus* showed the lowest tail-loss rate (45.16%), following by the mainland *H. frenatus* (65.38%), and *H. platyurus* (77.14%) (Table 6-1).

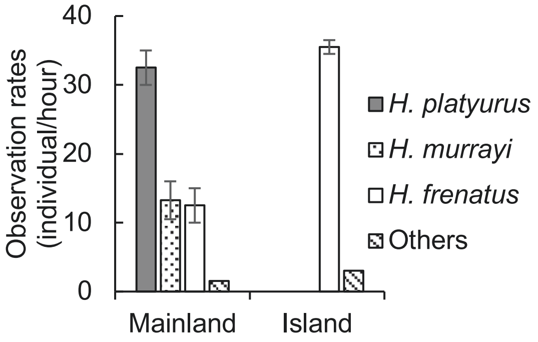

Figure 6-3 The abundance of house gecko species in Hat Yai (mainland) and Bulon Le Island (island).

Table 6-1 Mean (±SE) SVLs, mean (±SE) weights and tail-loss rates of *H. frenatus* from the mainland and the island populations, and *H. platyurus* from the mainland population.

	H. frenatus				*H. platyurus*	
	Mainland		Island		Mainland	
	Male (n=30)	Female (n=22)	Male (n=17)	Female (n=14)	Male (n=16)	Female (n=19)
SVL (mm)	51.4±0.6	47.8±0.7	49.9±1.0	47.0±0.7	52.6±1.2	51.7±0.8
Weight (g)	2.98±0.17	2.40±0.12	2.67±0.19	2.03±0.07	3.26±0.21	3.22±0.12
Tail-loss Rate	66.67%	63.64%	47.06%	42.86%	75.00%	78.95%

6.4.2. Agonistic expressions of *H. frenatus*

The mainland and the island populations of *H. frenatus* showed significant differences in frequencies of arch-back, tail-wave, and approach, regardless of competitor species (Fig. 6-4a, b, and c & Table 6-2a, b, and c). While the mainland geckos displayed arch-back and approached more often, the island geckos waved their tails more often. Additionally, the regression revealed a significant effect of interaction between populations and competitor species, which meant that the island geckos displayed tail-wave more often than the mainland geckos when they encountered *H. platyurus* ($\chi^2_1 = 12.62$, $P < 0.05$). On the other hand, the mainland geckos significantly fled more often when facing conspecifics ($\chi^2_1 = 7.92$, $P < 0.05$) despite the insignificant effect of populations of *H. frenatus* or competitor species alone (Fig. 6-4d & Table 6-2d).

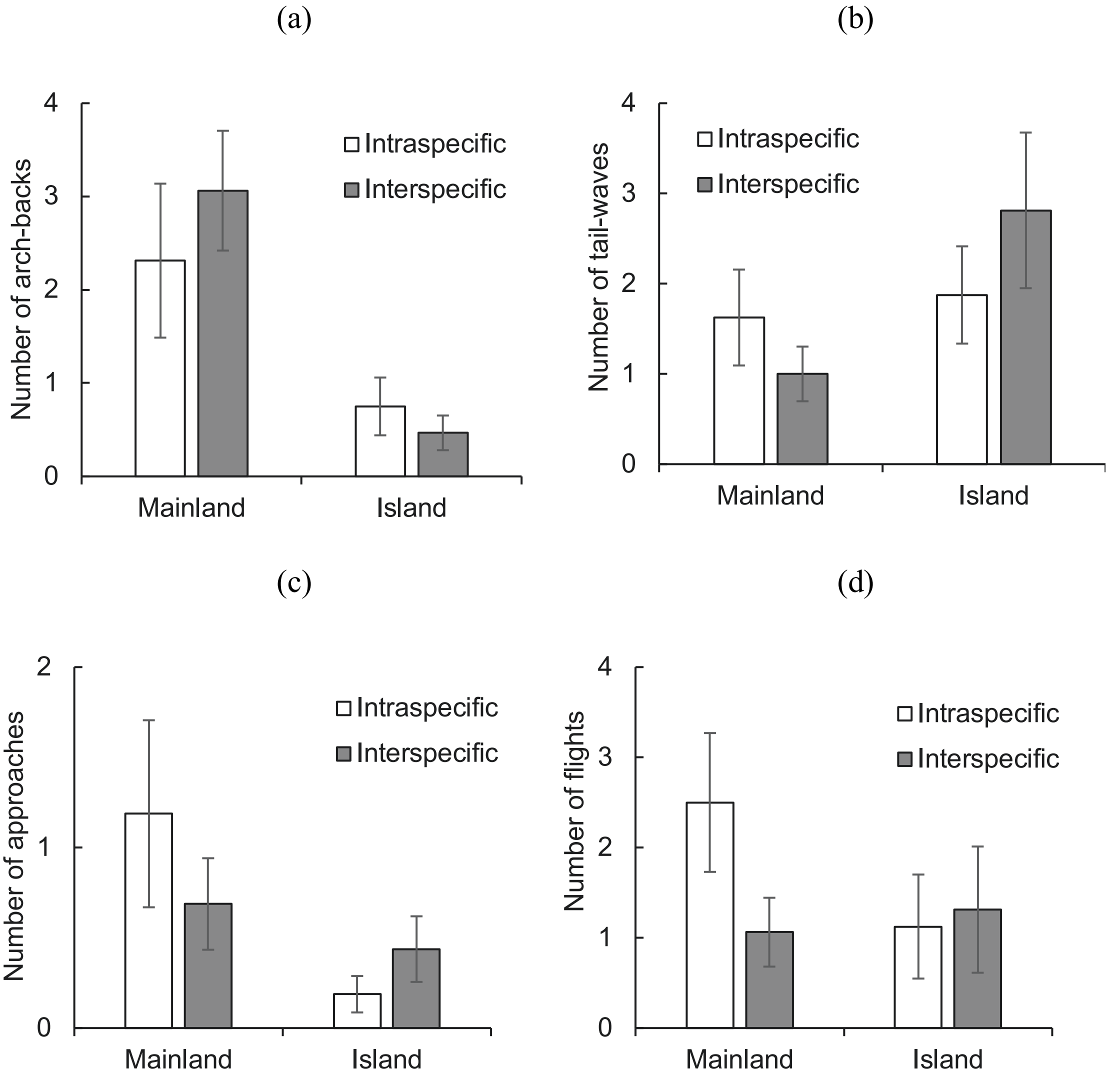

Figure 6-4 Mean (±SE) numbers of agonistic expressions within an hour of *H. frenatus* from the mainland (competitive community) and island (competitor release community); (a) arch-back, (b) tail-wave, (c) approach, and (d) flight. Open bars represent intraspecific interaction, and closed bars represent interspecific interaction.

Table 6-2 Results of Poisson regressions showing effects of populations (mainland vs. island), competitor species (*H. frenatus* vs. *H. platyurus*), and their interactions on agonistic expression frequencies of *H. frenatus*; (a) arch-back, (b) tail-wave, (c) approach, and (d) flight.

a) Arch-back

	Wald Chi-Square	*df*	Sig.	
Population	34.488	1	0.000	*
Competitor Species	0.243	1	0.622	
Population x Competitor Species	2.457	1	0.117	

b) Tail-wave

	Wald Chi-Square	*df*	Sig.	
Population	8.854	1	0.003	*
Competitor Species	0.041	1	0.840	
Population x Competitor Species	5.072	1	0.024	*

c) Approach

	Wald Chi-Square	*df*	Sig.	
Population	8.520	1	0.004	*
Competitor Species	0.146	1	0.702	
Population x Competitor Species	3.135	1	0.077	

d) Flight

	Wald Chi-Square	*df*	Sig.	
Population	1.844	1	0.174	
Competitor Species	2.632	1	0.105	
Population x Competitor Species	5.453	1	0.020	*

Asterisks (*) denotes statistical significance ($P < 0.05$)

6.4.3. Agonistic expressions of *H. platyurus*

While *H. frenatus* showed similar expressions regardless of competitor species (except for more flights when paired with conspecifics in the mainland population), *H. platyurus* displayed all expressions more often toward conspecifics (arch-back; Wald $\chi^2_1 = 43.42$, $P < 0.05$, tail-wave; Wald $\chi^2_1 = 7.20$, $P < 0.05$, approach; Wald $\chi^2_1 = 35.39$, $P < 0.05$, and flight; Wald $\chi^2_1 = 5.15$, $P < 0.05$) (Fig. 6-5).

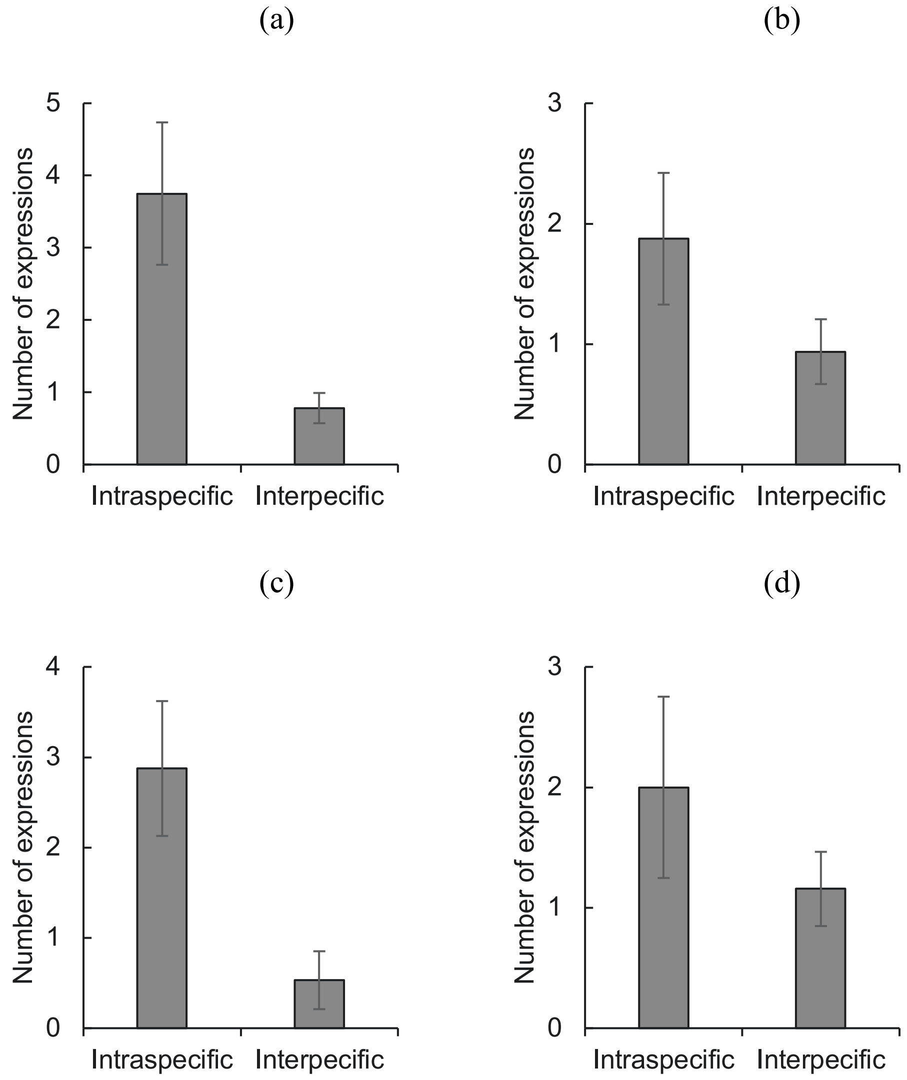

Figure 6-5 The number of agonistic expressions within an hour of *H. platyurus*; (a) arch-back, (b) tail-wave, (c) approach, and (d) flight.

6.5. Discussion

6.5.1. Competition intensity

Previous studies suggested that the lizard community on the island should have lower competition intensity than the one on the mainland (Lister 1976, Buckley and Jetz 2007). Adding to that knowledge, we confirmed that the urban mainland community of house geckos was more competitive than the rural island community since there were a higher diversity and abundance of competitors. In this study, we found that the mainland community of house gecko in Hat Yai comprised three dominant species from the genus *Hemidactylus*, and *H. platyurus* was the most dominant species, rather than *H. frenatus*. On the other hand, the absence of other *Hemidactylus* in Bulon Le Island could provide less competitor's diversity and density for *H. frenatus*. In addition, the higher tail-loss proportion of the mainland community confirmed that the mainland community was significantly more competitive than the island one.

6.5.2. Interpopulation divergence in the aggressiveness of *H. frenatus*

The early studies of introduced *H. frenatus* in the Pacific Islands suggested that the gecko relied on its aggressiveness to dominate the non-native community (Bolger and Case 1992, Dame and Petren 2006). Our results indicated that those conclusions were not ubiquitous because this behavioral trait varied among populations, depending on the ecological contexts. Correspondingly, a study by Michelangeli et al. (2018) found a different magnitude of behavioral expressions in a widespread reptile species, *Lampropholis delicata*, among geographically distinct populations. In our study, *H. frenatus* from the mainland community rigorously displayed their aggressive behaviors against conspecifics and heterospecifics, probably to compete for spaces and resources. At the same time, the gecko community in the island was less competitive so that *H. frenatus* became unaggressive.

Our finding could explain why introduced *H. frenatus* in Australia are less aggressive compared to those on the Pacific islands. The studies of the interactions between introduced *H. frenatus* and native *Gehyra australis* and *G. dubia* found that the invader was less aggressive against heterospecifics than natives (Yang et al. 2012, Cisterne et al. 2018). We suggested the low density of *Gehyra* spp. in urban Australia might provide a less competitive environment for the introduced *H. frenatus* so that it has lost aggressiveness through time, as has occurred on Bulon Le Island. According to the data from a competent citizen science database, iNaturalist.org, the house gecko community of northern and northeastern Australia (NT and QLD) was dominated exclusively by *H. frenatus*, with relatively low occurrences of other species (Fig. 6-6a) (iNaturalist 2020). Therefore, both *G. australis* and *G. dubia* should not be labeled as competitors of *H. frenatus,* since they are more common in bushland than in urban houses. A previous study on the western bluebird (*Sialia mexicana*) also found the lower aggressiveness of the long-term established population following the disappearance of native competitors (Duckworth and Badyaev 2007). Although Yang et al. (2012) suggested that *H. frenatus* were relatively unaggressive because they were smaller in size than the native *G. australis*, a study by Cisterne et al. (2018) in which *H. frenatus* was paired with the similarly sized *G. dubia*, also found a lack of aggressive behavior. Correspondingly, in our study, *H. frenatus* did not treat *H. platyurus* differently from their conspecifics despite *H. platyurus* being larger. Accordingly, we assumed that the aggressiveness of *H. frenatus* is more influenced by the density of competitors than the body size differences.

On the other hand, the Hawaiian house gecko community was dominated by two nocturnal species, *L. lugubris*, and *H. frenatus* (Fig. 6-6b). A behavioral study of genotypic ‘clone A’ of *L. lugubris* occurring in Hawaii confirmed that they were a bold competitor (Short and Petren 2008), which could be the reason behind its current abundance despite the long-term invasion of *H. frenatus*. In addition, according to the same database, another larger species of diurnal gecko, *P. laticauda*, widely spread across the Hawaiian landscape (iNaturalist 2020), could provide additional competition pressure to the community. Although being diurnal, a day gecko could have an overlapping active period and therefore compete with *H. frenatus* (Cole and Harris 2011). As a result, the introduced *H. frenatus* in Hawaii probably needed to maintain their aggressiveness because the recipient community was nearly as competitive as the native community (see mainland in Fig. 6-3).

A study on a related species, *H. turcicus*, by Briggs (2012) suggested that the decision to display behaviors relied on the self-assessment of the gecko. In our study, while *H. frenatus* reacted to the hostiles similarly regardless of species, *H. platyurus* responded less to the presence of *H. frenatus* than conspecifics. Therefore, we assumed that *H. platyurus* did not consider *H. frenatus* as a significant threat.

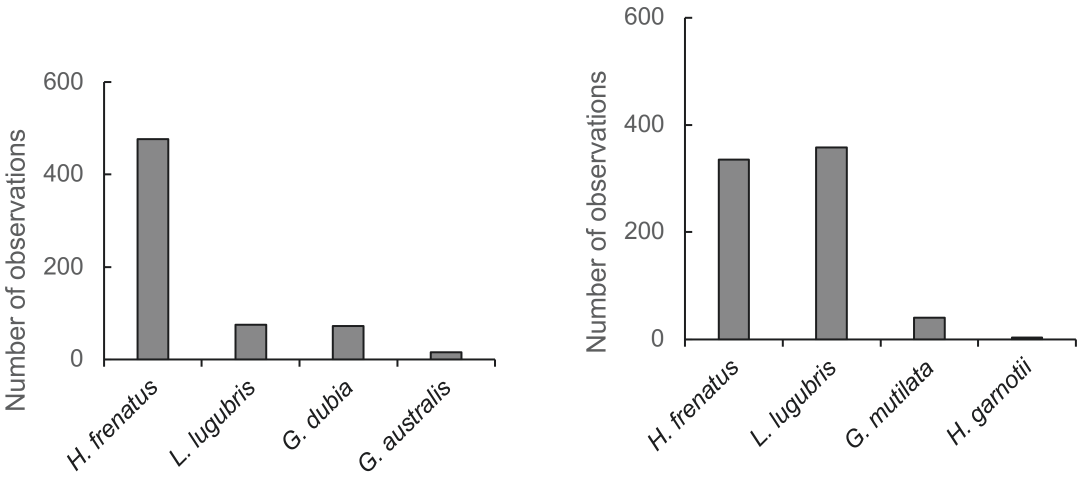
(a) (b)

Figure 6-6 Numbers of research-grade nocturnal house gecko observations in (a) northeastern Australia and (b) Hawaii, obtained from iNaturalist.org (iNaturalist 2020).

6.6. Conclusion

The early studies on the behavior of *H. frenatus* suggested that the gecko was exceptionally aggressive, which helped it to become an extraordinarily successful invasive species (Bolger and Case 1992, Case et al. 1994, Dame and Petren 2006). Our study confirmed that in its native range, *H. frenatus* is aggressive towards conspecifics and heterospecifics. However, we also found that the aggressiveness of *H. frenatus* is not a fixed specific trait, and it is positively correlated with the competition intensity in the community. Thus, geckos from a competitor-free island in Thailand were less aggressive than mainland geckos. By altering their behavior, house geckos are well suited to establishing in a range of novel competitive environments. Hence, the ability to shift their aggressiveness spatiotemporally, rather than aggressiveness per se, maybe the key to the geckos' widespread success across the globe.

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Chapter 7

Discussion and conclusion

The Asian house gecko is one of the most widespread invasive species in the world, yet little is known about how its thermal physiology or behavior has contributed to its success. Aside from its cosmopolitan distribution, the gecko has several traits, such as fast growth, high reproduction rate, high population density, short life cycle, and ease of care, which make it a good model for studying invasive terrestrial ectotherms. Future studies of this gecko should provide useful data that can be applied to other systems. Globally, many terrestrial ectotherms are spreading outside their native ranges and causing new problems (Gill et al. 2001, Meshaka 2011, Lee et al. 2019). For example, at least eight species of *Hemidactylus* have been reported from new geographic ranges (Jadin et al. 2009, Caicedo-Portilla and Dulcey-Cala 2011, Farr 2011, Torres-Carvajal and Tapia 2011, Heckard et al. 2013, Fierro-Cabo and Rentfro 2014, Bañuelos-Alamillo et al. 2016, Jairam et al. 2016, Boylan 2017, Weterings and Vetter 2017, Torres et al. 2018, Vásquez-Restrepo and Lapwong 2018). Therefore, future studies on the Asian house gecko should help us to understand more about the invasion process of terrestrial ectotherm so we could prevent and manage further introductions.

7.1. Thermal adaptations

Previous studies on the thermal biology of invasive species suggested that the invasive species supposedly have more extensive ranges of functional body temperatures, as well as high thermal tolerance so that they could outperform native species (Kelley 2014, Cortes et al. 2016, Geng et al. 2018). Therefore, thermal tolerance (CT_{min} and CT_{max}) has become a focus of studies which aim to determine the potential of a species to become successful outside its native range (Nyamukondiwa et al. 2010, Yu et al. 2012, Hu et al. 2014, Urquhart and Koetsier 2014, Cortes et al. 2016, Geng et al. 2018, Lenz et al. 2018). However, most of these studies took place in the recipient ecosystems where the invasive species had already established. Therefore, we know little about how those traits have shifted in response to new selection pressures. In this respect, several recent studies have demonstrated that some invasive species have adjusted their thermal biology after the initial introductions (Kolbe et al. 2012, Leal and Gunderson 2012). Consequently, the comparative study of thermal biology between the native and introduced ranges should shed light on the role of thermal biology in the biological invasion process, especially during the early stages. In Chapters 2, 3, and 4, I investigated whether the thermal physiology of the Asian house has changed since its introduction and spread into the temperate region of New South Wales, southeastern Australia.

During their initial invasion of southeastern Australia, Asian house geckos might have exploited the buffered climate of the urban areas to thermoregulate, thereby dodging selection on thermal traits (the Bogert effect). However, my results clearly showed that house geckos had shifted their thermal biology. In comparison with the native populations, the Asian house geckos in southeastern Australia could tolerate 1-2 °C colder temperatures. Also, in winter, these introduced geckos could extend both lower and upper thermal limits, giving them a broader range of functional body temperatures. After experiencing critical temperatures, the geckos from both native and introduced ranges could shift their thermal tolerances to a similar degree. However, the introduced geckos in southeastern Australia responded to the thermal stresses faster than the native geckos in Thailand. Although the geckos from both native and introduced ranges showed similar thermoregulation dynamics, the geckos from southeastern

Australia selected lower body temperatures. In addition, the thermal preference of the introduced geckos was lower in winter, confirming its ability to seasonally acclimate. While feeding status did not influence the preferred body temperatures of the geckos from Thailand, the introduced geckos from southeastern Australia selected higher body temperatures after feeding, presumably to stimulate their digestive function. In summary, the introduced geckos have shown a remarkably rapid shift in their thermal physiology to withstand the colder temperatures experienced in the temperate regions of Australia.

These rapid changes in thermal physiology were probably assisted by the geckos' high fecundity and fast growth rate (Ota 1994, Hoskin 2011, Nicholson et al. 2015), which enabled adaptation via natural selection to occur quickly. However, it is not easy to pinpoint precisely how those traits changed, nor how rapidly. Although a study on the thermal biology of the species along the introduction gradient would help to visualize the rate of phenotypic change, high rates of gene flow between populations due to human-associated dispersal may obscure the rate of change (Lenormand 2002). Nevertheless, if these thermal adaptations continue to occur, increasing urbanization and rises in temperature due to climate change will assist the spread of Asian house geckos further southward. Notably, Asian house geckos are also widespread in the Americas, and if similar adaptations occur in those countries, the gecko is likely to spread further into colder climates.

Besides experiencing lower and more variable temperatures than tropical regions, temperate regions provide less insect prey in winter (Lowman 1982). In Chapter 5, I found that the energy conservation strategy should be another critical factor contributing to the success of this invasive gecko in cold regions. Despite providing a wide range of temperatures in the thermal gradient, the introduced geckos captured in winter voluntarily selected low body temperatures. To cope with seasonal shortages of food, and lower temperatures, house geckos have shifted their body temperatures downwards, which would allow them to conserve energy. Interestingly, Christian et al. (1998) found that the tropical species of velvet gecko, *Oedura cincta* (or the tropical population of *O. marmorata* at that time), lacked seasonal energy modulation, while the temperate species, *O. marmorata*, showed lower energy expenditures during winter to conserve energy. Accordingly, despite being a tropical species, my study found that *H. frenatus* had adopted a thermal strategy similar to that of temperate species to survive in southeastern Australia.

7.2. Behavioral adaptations

A review of behavioral traits of invasive species found a common repertoire of behaviors among them, which were believed to facilitate their success (i.e., invasion syndrome). The major traits of successful invaders included aggressiveness, exploratory behavior, antipredator behavior, and foraging behavior (Chapple et al. 2012). However, most previous studies usually observed invasive species in their recipient ranges and made comparisons with native species (Petren and Case 1998, Cisterne et al. 2014, Williams et al. 2016). For example, all studies on the aggressiveness of the Asian house geckos were conducted outside their native range and produced contradicting results. While the studies in Hawaii suggested that the gecko was very aggressive against native species (Bolger and Case 1992, Case et al. 1994, Dame and Petren 2006), the studies in Australia found that the gecko was somewhat submissive (Yang et al. 2012, Cisterne et al. 2018). Those studies, while informative, cannot paint a complete picture of the invasion history of the species. My research is one of the few studies that has compared the behaviors of an invasive species in its native range and recipient range and in multiple populations.

In Chapter 5, I examined the gecko's exploratory behavior in divergent populations. I found that the geckos from core populations with higher competition and predation pressures tended to hide more and explore less to avoid being exposed in open areas. This shy personality would secure their safety and increase their probability of getting trapped and accidentally transported. On the other hand, the geckos from edge populations tended to hide less and explore more since the chances to encounter competitors and predators were minimal. This unwary personality would allow them to access necessary resources and quickly expand their range locally. Interestingly, the divergence in the exploratory behavior of the Asian house geckos does not only ensure their survival but also enhances their dispersal.

In Chapter 6, I examined the agonistic behavior of male geckos. I found that the Asian house geckos from a competitor-rich community were more aggressive than their conspecifics from a competitor-release community. In the community, where there are a lot of competitors, the aggressive geckos would be able to compete for spaces and foods, especially when those resources are clumped around artificial lights. In contrast, when there are not many competitors, the geckos can stay unaggressive and still get enough resources. In this manner, the geckos also save energy and can occur in high density. With this behavioral adaptation, the Asian house geckos should be able to co-occur with any other gecko species regardless of their competitiveness. My finding should explain the flourishes of the Asian house geckos in different ecosystems around the world.

7.3. Implications

By studying the thermal adaptations of an invasive species, we can make better predictions about their future range expansion. Current predictions using species distribution models rely on fixed traits, and while useful, they may fail to forecast future spread accurately. For example, a study by McCann et al. (2014) found that cane toads in Australia have reached colder areas than expected due to their ability to rapidly thermal acclimate. With the precise estimation of the distribution limit, the government would be able to design an effective management plan. In Australia, house geckos have the potential to migrate southwards in New South Wales, and could eventually establish populations in Sydney. Although the studies in Queensland suggested that house geckos are not aggressive towards native geckos, the situation could be quite different in New South Wales. In the Sydney region, a species of native gecko, the broad-tailed gecko (*Phyllurus platurus*), has adapted to urban areas and often occurs in and around houses (Wilson and Swan 2017), making them vulnerable to future invasions by Asian house geckos. Theoretically, house geckos might compete with, or prey on hatchlings of broad-tailed geckos. Furthermore, Barnett et al. (2018) suggested that the introduced house gecko could spread parasites to the native gecko community. The authors suggested that the equilibrium parasitic infection rate, which is maintained by the low density of the native species, could shift rapidly due to the high densities of introduced Asian house geckos. More importantly, the distribution range of the broad-tailed geckos is entirely restricted to the Sydney basin, so if the Asian house geckos become widespread in this area, they could cause the only population of the broad-tailed gecko to decline and became vulnerable to extinction.

In recent years, another species of house gecko, the Indo-Pacific house gecko (*Hemidactylus garnotii*), has established in Sydney and is becoming widespread (Boylan 2017). I hypothesize that the intense competition within the house gecko community could drive both introduced geckos to become more aggressive, and they could then negatively impact the native geckos. In addition, the high density of two species of introduced house geckos would increase the likelihood of transmission of parasites to the native lizard communities (Barnett et al. 2018). A study by Kelehear et al. (2013) even found a shift of Pentastomid parasite from Asian house geckos to cane toads. Therefore, it is likely that the future spread of Asian house geckos and also the Indo-Pacific house geckos will affect native ecosystems. Consequently, I propose that the prevention of further introduction of the Asian house gecko toward Sydney is essential.

During my specimen collections in Yamba, Coffs Harbour, Port Macquarie, and Taree, I have spoken with some residents and realized that they have minimal knowledge about the Asian house geckos despite their potential impacts on the Australian ecosystem (Hoskin 2011). I also confirmed the tendency of the geckos to get introduced unintentionally via travelers. Accordingly, I suggest that the government should provide information about those anticipated invasive species through media or educational programs, as a focus on early detection, and rapid response is the most effective strategy to control such species (Simpson et al. 2009). Fortunately, the Department of Primary Industry (DPI) of New South Wales already developed a platform to involve people in the prevention and management of early introduced species, called "Biosecurity Warrior." It should be easy for the department to add information about invasive house geckos into the platform. Citizen science applications will also be useful for tracking the range expansion of invasive species. For example, the hugely popular "FrogID” app, developed by the Australian Museum, allows the general public to upload frog calls and photographs. This platform has documented the spread of cane toads outside their known range. Interestingly, the scientist who developed this platform told me that the public has also uploaded many calls of the Asian house gecko (Jodi Rowley, personal communication).

During my review of the global invasion situation of the Asian house gecko, I exploited another comprehensive citizen science platform – iNaturalist. I found that another invasive gecko, the Indo-Pacific house gecko (*H. garnotii*), has established in Colombia for more than a century without being noticed because local biologists lacked experience with this group of geckos and misidentified them (Vásquez-Restrepo & Lapwong 2018). Moreover, during my collection trips in Thailand, I found a new record of a well-known invasive gecko, *Lepidodactylus lugubris*, despite its presence around houses (Lapwong & Juthong 2018). Both situations indicated that the invasive species could have gone undetected for years after the introductions because of insufficient human resources or expertise. However, this problem could be minimized with the help of citizen science, as mentioned above.

7.4. Further studies

Future molecular studies would be useful for understanding the genetic architecture underpinning the thermal adaptations that I documented. The understanding of the physiological changes during the invasion process should enlighten us on how organisms respond to the new environment. Although I tentatively suggested natural selection as the main contribution to this thermal adaptation, I cannot rule out the epigenetic expression as another possible contributor to the changes. In recent years, there has been growing knowledge of how thermal stress can induce histone acetylation and DNA methylation, which enable higher thermal tolerances, and which can be passed through generations (Norouzitallab et al. 2014, Hu et al. 2015, Weyrich et al. 2016, Hu and Barrett 2017, David et al. 2019). These sorts of studies would shed light on the molecular mechanisms that underpin the rapid upward shifts in thermal hardening responses that were present in the introduced populations. Also, future studies on the relationship between thermal preference and energy expenditure of the house geckos would confirm my prediction that selection of lower temperatures in winter is indeed an energy conservation strategy.

Climate matching is often seen as a primary indicator of the successful establishment of non-native amphibians and reptiles. However, a study by Bomford et al. (2008) predicted that based on climatic traits, *Hemidactylus flaviviridis* should be able to establish in non-native ranges quickly. Today, this species has still not established a successfully introduced population. This highlights the importance of understanding the behavioral traits that allow some species to be so successful. In this study, I showed that behavioral traits of house geckos vary between populations and ecological contexts, and these promote success during sequential stages of the invasion pathway. Future research on cognitive and other behavioral adaptations of invasive species in native and recipient ranges should provide a better understanding of the trait variation that promotes invasion success. With broader and more in-depth knowledge about those traits (or personalities), we would be able to predict and prevent emerging invasive species. Although I focused on exploratory behavior and aggressiveness, it is clearly of interest to focus on additional behavioral traits that may promote invasiveness.

Last but not least, the Asian house gecko has an extraordinarily large geographic range, so my study has focused on just a small part of its non-native range. Similar studies in different regions, such as East Asia and the Americas, would provide additional information, allowing us to not only evaluate the generality of my findings but to understand how it has adapted to dissimilar regions of the globe. For example, I recently gave a seminar at the World Congress of Herpetology in Dunedin, New Zealand, between 5th – 10th January 2020. At that conference, I met another Ph.D. student who is also working on the thermal biology of the Asian house gecko in temperate regions of Japan. After talking about our research, we realized that our results were somewhat different. Therefore, collaborations with other research teams from different geographic regions that study the same organism should generate more informative explanations of the focal phenomena.

7.5. Conclusion

Invasive species are a major environmental problem despite considerable efforts to prevent their spread or control established populations. Scientists have tried to understand the factors that help those species to overcome resistance and become successful in non-native ecosystems, notwithstanding the lack of co-evolution. The initial broad thermal tolerance, effective thermal acclimation, and bold personality (i.e., aggressive, explorative, etc.) are common characteristics of successful invasive species (Chapple et al. 2012, Kelley 2014). My study has extended our understanding of traits that facilitate the spread of invaders. In summary, the ability to shift thermal physiology and modulate exploratory and aggressive behaviors in different environments has likely contributed to the success of Asian House geckos. By exhibiting such flexibility in thermal physiology and behavior, this small reptile species has passed through different invasion stages and has become one of the world's most successful invasive species.

7.6. References

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