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斯文豪氏攀蜥與黃口攀蜥之運動生理與溫度特性：

跨海拔之物種內、種間及性別間之比較

Thermal sensitivity of locomotor performance and thermal profiles in two agamid lizards in Taiwan: Intraspecific, interspecific, intersexual comparisons across altitudes

陳哲豪

Che-Hao Chen

指導教授：林雨德 博士

Advisor: Yu-Teh Kirk Lin, Ph.D.

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本論文係 陳哲豪 君（學號R01B44021）在國立臺灣大學生態學與演化生物學研究所完成之碩士學位論文，於民國103年6月13日承下列考試委員審查通過及口試及格，特此證明

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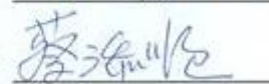
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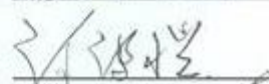
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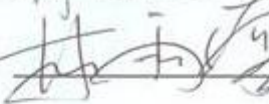
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何傳愷 博士



臺灣大學生態學與演化生物學研究所

林雨德 博士



所長



（簽名）

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摘要

外溫動物的生理表現隨著體溫變化，其中運動表現對個體的生存有重大的影響，而研究同一物種在不同溫度環境中族群的運動生理表現可讓我們了解溫度生理的適應性演化。本研究探討斯文豪氏攀木蜥蜴(*Japalura swinhonis*)與黃口攀木蜥蜴(*Japalura polygonata xanthostoma*)的中海拔族群和低海拔族群在運動生理及溫度特性上的差異，我測量攀木蜥蜴在六個溫度下的跑步速度與跳躍距離以畫出運動表現的溫度敏感度曲線(thermal sensitivity curve)，並算出表現寬度(B_{80})及理想表現溫度(T_0)。此外，我測量最高耐受溫度極限(CT_{max})、最低耐受溫度極限(CT_{min})及個體在野外環境中的體溫(T_b)，並且透過室內選溫實驗測量蜥蜴的選溫偏好(T_{sel})。結果發現兩種攀蜥在不同海拔的族群在溫度生理上都有適應性演化，但不同的運動型態的適應情形會隨著物種而不同，而雌雄在溫度生理上的差異只有在黃口攀蜥發現。然而不同海拔族群或不同性別的攀木蜥蜴在溫度偏好上並無差異。本研究顯示外溫動物族群在溫度生理上會適應不同的溫度環境。

關鍵字: 溫度敏感度、運動表現、溫度耐受極限、蜥蜴、海拔、雌雄差異

Abstract

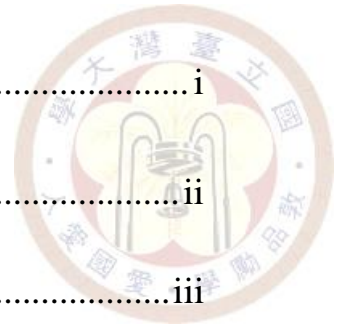


Physiological performance varies with body temperature in ectotherms, especially the locomotor performance which may influence their survivorship. Whether lizard populations in various thermal environments maintain similar thermal profiles and thermal performance curves has been debated. In this study, I compared the thermal characteristics between two populations from lowland and mid-altitude in *Japalura swinhonis* and *Japalura polygonata xanthostoma*. I measured lizard sprint speed and jump distance at 6 temperatures to calculate performance breadth (B_{80}) and thermal optimum (T_o). I also measured thermal tolerance limits (CT_{max} , CT_{min}), selected temperature (T_{sel}) and field body temperature (T_b). Results showed that in both species populations from different altitudes had different patterns of thermal sensitivity and thermal tolerance. Sexual difference in thermal physiology was only found in *J. polygonata xanthostoma*. However, there was no significant difference in T_{sel} between two altitudinal populations or sexes in both species. My results support the labile view on the evolution of thermal physiology for lizards.

Keywords: thermal sensitivity, locomotor performance, thermal tolerance, lizard, altitude, sexual difference

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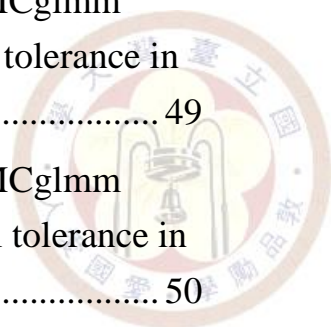
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Introduction



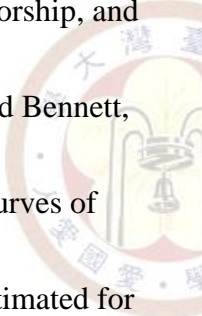
For ectotherms, their physiology and behavior, including locomotion (Bennett, 1980; Hirano and Rome, 1984; Weinstein, 1998; Ojanguren and Brana, 2000), immune function (Mondal and Rai, 2001), courtship (Navas and Bevier, 2001), foraging ability (Greenwald, 1974; Ayers and Shine, 1997; Carriere and Boivin, 2001), and rate of growth and development (Dutton et al., 1975; Kingsolver and Woods, 1997) are highly sensitive to body temperature. The relationship between body temperature and performance in ectotherms could be described by the thermal performance curve, or thermal sensitivity curve (Huey and Stevenson, 1979). The characteristics of thermal sensitivity curves reveal how organismal performance changes with body temperature. They generally include thermal optimum (T_o)—the body temperature when performance is at its maximum, performance breadth (B_{80})—the body temperature range that performance is greater than or equal to 80% of the maximum level, and critical thermal maximum (CT_{max}) and minimum (CT_{min})—the highest and lowest body temperature at which the organism loss its ability to perform.

Since environmental temperature may vary spatially and temporally, ectotherms often use thermoregulation to cope with temperature heterogeneity. They regulate body temperature within a specific range through behavioral, physiological, or morphological changes to maintain high level of performance (Avery, 1982; Hutchison and Dupre,

1992). However, thermoregulation may incur costs, such as increased risk of predation (Huey and Slatkin, 1976). In addition, thermoregulation may not be effective under certain circumstances, such as constant low or highly fluctuating environmental temperature or competition for basking perches among individuals. Ectotherms, thus, may fail to maintain proper body temperature for daily activities, such as feeding, reproduction, and escaping predators (Huey and Slatkin, 1976). Therefore, one would expect ectotherms evolve to adapt to different thermal environments (Kingsolver and Huey, 1998). Thermal adaptation should alter the parameters of thermal sensitivity curves including T_o , B_{80} , CT_{max} , or CT_{min} .

To understand thermoregulation and its evolution, one needs to know the thermal profiles of ectotherms as well (Huey and Slatkin, 1976; Hertz et al., 1993), which includes three important variables: the environmental temperature (T_e , or operative temperature); the field body temperature (T_b) that ectotherms achieve in the environment; and the selected body temperature (T_{sel}) that ectotherms choose under ideal thermal gradient conditions. T_b does not necessarily conform to T_{sel} , and may be seen as the result of the compromise between the T_{sel} and T_e .

Many types of individual performance could be examined to construct the thermal performance curves. Among them, locomotor performance such as swimming, jumping, and sprinting that involve whole-organism performance (Bennett, 1990) is often



adopted because it affects foraging efficiency, predator avoidance, survivorship, and finally the fitness (Greenwald, 1974; Christian and Tracy, 1981; Jayne and Bennett, 1990; Robson and Miles, 2000; Husak, 2006). . The thermal sensitivity curves of locomotor performance in association with thermal profiles have been estimated for many species. For example, in *Anolis* lizards, the T_o for sprint speed was correlated with field T_b , and both the 95% performance breadth (B_{95}) and the thermal tolerance ($CT_{max} - CT_{min}$) were positively correlated with the range of field T_b (van berkum, 1986). Similarly, Huey and Kingsolver (1993) conducted a comparative study on thermal sensitivities for sprinting speed among iguanid lizards, and found that T_o was positively correlated with field T_b , and with CT_{max} . These results indicated that evolutionary responses to thermal environments (T_e) have occurred. Previous studies on amphibians have also shown similar patterns in thermal physiology. Navas (1996a, b, 1997) compared thermal sensitivity curves of swimming among families: Dendrobatidae, Hylidae, Bufonidae, and Leptodactylidae. He found that high-elevation species had lower T_o and wider B_{80} than their congener from low-elevation.

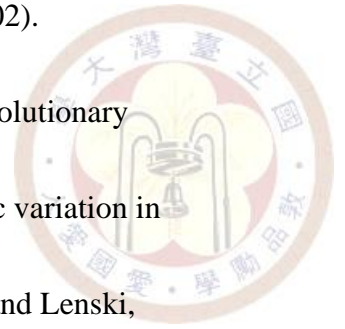
These interspecific comparative studies in reptiles and amphibians indicated that thermal sensitivity of locomotor performance could adapt to thermal variations along the altitude or latitude cline (Huey et al., 1989). That is, many thermal physiological parameters are labile, at least in some taxa. However, interspecific comparison may be

influenced by variables other than habitat differences (Pearson et al., 2002).

Intraspecific comparison is better than interspecific ones for inferring evolutionary adaptation in response to changes in thermal environments or geographic variation in climate (Van Damme et al., 1989; Huey and Kingsolver, 1993; Bennett and Lenski,

1999; Feder et al., 2000; Qualls and Shine, 2000; Angilletta et al., 2002; Kiefer et al., 2005). Yet, few studies have been conducted that examined intraspecific comparisons.

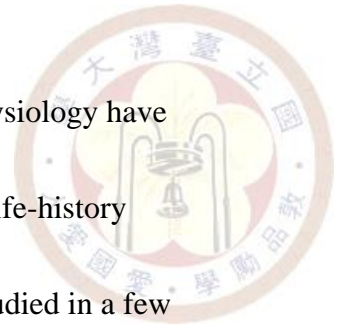
For example, eastern fence lizard (*Sceloporus undulatus*) from two altitudinal populations had identical T_o for sprinting speed despite the difference in field T_b (Crowley, 1985). A research on the wall lizard (*Podarcis tiliguerta*) found that field T_b differed between low- and high-elevation populations, but T_o and B_{80} for sprinting speed were identical in both populations (Van Damme et al., 1989). These results indicate that the evolution of thermal sensitivity of locomotor performance may be conservative within species even though there exists great divergence in the thermal environment. In contrast, a labile view of evolutionary thermal physiology has its support. For example, Beuchat et al. (1984) found the Puerto Rican robber frog (*Eleutherodactylus portoricensis*) in the montane area jumped poorly at high T_b while jumped well at low T_b , compared to its lowland congener. In all, more intraspecific comparative studies along latitude or altitude clines are needed to reveal the relationship between the characteristics of thermal sensitivities and thermal environments. This is a major gap in



the studies of evolution of thermal physiology.

Another major gap is that most studies of evolution of thermal physiology have ignored the intersexual difference within species. Sexual differences in life-history (Shine, 2005), behavior, and activity (Kerr and Bull, 2006) have been studied in a few reptilian species. They suggested that males and females might prefer different T_b , and use different thermoregulatory strategies. Indeed, several studies have shown sex differences in thermal tolerance (Lailvaux and Irschick, 2007), T_{sel} (Sievert and Hutchison, 1989), field T_b (Brown and Weatherhead, 2000; Singh et al., 2002; Fitzgerald et al., 2003), and sprint speed (Cullum, 1998; Lailvaux et al., 2003). These results indicated that we should routinely consider sex a variable when conducting studies on thermal physiology.

To fill the two gaps, I studied the thermal physiology of two agamid lizards, *Japalura swinhonis* and *Japalura polygonata xanthostoma*. They are endemic species and subspecies of Taiwan, respectively. *J. swinhonis* distributes the whole island, while *J. polygonata xanthostoma* distributes in northern Taiwan. Both species occur from lowland to mid-altitude (Ota, 1991; Hsiang, 1997; Kuo et al., 2007), and provide an altitudinal cline for investigating intraspecific variation. Both *Japalura* lizards have sexual dimorphism, especially *J. swinhonis* (Lin and Lu, 1982; Kuo et al., 2007; Kuo et al., 2009). However, the two species dwell in different habitat types. *J. swinhonis* occurs



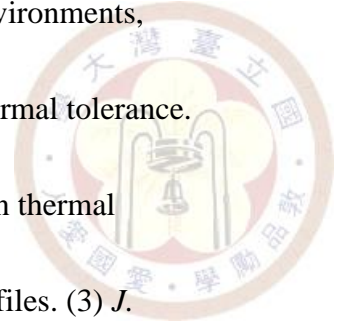
more often in human-inhabited areas, while *J. polygonata xanthostoma* in forested areas (Shan, 2013). Since human-inhabited areas are generally more open, thus have higher air temperatures than forested areas, the two species encounter different thermal environments both within and across altitudes. It offers a great opportunity to examine the inter-specific, intra-specific, and inter-sexual variations in thermal sensitivity curves, thermal profiles, and their relationships. Overall, my research goals are as follows: (1) To examine the evolutionary pattern of thermal physiology by comparing intra-specifically between lowland and mid-altitude populations in both *J. swinhonis* and *J. polygonata xanthostoma*; (2) To examine sexual difference in thermal physiology in *J. swinhonis* and *J. polygonata xanthostoma*; and (3) To compare the extent of thermal adaptation between *J. swinhonis* and *J. polygonata xanthostoma*. Figure 1 gives the concept map of the current study.

To fulfill the goals, I compared the thermal sensitivity in locomotor performance between lowland and mid-altitude populations as well as between two sexes in both *J. swinhonis* and *J. polygonata xanthostoma*. I measured sprint speed and jump distance as locomotor performance. Both types of locomotion are important for arboreal lizards (Losos and Irschick, 1996; Irschick and Losos, 1998). I also measured the thermal profiles: field body temperature (T_b), operative temperature (T_e), and selected body temperature (T_{sel}) of *Japalura* lizards. I tested the following hypotheses: (1)

Mid-altitude and lowland population lizards inhabit different thermal environments, thus have different thermal sensitivity of locomotor performance and thermal tolerance.

(2) *J. swinhonis* and *J. polygonata xanthostoma* have sexual difference in thermal sensitivity of locomotor performance, thermal tolerance and thermal profiles. (3) *J.*

swinhonis and *J. polygonata xanthostoma* have different extent of thermal adaptation across altitudes.



Materials and Methods

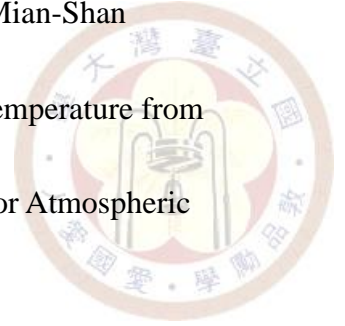


Study locations

The study was conducted, for each species, in one mid-altitude and two lowland locations, each. The mid-altitude location for *Japalura swinhonis* was the Xi-Tou Nature Education Area (23°67'N, 120°80'E) at an altitude of 1100–1150m. The mean temperature from June to September is 20.42±0.43°C (data obtained from Xi-Tou weather station, Experimental Forest of National Taiwan University, 2005-2013). The survey trail was about 2 km in length. The lowland locations for *Japalura swinhonis* were at the general area encompassed by the Fu-Yang Eco Park (25°00'N, 121°33'E) and Fu-Jou-Shan Park (25°10'N, 121°33'E) at an altitude of 25-40m and 20-55m, respectively. The mean temperature from June to September is 28.48±1.09°C (data obtained from Data Bank for Atmospheric Research, 1998-2010). The survey trail was about 3 km in length.

The mid-altitude location for *Japalura polygonata xanthostoma* was the Ming-Chih Forest Recreation Area (24°39'N, 121°28'E) at an altitude of 1150-1180m. The mean temperature from June to September is 16.75±1.50°C (data obtained from the Ecological and Environmental GIS database for Taiwan, Council of Agriculture, 1997-2010). The survey trail was about 2 km in length. The lowland locations for *Japalura polygonata xanthostoma* was at the general area that covered Min-Jiu-Shan

Mountain Trail (25 °05'N, 121°37'E) at an altitude of 30-40m, and Jin-Mian-Shan Hiking Trail (25 °09'N, 121°58'E) at an altitude of 25-30m. The mean temperature from June to September is $27.68 \pm 1.36^{\circ}\text{C}$ (data obtained from the Data Bank for Atmospheric Research, 1998-2010). The survey trail was about 2 km in length.



Field temperatures (T_b and T_e) and lizard collection

I sampled the lowland populations of *Japalura swinhonis* and *Japalura polygonata xanthostoma* from June to October, and the mid-altitude populations from July to September in 2013. I surveyed at least three times at each location. Generally, a survey began at 0800~0830 in the morning or 1400~1430 in the afternoon, depending on weather conditions. During surveys, I walked leisurely along trails, and captured lizards by hand or noose. Each captured lizard was measured field body temperature (T_b) immediately by inserting a thermocouple probe (DTM317, TECPEL, Inc., Taipei, Taiwan) into their cloaca. The operative temperature (T_e , or environmental temperature) was recorded by measuring the substrate where the lizard was perching on using a portable infrared thermometer (LS-E2006-01-A, OPTRIS, Inc., Berlin, Germany). I also recorded species, sex, snout vent length, and initial perch height of the lizard. The lizard was then put in a cloth bag, and brought back to the laboratory within 24 hrs. Lizards that were pregnant, or had tail loss or injury were released at site.



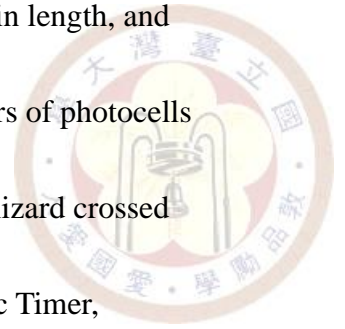
Laboratory housing

Upon returning to the laboratory, I housed lizards individually in glass tanks (L×W×H: 35×21×26 cm³) with 3-cm-depth potting soil substrate and a leaning rod for perching. Tanks were maintained in growth chambers (CK-68E, CHANG-KUANG, Inc., Taipei, Taiwan) with a L:D=13:11 light cycle. The temperature was set at 30°C at light and 25°C at dark for lowland populations; 26°C at light and 20°C at dark for mid-altitude populations. The settings followed the average temperatures in the field. I monitored the health of lizards daily, and provided two small crickets with calcium powder and *ad lib* water to each lizard daily. Lizards from each population were randomly divided into two groups: one is for measuring the locomotor performance: sprint speed and jump distance; the other for measuring thermal tolerance and selected body temperature (T_{sel}). The reason for dividing the lizards into two groups was to reduce the housing period, and the potential for laboratory temperature acclimation. All laboratory trials were completed within 10 days of capture of lizards.

Thermal performance curve

I obtained thermal performance curve (thermal sensitivity curve) by measuring the sprint speed and jump distance of lizards in performance trials. I measured the sprint

speed by chasing lizards up a 10-cm-diameter rod. The rod was 250-cm in length, and held at a 60° incline angle. Along the length of the rod, I set up eight pairs of photocells at 10-cm intervals at the mid-section of the rod (Fig. 17). As a sprinting lizard crossed the consecutive light beams of the photocells (Nine Section Photoelectric Timer, POWCHUNG, Inc., Taipei, Taiwan), the time it crossed each beam would be recorded by a photoelectric timer. I calculated the sprint speed from the travel distance and time recorded. The sprint speed of each lizard was measured at six different body temperatures: 20, 25, 27.5, 30, 32.5, 35°C in random order. In the beginning of a trial, I placed a lizard in a growth chamber set at the target temperature for 1 hour. The lizard was then removed from the growth chamber, its body temperature measured with a thermocouple probe to be sure it reached the target temperature. Immediately, I placed the lizard on the race rod, and chased the lizard up the rod. I measured lizard body temperature immediately after the trial to ensure it did not deviate more than 1°C from the target temperature. The sprint speed of each lizard was measured three times per temperature with a 1-hour rest in the growth chamber between trials. The average sprint speed measured for each individual at a given temperature entered the subsequent analyses. The lizards get a full day's rest between trials performed at different temperatures. Overall, there were six average sprint speeds (one at each temperature) for each lizard.

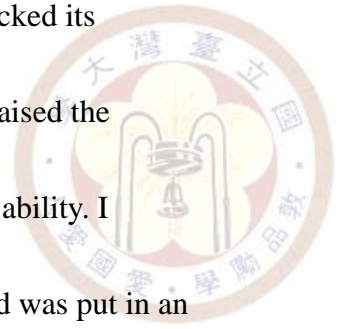


I measured the jump distance by probing lizards to jump from a platform ($L \times W \times H$: $10 \times 10 \times 9 \text{ cm}^3$) in an arena ($L \times W \times H$: $98 \times 30 \times 30 \text{ cm}^3$). The platform was at one end of the arena, and a shelter (a halved flowerpot) at the other end. Lizards were induced to jump toward the shelter, and the jump distances were recorded by a video camera (HDR-SR12, SONY, Inc., Tokyo, Japan). Similar to the procedures used for measuring sprint speed, jump distance of each lizard was measured three times at each temperature on the same days upon the completion of sprint speed trials. The maximum jump distance measured for each individual at a given temperature entered the subsequent analyses. Overall, there were six maximum jump distances (one at each temperature) for each lizard.

Thermal tolerance

The two ends of a thermal performance curves are the critical thermal minimum (CT_{\min}) and the critical thermal maximum (CT_{\max}). I determined the two critical values by measuring the temperatures at which a lizard lost righting response (Lutterschmidt and Hutchison, 1997a, b). In the beginning of a trial, a lizard, still in the housing tank, would be moved from growth chamber and placed in room temperature for an hour to allow the lizard adjust to the ambient temperature. To determine the CT_{\max} , I inserted a thermocouple probe into the lizard's cloaca, then placed the lizards under a ceramic heat

lamp (7Z-JT-250W, ZOOLIFE, Inc., Taipei, Taiwan), and constantly checked its righting response. By adjusting the distance between lizard and lamp, I raised the lizard's body temperature at approximately 1 °C/min until it lost righting ability. I followed similar procedures to determine the CT_{min} , except that the lizard was put in an open ziplock bag and submerged in 1 °C ice water. By adjusting the submerge time, I lowered the lizard's body temperature at approximately 1 °C/min until it lost righting ability. The CT_{max} and CT_{min} trials were conducted one day apart.



Selected body temperature (T_{sel})

This experiment was conducted in a cold room in which temperature was maintained at 18°C. I fitted four steel temperature gradient troughs ($L \times W \times H$: 98×30×30cm³) with 3-cm-depth potting soil substrate in the room. Two ceramic heat lamps (250W and 150W, respectively) were suspended at one end and 1/4 length, respectively, of each trough as heat sources, to create a thermal gradient ranged from 18 to 60°C. Lizards would be moved from growth chamber, and randomly placed into troughs at 0700 hour, one in each. They were free to move around within troughs. At 1500 hour, I measured the body temperatures of lizards as their selected body temperatures (T_{sel}), and replaced the lizards back to its housing chamber. The trial was repeated on the second day, so the selected body temperature was measured twice for

each lizard. I used the mean of the two readings as the selected body temperature (Ji et al., 1996; Ji et al., 1997; Xu et al., 1999; Du et al., 2000; Chen et al., 2003; Zhang and Ji, 2004).



Morphological measurement

I recorded 13 morphological variables for each lizard using an electronic vernier caliper. I measured: head length (HL, measured from quadrate to the tip of snout), head width (HW, the distance between jaw joints on each sides), head height (HH, measured from lower dentary to the parietal), body width (BW, measured from the longest distance between each side of body), body height (BH, longest distance between dorsal and ventral), snout-ventral length (SVL, measured from the cloacal opening to the tip of snout), tail length (TL, measured from cloacal opening to the tip of tail), right forelimb length (Flimb, measured from the upper arm joint to wrist), right forelimb palm length (Fpalm, measured from wrist to the base of longest toe), length of the longest toe of right forelimb (Ftoe, measured from toe base to tip, claws were not included), right hindlimb length (Hlimb, measured from the upper leg joint to ankle), right hindlimb palm length (Hpalm, measured from wrist to the base of longest toe), length of the longest toe of right hindlimb (Htoe, measured from toe base to tip, claws were not included).



Constructing the thermal performance curve

There were six body temperature-specific average sprint speeds for each lizard. First, I transformed the absolute average sprint speeds (cm/sec) into relative sprint speeds (%) by dividing each value by the highest value. Ideally, the six relative sprint speeds could be connected by a minimum convex polygon on a speed-by-temperature space (van Berkum 1985). If a sprint speed fell inside the polygon, it would be considered an underestimation, and replaced by a value interpolated from other values that fitted the polygon (van Berkum 1985). After I connected the six relative sprint speeds on the speed-by-temperature space, I joint them to thermal tolerance. Since the lizards that I measured sprint speeds and those I measured thermal tolerance were not the same individuals, I used universal CT_{\min} and CT_{\max} (mean CT_{\min} and mean CT_{\max} per sex per population per species) as the two end points of all thermal performance curves. After completing a thermal performance curve on the speed-by-temperature space, I extracted the lower and higher bound of body temperature at which lizard can sprint at 80% of its maximum (L_{80} and H_{80} , respectively) and 95% of its maximum (L_{95} and H_{95} , respectively). From them, I obtained two performance breadth readings: B_{80} and B_{95} , calculated as the difference between L_{80} and H_{80} , and between L_{95} and H_{95} , respectively. Finally, T_o , defined as the body temperature at which individual

performance is at maximum, was calculated as the midpoint of the B_{95} . Following the same procedures, I also constructed the thermal performance curve based on the six body temperature-specific maximum jump distances for each lizard.

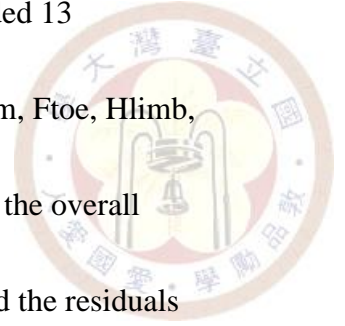


Statistical analyses

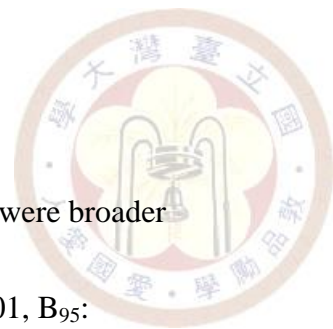
To test the effects of altitude and sex on the temperature-specific locomotor performance, thermal tolerance, and thermal profiles, I conducted two-way ANOVAs using Markov chain Monte Carlo (MCMC) generalized linear mixed models (implemented in the *R* 3.0.2 package R2WinBUGS running WinBUGS 1.4.3). With priors set at 'uninformative' and intercept set at 'lowland female', I ran three parallel MCMC sampling chains of 30000 iterations each, and saved one per 15 iterations as samples, a total of 6000 samples. Autocorrelation between successive stored iterations for all chains were low ($ACF < 0.1$ in all chains). For all parameters (H_{95} , L_{95} , H_{80} , L_{80} , B_{95} , B_{80} , T_o) I tested, the 3 chains (models) showed sufficient convergence ($Rhat < 1.05$ in all parameters). I carried out permutation t-tests (5000 permutations) to evaluate the differences between two types of locomotion in parameters of thermal sensitivity. I also used permutation t-tests (5000 permutations) to evaluate the differences between thermal profiles (T_b , T_e and T_{sel}).

I generated size-independent estimates of morphological traits by the following

procedures. First, I performed a principal component analysis that included 13 morphological variables (HL, HW, HH, BW, BH, SVL, TL, Flimb, Fpalm, Ftoe, Hlimb, Hpalm, Htoe), and used the first principal component (PC1) to represent the overall body size. I regressed each morphological variable against PC1, and used the residuals against regression line as size-independent estimates of morphological traits (standardized traits, hereafter). I used two-way ANOVAs to compare the standardized traits between two altitudinal populations and sexes.



Results



Thermal sensitivity of sprint speed

In *Japalura swinhonis*, both B_{80} and B_{95} of mid-altitude population were broader than those of lowland population (two-way ANOVAs, B_{80} : $pMCMC < 0.01$, B_{95} : $pMCMC < 0.05$, Table 1 and 9, Fig. 2). In addition, H_{95} , L_{95} , H_{80} , L_{80} , and T_o (Table 1) of mid-altitude population were lower than those of lowland population ($pMCMC < 0.001$ in all cases, Table 9, Fig. 2). However, there was no sexual difference in thermal sensitivity of sprint speed in *J. swinhonis*.

In *Japalura polygonata xanthostoma*, there was no difference in L_{95} and L_{80} between altitudes or sexes (two-way ANOVAs, Table 2 and 10, Fig. 3). There was no altitude effect in B_{95} ($pMCMC = 0.94$) or B_{80} ($pMCMC = 0.21$, Table 10). Sexual difference occurred in B_{95} ($pMCMC < 0.05$), and marginally in B_{80} ($pMCMC = 0.06$, Table 10). B_{95} or B_{80} of males was broader than that of females (Fig. 3). Interactions occurred between altitude and sex. In males, H_{95} , H_{80} , and T_o of mid-altitude population were lower than those of lowland population (H_{95} : $pMCMC < 0.001$, H_{80} : $pMCMC < 0.001$, T_o : $pMCMC < 0.01$); whereas there was no altitudinal difference in females (Table 17, Fig. 3).

Thermal sensitivity of jump distance

In *J. swinhonis*, there was no difference in L_{95} , B_{95} , and B_{80} between altitudes or sexes (Table 3 and 11, Fig. 4). H_{95} , H_{80} , L_{80} , and T_o of mid-altitude population were lower than those of lowland population (two-way ANOVAs, H_{95} : $pMCMC < 0.01$, H_{80} : $pMCMC < 0.01$, L_{80} : $pMCMC < 0.05$, T_o : $pMCMC < 0.05$, Table 11, Fig. 4). There was no sexual difference in jump distance (Table 11, Fig. 4).

In *J. polygonata xanthostoma*, L_{80} , L_{95} , and T_o of mid-altitude population were lower than those of lowland population (two-way ANOVA, L_{80} : $pMCMC < 0.01$, L_{95} : $pMCMC < 0.001$, T_o : $pMCMC < 0.01$, Table 4 and 12, Fig. 5); L_{80} of males was lower than that of females ($pMCMC < 0.05$, Table 12, Fig. 5). B_{80} of mid-altitude population was broader than that of lowland population ($pMCMC < 0.001$, Table 12, Fig. 5); B_{80} of males was broader than that of females ($pMCMC < 0.01$, Table 12, Fig. 5). There were interactions between altitude and sex in H_{95} and B_{95} (H_{95} : $pMCMC < 0.05$, B_{95} : $pMCMC < 0.05$, Table 12, Fig. 5). In males, H_{95} of mid-altitude population was lower than that of lowland population; whereas there was no altitudinal difference in females (Table 18, Fig. 5). B_{95} of mid-altitude population was broader than that of lowland population in males; whereas there was no altitudinal difference in females (Table 18, Fig. 5). There was no significant difference in H_{80} between altitudes or sexes (Table 12, Fig. 5).

Thermal tolerance

There was a significant difference in CT_{max} between altitudes in *J. swinhonis* (Table 5). CT_{max} of lowland population was higher than that of mid-altitude population (ANOVA, $pMCMC < 0.05$, Table 13, Fig. 6). In *J. polygonata xanthostoma* (Table 6), CT_{max} of males was higher than that of females, and CT_{min} of mid-altitude population was lower than that of lowland population (ANOVA, CT_{max} : $pMCMC < 0.01$, CT_{min} : $pMCMC < 0.001$, Table 14, Fig. 8, Fig. 9).

Thermal profiles

Field T_b and T_e of mid-altitude population were lower than those of lowland population in *J. swinhonis* (Two-way ANOVAs, T_b : $pMCMC < 0.001$, T_e : $pMCMC < 0.001$, Table 7 and 15). *J. polygonata xanthostoma* had a similar pattern. Field T_b and T_e of mid-altitude population were lower than those of lowland population (T_b : $pMCMC < 0.001$, T_e : $pMCMC < 0.01$, Table 8 and 16). However, in both species, there was no sexual difference in T_b or T_e (Table 15 and 16). In both species, there was no difference between altitudes or sexes in T_{sel} (Table 15 and 16).

Discussion



In Taiwan, both *Japalura swinhonis* and *J. polygonata xanthostoma* can be found in drastically different thermal environments. The mid-altitude populations inhabit thermal environments that have much lower and more variable mean temperatures (20.42 ± 0.43 and 16.75 ± 1.50 °C, respectively) than those of lowland populations (28.48 ± 1.09 and 27.68 ± 1.36 °C, respectively). Ectotherms in low body temperature states would have low level of locomotor performance. The impairment of locomotor performance might result in serious consequences for capturing prey (Greenwald, 1974; Avery et al., 1982), escaping predation (Webb, 1976; Christian and Tracy, 1981; Hirano and Rome, 1984), and other fitness-related functions. I observed that both *Japalura* species thermo-regulated by choosing micro thermal habitats (T_e , 25.09 ± 2.49 and 30.08 ± 1.29 °C for mid-altitude and lowland habitats, respectively, for *J. swinhonis*; 25.34 ± 5.21 and 28.72 ± 2.25 °C for mid-altitude and lowland habitats, respectively, for *J. polygonata xanthostoma*, Table 19) that had much higher temperature than the general areas could offer. They obtained field body temperatures (T_b) that were in fact significantly higher than T_e , which indicated the two species likely thermo-regulated not only behaviorally, but also physiologically. However, only the lowland individuals were able to reach T_b s that were close to the preferred body temperatures (T_{sel} , 31.19 ± 2.35 and 31.67 ± 2.14 °C for mid-altitude and lowland habitats, respectively, for *J. swinhonis*;

29.82±2.10 and 29.86±1.88°C for mid-altitude and lowland habitats, respectively, for *J. polygonata xanthostoma*, Table 7 and 8), which were similar between populations and sexes (Table 15 and 16) within species. Nevertheless, mid-altitudinal populations in both species have adapted their thermal physiology toward their respective thermal environments by changing the thermal sensitivity curves and critical temperature limits (Fig. 2–5). The hypothesis that mid-altitude and lowland population lizards have different thermal sensitivity of locomotor performance and thermal tolerance is supported.

While previous studies have failed to find intraspecific difference (Crowley, 1985; Van Damme et al., 1989), a study on eastern fence lizard, *Sceloporus undulates*, suggested that high level of insect densities in high-altitude may allow successful foraging despite the impairment of locomotor performance (Crowley, 1985). Moreover, the reduced predator pressure enhanced the survivorship at high elevations and latitudes in lizards may also contribute to different strength of the relationships between locomotor performance and fitness among populations (Tinkle, 1969; Pianka, 1970; Ballinger et al., 1979; Schall and Pianka, 1980). My results suggest that *J. swinhonis* and *J. polygonata xanthostoma* in mid-altitude and lowland might have same prey availability and predator pressure. Hence, they evolve adaptive thermal sensitivity of locomotor performance under mid-altitude thermal habitat where temperature is lower

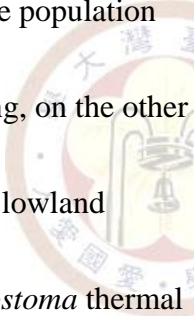
and variable.



Intraspecific comparison

I found that generally, several, if not all, parameters of the thermal sensitivity curves and critical temperature limits of the mid-latitude populations are lower (in H_{80} , H_{95} , L_{80} , L_{95} , T_o , CT_{max} and CT_{min}) and/or broader (in B_{80} and B_{95}) than those of the lowland populations. This is particularly true in *J. swinhonis*. Both in sprinting and jumping, thermal optimum (T_o) of mid-altitude *J. swinhonis* population is lower than that of lowland population. Moreover, performance breadth (B_{80}) of mid-altitude population not only shifts to the cold end of thermal sensitivity curve, but also is broader than that of lowland population. The effect of altitude on B_{80} occurs significantly in sprinting (Table 9), but not jumping (Table 11), while the trends are in the same direction (Table 1 and 3). Since B_{80} of jumping is generally broader than that of sprinting (Table 20), it indicates that jumping is less sensitive to body temperature than sprinting is in *J. swinhonis*. This is likely due to the weak influence on fitness by jumping (Huey and Kingsolver, 1993), and may contribute to different evolutionary patterns between sprinting and jumping.

Compared to *J. swinhonis*, *J. polygonata xanthostoma* showed a different pattern of the thermal sensitivity of locomotor performance. The effect of altitude is not as

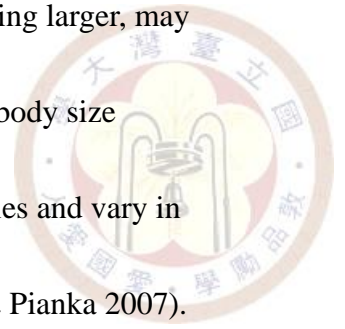


ubiquitous on the former as on the latter species. In sprinting, mid-altitude population has lower T_o than lowland population only in males (Table 10). In jumping, on the other hand, mid-altitude population has broader B_{80} and lower T_o than those of lowland population in both sexes (Table 12). It seems that in *J. polygonata xanthostoma* thermal sensitivity of jump distance is more adaptive than sprint speed to the thermal environment. It has been suggested that lizards prefer different types of locomotion when temperature resource is limited (Ibarguengoytia et al., 2007; Aguilar and Cruz, 2010; Fernandez et al., 2011). *J. polygonata xanthostoma* might prefer jumping to sprinting while the thermal quality of habitat is low. I expect that *J. polygonata xanthostoma* use more jumping movements in the mid-altitude than lowland habitats. Unfortunately, the frequency of each types of locomotion which *J. polygonata xanthostoma* used in natural circumstances is unclear to test such a prediction.

Intersexual comparison

Both *J. swinhonis* and *J. polygonata xanthostoma* are sexually dimorphic, with males having larger body sizes than females, particularly in the former species. Individuals with large body size have a small volume to surface area ratio, the thermal inertia of the bodies (trend of a body to resist to changes in its temperature) should be high. That is, they take longer to reach desired body temperature from exterior heat

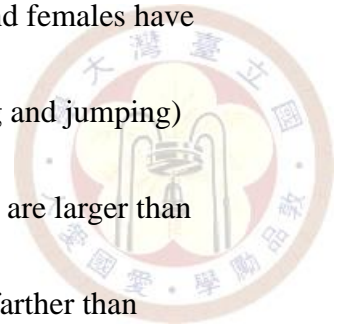
source, yet could retain body heat longer. Thus, I expect male lizards, being larger, may be able to thermo-regulate more effectively than females. Regardless of body size differences, different sexes could also have different physiological abilities and vary in thermoregulation needs due to differences in reproductive roles (Huey & Pianka 2007).



For example, males are territorial and often fight between individuals. Previous studies revealed that dominance correlates with activity level in lizards (Brackin, 1978) and activity level are related to locomotor performance (Bennett et al., 1984; Hertz et al., 1988; Garland et al., 1990). Thus, males and females could have different field body temperatures (T_b) and T_{sel} , and thermal sensitivities.

Although I did not detected sexual difference in T_b or T_{sel} , I did observe sexual differences in thermal sensitivity. As stated above, in *J. polygonata xanthostoma*, I found altitudinal difference in T_o of sprint speed occurred only in males. In addition, males have broader B_{80} in both sprint speed (though marginally) and jump distance (Table 10 and 12), and higher CT_{max} than those of females in both altitudinal populations (Table 14). It suggested that the adaptation of thermal sensitivity to local thermal environments is likely constrained for *J. polygonata xanthostoma* females, especially in mid-altitude. Therefore, females potentially use different strategies or change active period for daily activities (Lailvaux et al., 2003). Interestingly, *J. swinhonis*, with a much stronger sexually dimorphism than *J. polygonata xanthostoma*,


did not show any sexual difference in thermal physiology. Both males and females have the same thermal sensitivity of locomotor performance (in both sprinting and jumping) and thermal tolerance (Table 9, 11 and 13). Since all body parts of males are larger than those of females (Kuo et al., 2009), enabling males run faster and jump farther than females. Overall, the hypothesis that *J. swinhonis* and *J. polygonata xanthostoma* have sexual difference in thermal sensitivity of locomotor performance, thermal tolerance and thermal profiles is partially supported.



Interspecific comparison

As I have discussed in previous paragraphs, *J. swinhonis* and *J. polygonata xanthostoma* revealed different patterns in thermal sensitivity of locomotor performance. Generally, *J. swinhonis* has adaptive thermal physiological changes in sprinting while *J. polygonata xanthostoma* has changes in jumping. Such a difference could be explained by different habitat types (Shan, 2013) which may affect locomotor ability (Losos and Sinervo, 1989; Spezzano and Jayne, 2004). *J. swinhonis* occurs in wooded areas with abundant canopy gaps, while *J. polygonata xanthostoma* in forested areas with relatively closed canopy (Tao, 2013). Although sprinting is important to both arboreal lizards for escaping predation and foraging on the trunk, *J. polygonata xanthostoma* has more opportunity to use jump ability in its forested habitats, which often have shrubby

undergrowth.



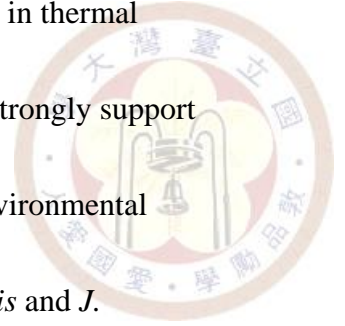
The patterns of thermal tolerance differ between the two species. Mid-altitude *J. polygonata xanthostoma* has lower critical thermal minimum (CT_{\min}) than that of lowland population (Table 14), whereas *J. swinhonis* has no difference in CT_{\min} between two altitudinal populations (Table 13). It might be attributed to the fact that the mean temperature in Mingchih Forest Recreation Area from December to March can drop below the CT_{\min} of *J. polygonata xanthostoma*. The winter temperature can be a strong selective force. In contrary, *J. swinhonis* has higher CT_{\max} of lowland population than mid-altitude population. *J. swinhonis* prefer relatively open areas which have high temperature, particularly during the breeding season. The species in lowland might be often confronted by environmental temperatures that are very close to CT_{\max} . Hence, an adaptive shift in CT_{\max} is important to *J. swinhonis*. Such a finding of geographic difference in thermal tolerance is also found in several studies (Miller and Packard, 1977; Hertz, 1979a; Hertz et al., 1979; Hertz and Huey, 1981), but not others (Huey and Webster, 1976; Hertz, 1979b; Gvozdik and Castilla, 2001). Nevertheless, thermal tolerance may respond to not only habitat temperature but also other factors such as microclimate, seasonal cycle and diet (Lutterschmidt and Hutchison, 1997b; Leal and Gunderson, 2012), and should be explored further.

Regarding thermal profiles, *J. swinhonis* has higher selected body temperature (T_{sel})


and T_b compared to those of *J. polygonata xanthostoma* (Table 23, 24, 25 and 26). It indicates that *J. swinhonis* prefer higher temperature than *J. polygonata xanthostoma*. It conforms to the fact that *J. swinhonis* often occurs in relatively open areas. Although both *J. swinhonis* and *J. polygonata xanthostoma* have changed thermal sensitivity curves of locomotor performance to compensate for the challenge of mid-altitude, there is no difference in T_{sel} between mid-altitude population and lowland population (Table 15 and 16). Numerous species of reptiles have been reported that temporal, spatial variation and individual status may affect T_{sel} (Gatten, 1974; Ellner and Karasov, 1993; Christian and Bedford, 1995; Andrews, 1998; Firth and Belan, 1998). Why is there no intraspecific difference in T_{sel} despite different thermal habitats? A possibility is that lizards selected their preferred body temperature may not only consider the locomotor performance but other physiological functions which might have different thermal sensitivity curve, such as food assimilation and immune function (Van Damme et al., 1991; Ji et al., 1996; Angilletta et al., 2002). Overall, the hypothesis that *J. swinhonis* and *J. polygonata xanthostoma* have different extent of thermal adaptation across altitudes is supported.

Conclusion

In this thesis, I reported interspecific, intraspecific, and sexual variations in thermal physiology of *J. swinhonis* and *J. polygonata xanthostoma*. The results strongly support the labile view of the evolution of thermal physiology in ectotherms. Environmental temperatures have strongly influenced thermal physiology of *J. swinhonis* and *J. polygonata xanthostoma*, shaping their thermal sensitivity curve of locomotor performance and thermal tolerance. The extent of adaptation between different types of locomotion may vary with species and sex. Future work should focus on the escape and foraging behavior in the field environment to evaluate the differences between sexes, species and population. Furthermore, other environmental factors, prey availability and predator pressure of habitat should be taken into consideration.



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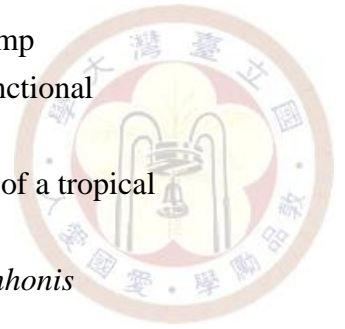
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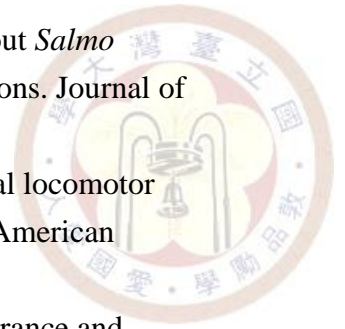
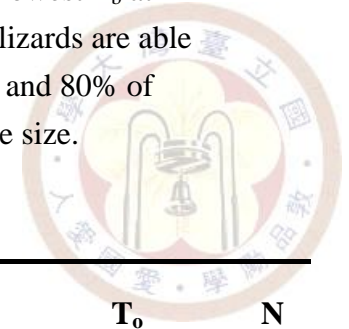
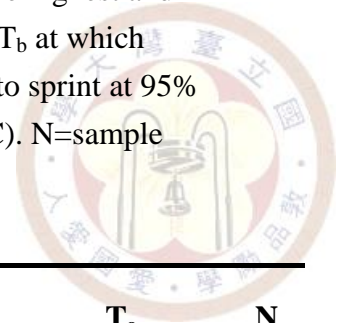


Table 1. Parameters related to the thermal sensitivity of sprint speed in *Japalura swinhonis*. H₉₅ and L₉₅ are the highest and lowest T_b at which lizards are able to sprint at 95% of maximum speed, respectively. H₈₀ and L₈₀ are the highest and lowest T_b at which lizards are able to sprint at 80% of maximum speed, respectively. B₉₅ and B₈₀ are the ranges of T_b at which lizards are able to sprint at 95% and 80% of maximum speed, respectively. T_o is the T_b at which lizards sprint at maximum speed. Values give mean±1se (°C). N=sample size.



Altitude	Sex	H₉₅	L₉₅	H₈₀	L₈₀	B₉₅	B₈₀	T_o	N
Mid-altitude	Male	32.98 ± 0.36	29.10 ± 0.40	34.90 ± 0.20	24.94 ± 0.37	3.88 ± 0.37	9.96 ± 0.45	31.04 ± 0.33	27
	Female	32.43 ± 0.45	27.40 ± 0.48	34.76 ± 0.24	23.54 ± 0.38	5.03 ± 0.52	11.23 ± 0.43	29.91 ± 0.39	26
Lowland	Male	33.85 ± 0.34	30.95 ± 0.48	35.55 ± 0.12	26.79 ± 0.52	2.90 ± 0.30	8.76 ± 0.51	32.40 ± 0.39	25
	Female	34.17 ± 0.26	30.33 ± 0.41	35.66 ± 0.09	26.44 ± 0.42	3.84 ± 0.38	9.28 ± 0.49	32.25 ± 0.29	29

Table 2. Parameters related to the thermal sensitivity of sprint speed in *Japalura polygonata xanthostoma*. H₉₅ and L₉₅ are the highest and lowest T_b at which lizards are able to sprint at 95% of maximum speed, respectively. H₈₀ and L₈₀ are the highest and lowest T_b at which lizards are able to sprint at 80% of maximum speed, respectively. B₉₅ and B₈₀ are the ranges of T_b at which lizards are able to sprint at 95% and 80% of maximum speed, respectively. T_o is the T_b at which lizards sprint at maximum speed. Values give mean±1se (°C). N=sample size.



Altitude	Sex	H ₉₅	L ₉₅	H ₈₀	L ₈₀	B ₉₅	B ₈₀	T _o	N
Mid-altitude	Male	32.26 ± 0.49	28.40 ± 0.52	35.01 ± 0.23	25.10 ± 0.47	3.86 ± 0.43	9.91 ± 0.48	30.33 ± 0.45	17
	Female	34.32 ± 0.34	31.01 ± 0.55	35.71 ± 0.11	26.57 ± 0.47	3.31 ± 0.42	9.14 ± 0.47	32.66 ± 0.41	21
Lowland	Male	34.57 ± 0.27	30.10 ± 0.52	35.77 ± 0.12	26.35 ± 0.54	4.47 ± 0.47	9.42 ± 0.54	32.34 ± 0.34	25
	Female	34.14 ± 0.24	30.88 ± 0.44	35.62 ± 0.09	27.35 ± 0.48	3.26 ± 0.32	8.28 ± 0.45	32.51 ± 0.32	28

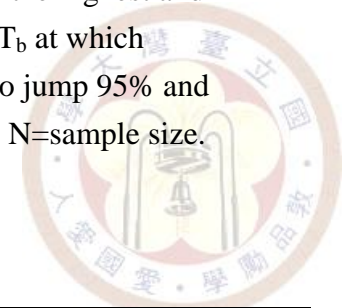
Table 3. Parameters related to the thermal sensitivity of jump distance in *Japalura swinhonis*. H₉₅ and L₉₅ are the highest and lowest T_b at

which lizards are able to jump 95% of maximum distance, respectively. H_{80} and L_{80} are the highest and lowest T_b at which lizards are able to jump 80% of maximum distance, respectively. B_{95} and B_{80} are the ranges of T_b at which lizards are able to jump 95% and 80% of maximum distance, respectively. T_0 is the T_b at which lizards jump maximum distance. Values give mean \pm 1 se ($^{\circ}$ C). N=sample size.



Altitude	Sex	H₉₅	L₉₅	H₈₀	L₈₀	B₉₅	B₈₀	T₀	N
Mid-altitude	Male	32.73 \pm 0.38	27.98 \pm 0.63	34.70 \pm 0.21	23.71 \pm 0.64	4.75 \pm 0.43	10.99 \pm 0.64	30.35 \pm 0.47	27
	Female	33.08 \pm 0.39	28.40 \pm 0.54	34.84 \pm 0.22	23.53 \pm 0.54	4.68 \pm 0.41	11.31 \pm 0.57	30.74 \pm 0.42	26
Lowland	Male	34.16 \pm 0.38	30.38 \pm 0.53	35.52 \pm 0.19	25.31 \pm 0.65	3.77 \pm 0.41	10.21 \pm 0.64	32.27 \pm 0.41	25
	Female	34.44 \pm 0.19	29.65 \pm 0.44	35.68 \pm 0.08	25.32 \pm 0.58	4.79 \pm 0.46	10.35 \pm 0.58	32.05 \pm 0.25	29

Table 4. Parameters related to the thermal sensitivity of jump distance in *Japalura polygonata xanthostoma*. H₉₅ and L₉₅ are the highest and lowest T_b at which lizards are able to jump 95% of maximum distance, respectively. H₈₀ and L₈₀ are the highest and lowest T_b at which lizards are able to jump 80% of maximum distance, respectively. B₉₅ and B₈₀ are the ranges of T_b at which lizards are able to jump 95% and 80% of maximum distance, respectively. T_o is the T_b at which lizards jump maximum distance. Values give mean ± 1 se (°C). N=sample size.



Altitude	Sex	H₉₅	L₉₅	H₈₀	L₈₀	B₉₅	B₈₀	T_o	N
Mid-altitude	Male	33.20 ± 0.46	28.69 ± 0.79	35.33 ± 0.20	23.14 ± 0.57	4.51 ± 0.59	12.19 ± 0.50	30.95 ± 0.58	17
	Female	34.42 ± 0.26	29.09 ± 0.53	35.74 ± 0.08	23.43 ± 0.48	5.33 ± 0.53	12.31 ± 0.48	31.76 ± 0.32	21
Lowland	Male	34.73 ± 0.23	30.13 ± 0.53	35.74 ± 0.17	24.06 ± 0.60	4.60 ± 0.54	11.68 ± 0.63	32.43 ± 0.30	25
	Female	34.65 ± 0.24	31.52 ± 0.40	35.82 ± 0.06	26.17 ± 0.65	3.13 ± 0.37	9.65 ± 0.67	33.08 ± 0.27	28

Table 5. The thermal tolerance of *Japalura swinhonis*. CT_{max} and CT_{min} are the highest and lowest T_b at which lizards loss righting response, respectively. Thermal tolerance is the T_b width from CT_{max} to CT_{min} . Values are mean \pm 1se ($^{\circ}C$) for two altitudinal populations and two sexes.

Altitude	Sex	Thermal tolerance	CT_{max}	CT_{min}	N
Mid-altitude	Male	31.36 \pm 0.46	39.54 \pm 0.38	8.16 \pm 0.29	28
	Female	30.30 \pm 0.46	39.18 \pm 0.35	8.88 \pm 0.30	26
Lowland	Male	31.73 \pm 0.44	40.34 \pm 0.20	8.63 \pm 0.29	26
	Female	31.12 \pm 0.28	40.14 \pm 0.20	9.02 \pm 0.27	27

Table 6. The thermal tolerance of *Japalura polygonata xanthostoma*. CT_{max} and CT_{min} are the highest and lowest T_b at which lizards loss righting response, respectively. Thermal tolerance is the T_b width from CT_{max} to CT_{min} . Values are mean \pm 1se ($^{\circ}C$) for two altitudinal populations and two sexes.

Altitude	Sex	Thermal tolerance	CT_{max}	CT_{min}	N
Mid-altitude	Male	33.40 \pm 0.43	40.34 \pm 0.24	6.94 \pm 0.30	17
	Female	33.03 \pm 0.54	40.15 \pm 0.22	7.12 \pm 0.36	22
Lowland	Male	32.75 \pm 0.40	40.73 \pm 0.21	7.98 \pm 0.27	26
	Female	31.34 \pm 0.43	39.97 \pm 0.18	8.63 \pm 0.30	25

Table 7. The thermal profile of *Japalura swinhonis*. Field T_b is the body temperature at which lizards achieve in the field. T_e is the operative temperature (or environmental temperature). T_{sel} is the temperature lizards select under an unconstrained condition. Values are mean \pm 1se ($^{\circ}$ C) for two altitudinal populations and two sexes.

Altitude	Sex	Field T_b	T_e	N	T_{sel}	N
Mid-altitude	Male	26.32 \pm 0.33	25.19 \pm 0.36	33	31.10 \pm 0.47	25
	Female	25.96 \pm 0.37	24.95 \pm 0.59	26	31.19 \pm 0.48	25
Lowland	Male	32.02 \pm 0.25	30.35 \pm 0.23	35	31.93 \pm 0.41	26
	Female	31.92 \pm 0.24	29.82 \pm 0.20	37	31.49 \pm 0.46	24

Table 8. The thermal profile of *Japalura polygonata xanthostoma*. Field T_b is the body temperature at which lizards achieve in the field. T_e is the operative temperature (or environmental temperature). T_{sel} is the temperature lizards select under an unconstrained condition. Values are mean \pm 1se ($^{\circ}$ C) for two altitudinal populations and two sexes.

Altitude	sex	Field T_b	T_e	N	T_{sel}	N
Mid-altitude	Male	26.73 \pm 0.61	25.70 \pm 0.99	12	30.70 \pm 0.44	17
	Female	26.93 \pm 0.82	25.00 \pm 0.84	13	29.11 \pm 0.45	22
Lowland	Male	30.02 \pm 0.26	28.29 \pm 0.36	37	30.12 \pm 0.29	26
	Female	30.32 \pm 0.33	29.34 \pm 0.45	25	29.58 \pm 0.45	25

Table 9. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex on parameters related to the thermal sensitivity of sprint speed in *Japalura swinhonis*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Thermal Sensitivity Parameters		Mean	95% CI	pMCMC
H ₉₅	Intercept (lowland, female)	34.16	33.49 to 34.84	<0.001
	Altitude (lowland→mid-altitude)	-1.73	-2.71 to -0.73	<0.001
	Sex (female→male)	-0.31	-1.34 to 0.69	0.55
	Altitude*Sex	0.87	-0.64 to 2.29	0.22
L ₉₅	Intercept (lowland, female)	30.33	29.50 to 31.21	<0.001
	Altitude (lowland→mid-altitude)	-2.94	-4.15 to -1.66	<0.001
	Sex (female→male)	0.63	-0.65 to 1.89	0.33
	Altitude*Sex	1.06	-0.67 to 2.86	0.25
H ₈₀	Intercept (lowland, female)	35.66	35.35 to 35.97	<0.001
	Altitude (lowland→mid-altitude)	-0.89	-1.34 to -0.42	<0.001
	Sex (female→male)	-0.11	-0.57 to 0.39	0.65
	Altitude*Sex	0.24	-0.45 to 0.92	0.47
L ₈₀	Intercept (lowland, female)	26.44	25.63 to 27.28	<0.001
	Altitude (lowland→mid-altitude)	-2.89	-4.07 to -1.66	<0.001
	Sex (female→male)	0.35	-0.89 to 1.54	0.57
	Altitude*Sex	1.05	-0.67 to 2.74	0.21
B ₉₅	Intercept (lowland, female)	3.84	3.09 to 4.64	<0.001
	Altitude (lowland→mid-altitude)	1.21	0.07 to 2.28	<0.05
	Sex (female→male)	-0.93	-2.04 to 0.18	0.09
	Altitude*Sex	-0.24	-1.88 to 1.41	0.76
B ₈₀	Intercept (lowland, female)	9.25	8.40 to 10.13	<0.001
	Altitude (lowland→mid-altitude)	1.98	0.75 to 3.29	<0.01
	Sex (female→male)	-0.49	-1.72 to 0.77	0.47
	Altitude*Sex	-0.78	-2.66 to 1.02	0.41
T ₀	Intercept (lowland, female)	32.24	31.60 to 32.92	<0.001
	Altitude (lowland→mid-altitude)	-2.33	-3.27 to -1.30	<0.001
	Sex (female→male)	0.16	-0.80 to 1.11	0.75
	Altitude*Sex	0.96	-0.40 to 2.28	0.16

Table 10. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex on parameters related to the thermal sensitivity of sprint speed in *Japalura polygonata xanthostoma*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Thermal Sensitivity Parameters		Mean	95% CI	pMCMC
H ₉₅	Intercept (lowland, female)	34.15	33.59 to 34.70	<0.001
	Altitude (lowland→mid-altitude)	0.17	-0.70 to 1.02	0.71
	Sex (female→male)	0.41	-0.47 to 1.25	0.32
	Altitude*Sex	-2.48	-3.79 to -1.18	<0.001
L ₉₅	Intercept (lowland, female)	30.87	29.94 to 31.80	<0.001
	Altitude (lowland→mid-altitude)	0.14	-1.25 to 1.52	0.86
	Sex (female→male)	-0.77	-2.11 to 0.63	0.24
	Altitude*Sex	-1.85	-4.08 to 0.18	0.07
H ₈₀	Intercept (lowland, female)	35.63	35.39 to 35.86	<0.001
	Altitude (lowland→mid-altitude)	0.09	-0.29 to 0.43	0.63
	Sex (female→male)	0.14	-0.20 to 0.50	0.40
	Altitude*Sex	-0.85	-1.38 to -0.31	<0.01
L ₈₀	Intercept (lowland, female)	27.35	26.45 to 28.30	<0.001
	Altitude (lowland→mid-altitude)	-0.80	-2.26 to 0.66	0.28
	Sex (female→male)	-1.01	-2.35 to 0.31	0.14
	Altitude*Sex	-0.46	-2.58 to 1.54	0.66
B ₉₅	Intercept (lowland, female)	3.27	2.55 to 3.99	<0.001
	Altitude (lowland→mid-altitude)	0.06	-1.04 to 1.18	0.94
	Sex (female→male)	1.19	0.14 to 2.24	<0.05
	Altitude*Sex	-0.66	-2.27 to 1.06	0.43
B ₈₀	Intercept (lowland, female)	8.28	7.39 to 9.13	<0.001
	Altitude (lowland→mid-altitude)	0.85	-0.46 to 2.22	0.21
	Sex (female→male)	1.15	-0.07 to 2.50	0.06
	Altitude*Sex	-0.37	-2.45 to 1.68	0.70
T _o	Intercept (lowland, female)	32.52	31.83 to 33.17	<0.001
	Altitude (lowland→mid-altitude)	0.14	-0.87 to 1.12	0.78
	Sex (female→male)	-0.19	-1.19 to 0.83	0.68
	Altitude*Sex	-2.13	-3.62 to -0.62	<0.01

Table 11. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex on various parameters related to the thermal sensitivity of jump distance in *Japalura swinhonis*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Thermal Sensitivity Parameters		mean	95% CI	pMCMC
H ₉₅	Intercept (lowland, female)	34.43	33.77 to 35.08	<0.001
	Altitude (lowland→mid-altitude)	-1.34	-2.33 to -0.42	<0.01
	Sex (female→male)	-0.28	-1.22 to 0.69	0.56
	Altitude*Sex	-0.08	-1.41 to 1.26	0.89
L ₉₅	Intercept (lowland, female)	29.64	29.50 to 31.21	<0.001
	Altitude (lowland→mid-altitude)	-1.25	-2.70 to 0.28	0.10
	Sex (female→male)	0.74	-0.72 to 2.22	0.33
	Altitude*Sex	-1.16	-3.33 to 0.98	0.29
H ₈₀	Intercept (lowland, female)	35.68	35.33 to 36.02	<0.001
	Altitude (lowland→mid-altitude)	-0.84	-1.36 to -0.33	<0.01
	Sex (female→male)	-0.16	-0.66 to 0.36	0.52
	Altitude*Sex	0.02	-0.74 to 0.75	0.48
L ₈₀	Intercept (lowland, female)	25.32	24.16 to 26.52	<0.001
	Altitude (lowland→mid-altitude)	-1.75	-3.34 to -0.07	<0.05
	Sex (female→male)	-0.02	-1.79 to 1.76	0.99
	Altitude*Sex	0.15	-2.33 to 2.54	0.89
B ₉₅	Intercept (lowland, female)	4.78	3.97 to 5.64	<0.001
	Altitude (lowland→mid-altitude)	-0.10	-1.32 to 1.15	0.88
	Sex (female→male)	-1.02	-2.20 to 0.21	0.11
	Altitude*Sex	1.09	-0.69 to 2.86	0.22
B ₈₀	Intercept (lowland, female)	10.37	9.24 to 11.60	<0.001
	Altitude (lowland→mid-altitude)	0.94	-0.80 to 2.58	0.28
	Sex (female→male)	-0.17	-1.91 to 1.51	0.87
	Altitude*Sex	-0.14	-2.50 to 2.31	0.90
T ₀	Intercept (lowland, female)	32.03	31.27 to 32.77	<0.001
	Altitude (lowland→mid-altitude)	-1.31	-2.47 to -0.22	<0.05
	Sex (female→male)	0.24	-0.90 to 1.31	0.66
	Altitude*Sex	-0.61	-2.19 to 0.97	0.43

Table 12. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex on various parameters related to the thermal sensitivity of jump distance in *Japalura polygonata xanthostoma*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Thermal Sensitivity Parameters		mean	95% CI	pMCMC
H ₉₅	Intercept (lowland, female)	34.65	34.13 to 35.19	<0.001
	Altitude (lowland→mid-altitude)	-0.23	-1.02 to 0.61	0.55
	Sex (female→male)	0.07	-0.70 to 0.84	0.85
	Altitude*Sex	-1.28	-2.50 to -0.06	<0.05
L ₉₅	Intercept (lowland, female)	31.52	30.52 to 32.52	<0.001
	Altitude (lowland→mid-altitude)	-2.44	-3.94 to -1.00	<0.001
	Sex (female→male)	-1.37	-2.85 to 0.13	0.07
	Altitude*Sex	0.98	-1.38 to 3.26	0.37
H ₈₀	Intercept (lowland, female)	35.83	35.58 to 36.07	<0.001
	Altitude (lowland→mid-altitude)	-0.08	-0.44 to 0.30	0.63
	Sex (female→male)	-0.09	-0.41 to 0.27	0.62
	Altitude*Sex	-0.32	-0.87 to 0.20	0.24
L ₈₀	Intercept (lowland, female)	26.17	25.08 to 27.23	<0.001
	Altitude (lowland→mid-altitude)	-2.72	-4.41 to -1.04	<0.01
	Sex (female→male)	-2.12	-3.67 to -0.48	<0.05
	Altitude*Sex	1.79	-0.66 to 4.30	0.16
B ₉₅	Intercept (lowland, female)	3.13	0.46 to 4.05	<0.001
	Altitude (lowland→mid-altitude)	2.18	0.81 to 3.59	<0.001
	Sex (female→male)	1.47	0.15 to 2.82	<0.05
	Altitude*Sex	-2.25	-4.21 to -0.30	<0.05
B ₈₀	Intercept (lowland, female)	9.65	8.52 to 10.03	<0.001
	Altitude (lowland→mid-altitude)	2.65	0.94 to 4.40	<0.001
	Sex (female→male)	2.03	0.44 to 3.65	<0.01
	Altitude*Sex	-2.16	-4.63 to 0.39	0.07
T ₀	Intercept (lowland, female)	33.06	32.42 to 33.72	<0.001
	Altitude (lowland→mid-altitude)	-1.33	-2.27 to -0.35	<0.01
	Sex (female→male)	-0.64	-1.54 to 0.26	0.16
	Altitude*Sex	-0.14	-1.58 to 1.29	0.84

Table 13. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex on thermal tolerance in *Japalura swinhonis*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Parameter	mean	95% CI	pMCMC	
CT _{max}	Intercept (lowland, female)	40.15	39.55 to 40.71	<0.001
	Altitude (lowland→mid-altitude)	-0.97	-1.78 to -0.12	<0.05
	Sex (female→male)	0.20	-0.66 to 1.04	0.64
	Altitude*Sex	0.17	-0.99 to 1.34	0.76
CT _{min}	Intercept (lowland, female)	9.03	8.46 to 9.62	<0.001
	Altitude (lowland→mid-altitude)	-0.14	-0.99 to 0.69	0.74
	Sex (female→male)	-0.42	-1.24 to 0.41	0.34
	Altitude*Sex	-0.29	-1.47 to 0.92	0.60

Table 14. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex the thermal tolerance in *Japalura polygonata xanthostoma*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Parameter		Mean	95% CI	pMCMC
CT _{max}	Intercept (lowland, female)	39.96	39.56 to 40.35	<0.001
	Altitude (lowland→mid-altitude)	0.19	-0.39 to 0.79	0.50
	Sex (female→male)	0.78	0.22 to 1.34	<0.01
	Altitude*Sex	-0.59	-1.50 to 0.27	0.17
CT _{min}	Intercept (lowland, female)	8.63	8.02 to 9.21	<0.001
	Altitude (lowland→mid-altitude)	-1.50	-2.38 to -0.66	<0.001
	Sex (female→male)	-0.66	-1.47 to 0.16	0.12
	Altitude*Sex	0.47	-0.75 to 1.73	0.48

Table 15. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex on various parameters related to the thermal profiles in *Japalura swinhonis*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Parameter		Mean	95% CI	pMCMC
T _b	Intercept (lowland, female)	31.92	31.38 to 32.45	<0.001
	Altitude (lowland→mid-altitude)	-5.96	-6.82 to -5.11	<0.001
	Sex (female→male)	0.11	-0.68 to 0.90	0.80
	Altitude*Sex	0.25	-0.95 to 1.42	0.69
T _e	Intercept (lowland, female)	29.81	29.21 to 30.41	<0.001
	Altitude (lowland→mid-altitude)	-4.85	-5.87 to -3.89	<0.001
	Sex (female→male)	0.54	-0.37 to 1.41	0.22
	Altitude*Sex	-0.30	-1.66 to 1.06	0.64
T _{sel}	Intercept (lowland, female)	31.43	30.50 to 32.31	<0.001
	Altitude (lowland→mid-altitude)	-0.15	-1.41 to 1.11	0.78
	Sex (female→male)	0.45	-0.79 to 1.74	0.49
	Altitude*Sex	-0.62	-2.36 to 1.14	0.47

Table 16. Statistical results of two-way ANOVAs using MCMCglmm examining the effects of altitude and sex on various parameters related to the thermal profiles in *Japalura polygonata xanthostoma*. The mean values (in °C) indicate the strength and direction of the main effects and the interaction.

Parameter		Mean	95% CI	pMCMC
T _b	Intercept (lowland, female)	30.32	29.55 to 31.11	<0.001
	Altitude (lowland→mid-altitude)	-3.41	-4.68 to -2.10	<0.001
	Sex (female→male)	-0.29	-1.29 to 0.70	0.55
	Altitude*Sex	0.11	-1.74 to 1.97	0.90
T _e	Intercept (lowland, female)	29.35	27.97 to 30.66	<0.001
	Altitude (lowland→mid-altitude)	-3.14	-5.44 to -0.93	<0.01
	Sex (female→male)	-1.03	-2.72 to 0.72	0.25
	Altitude*Sex	0.54	-2.65 to 3.62	0.73
T _{sel}	Intercept (lowland, female)	29.58	28.80 to 30.35	<0.001
	Altitude (lowland→mid-altitude)	-0.47	-1.58 to 0.66	0.42
	Sex (female→male)	0.54	-0.51 to 1.63	0.33
	Altitude*Sex	1.05	-0.55 to 2.69	0.21

Table 17. Means and 95% confident intervals of the thermal sensitivity of sprint speed in *Japalura polygonata xanthostoma* that showed interaction between altitude and sex.

Parameter	Altitude	Sex	mean	95% CI
H ₉₅	Mid-altitude	Male	32.25 ^b	31.51 – 33.02
	Mid-altitude	Female	34.32 ^a	33.66 – 34.97
	Lowland	Male	34.56 ^a	33.96 – 35.18
	Lowland	Female	34.15 ^a	33.59 – 34.73
H ₈₀	Mid-altitude	Male	35.01 ^b	34.69 – 35.29
	Mid-altitude	Female	35.71 ^a	35.43 – 35.98
	Lowland	Male	35.77 ^a	35.52 – 36.02
	Lowland	Female	35.63 ^a	35.39 – 35.86
T _o	Mid-altitude	Male	30.34 ^b	29.49 – 31.18
	Mid-altitude	Female	32.34 ^a	31.90 – 33.43
	Lowland	Male	32.67 ^a	31.58 – 33.07
	Lowland	Female	32.52 ^a	31.83 – 33.17

Table 18. Means and 95% confident intervals of the thermal sensitivity of jump distance in *Japalura polygonata xanthostoma* that showed interaction between altitude and sex.

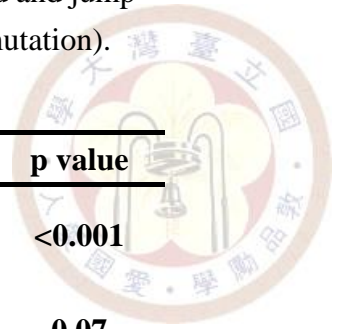
Parameter	Altitude	Sex	mean	95% CI
H ₉₅	Mid-altitude	Male	33.21 ^b	32.53 – 33.88
	Mid-altitude	Female	34.42 ^{ab}	33.80 – 35.03
	Lowland	Male	34.73 ^a	34.18 – 35.26
	Lowland	Female	34.65 ^a	34.13 – 35.19
B ₉₅	Mid-altitude	Male	4.54 ^{ab}	3.42 – 5.70
	Mid-altitude	Female	5.32 ^a	4.26 – 6.41
	Lowland	Male	4.61 ^{ab}	3.67 – 5.60
	Lowland	Female	3.13 ^b	2.22 – 4.05

Table 19. Comparison of field body temperature (T_b) and operative temperature (T_e) at mid-altitude and lowland in two *Japalura* lizards. Based on permutation t-tests (5000 permutation). Values are temperature \pm 1sd($^{\circ}$ C).

Species	Altitude	T_b	T_e	p value
<i>Japalura swinhonis</i>	Mid-altitude	26.17 \pm 1.89	25.09 \pm 2.49	<0.01
	Lowland	31.97 \pm 1.46	30.08 \pm 1.29	<0.001
<i>J. polygonata xanthostoma</i>	Mid-altitude	26.83 \pm 2.54	25.34 \pm 5.21	<0.05
	Lowland	30.14 \pm 1.59	28.72 \pm 2.25	<0.001

Table 20. Comparison of performance breadth (B_{80}) between sprint speed and jump distance in *Japalura swinhonis*. Based on permutation t-tests (5000 permutation). Values are temperature ($^{\circ}\text{C}$).

Species	Altitude	Jump distance	Sprint speed	p value
<i>J. swinhonis</i>	Mid-altitude	11.15	10.58	<0.001
	Lowland	10.29	9.01	0.07



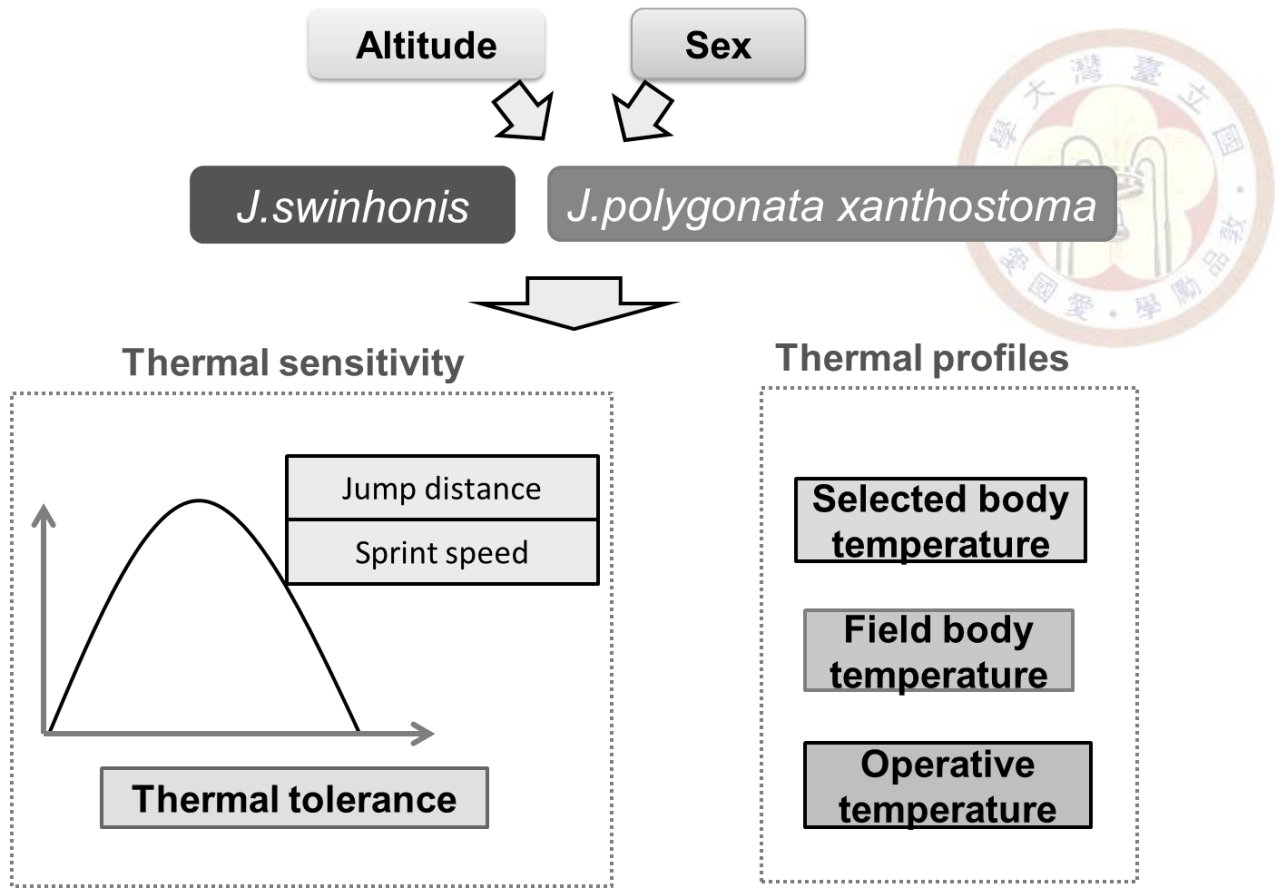


Figure 1. Concept map of the current study.

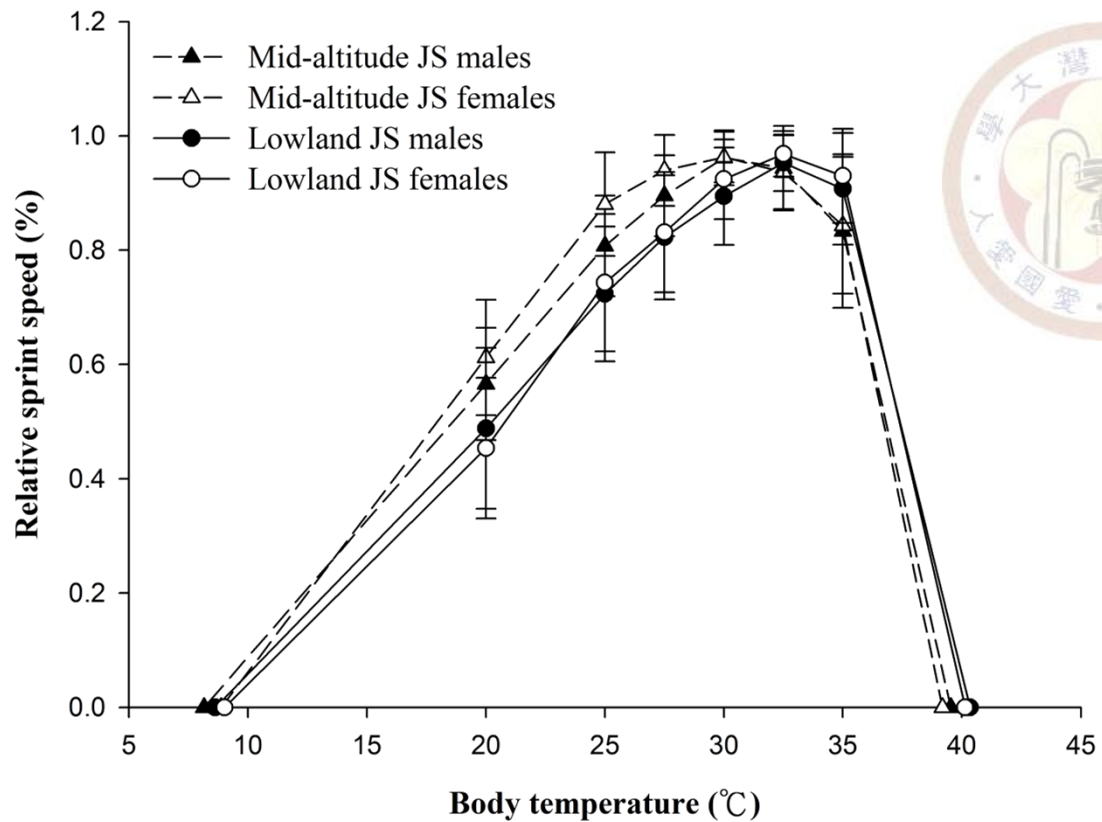


Figure 2. The thermal sensitivity curves of sprint speed in *Japalura swinhonis* (JS). Values at two ends are CT_{max} and CT_{min} , the highest and lowest body temperature at which lizards loss righting response, respectively. Values (mean \pm 1se) in between are temperature-specific relative sprint speed.

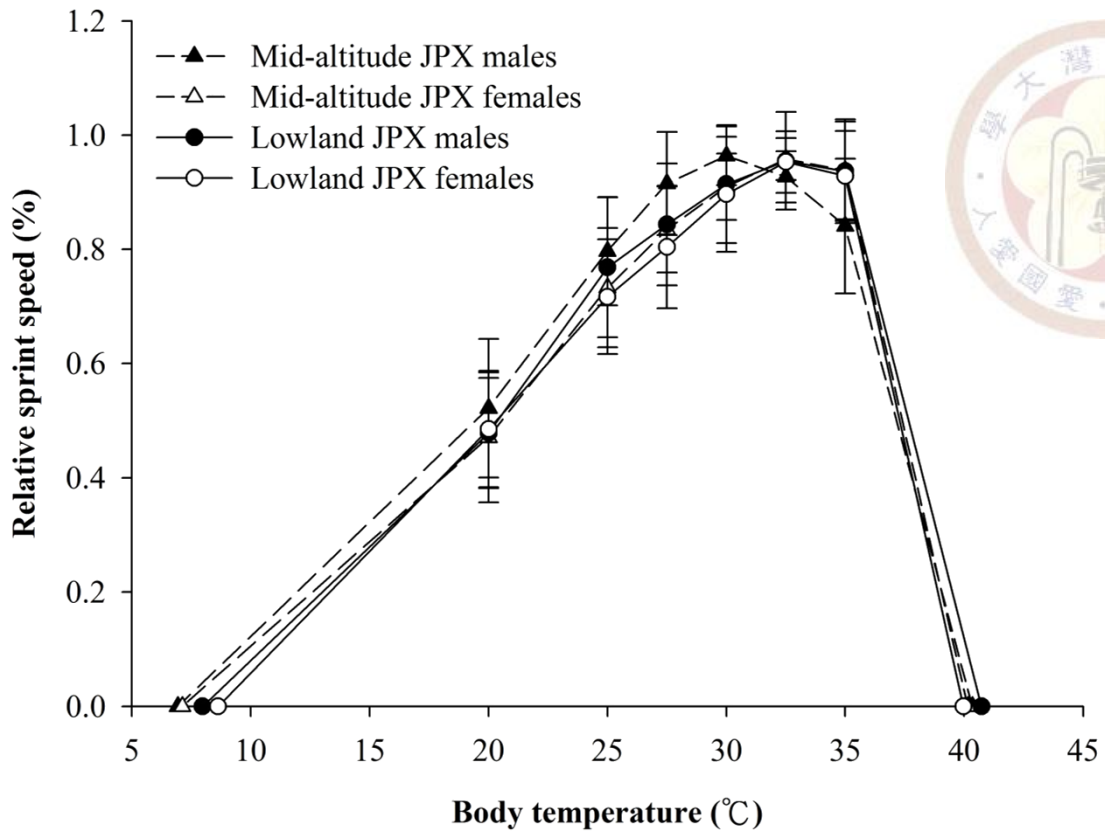


Figure 3. The thermal sensitivity curves of sprint speed in *Japalura polygonata xanthostom* (JPX). Values at two ends are CT_{max} and CT_{min} , the highest and lowest body temperature at which lizards loss righting response, respectively. Values (mean \pm 1se) in between are temperature-specific relative sprint speed.

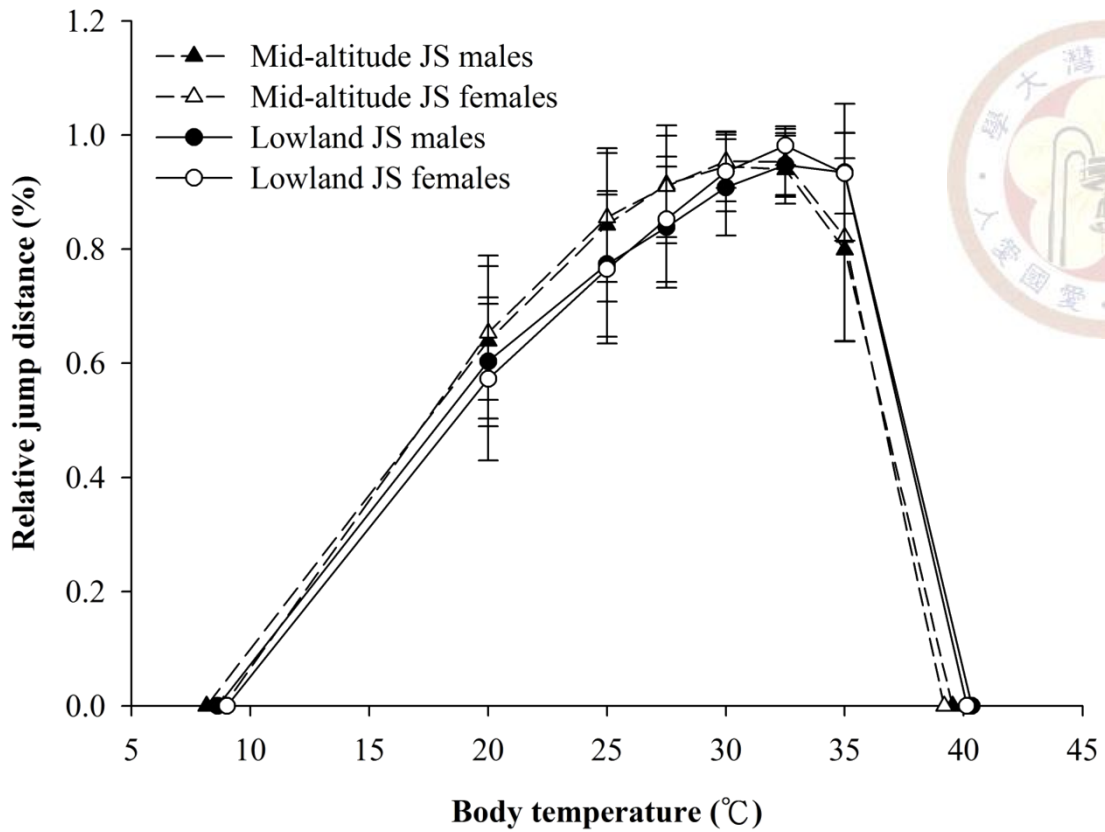


Figure 4. The thermal sensitivity curves of jump distance in *Japalura swinhonis* (JS). Values at two ends are CT_{max} and CT_{min} , the highest and lowest body temperature at which lizards loss righting response, respectively. Values (mean \pm 1se) in between are temperature-specific relative jump distance.

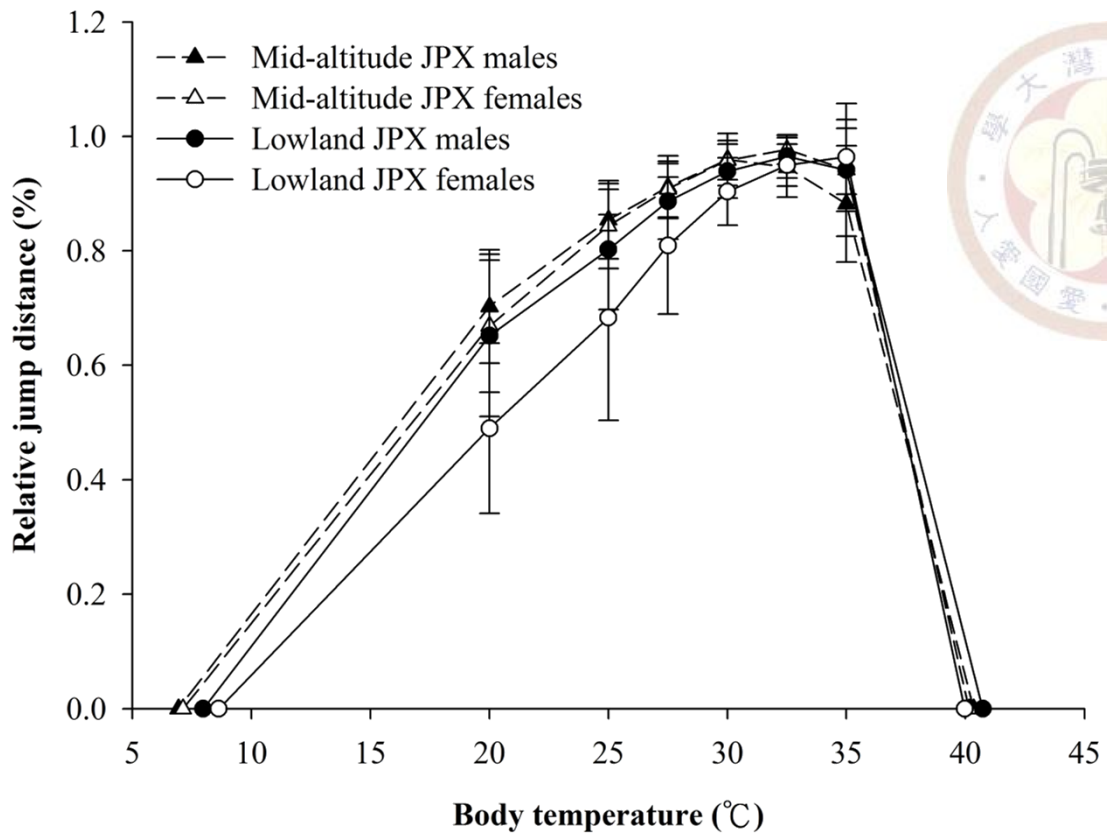


Figure 5. The thermal sensitivity curves of jump distance in *Japalura polygonata xanthostoma* (JPX). Values at two ends are CT_{max} and CT_{min} , the highest and lowest body temperature at which lizards loss righting response, respectively. Values (mean \pm 1se) in between are temperature-specific relative jump distance..

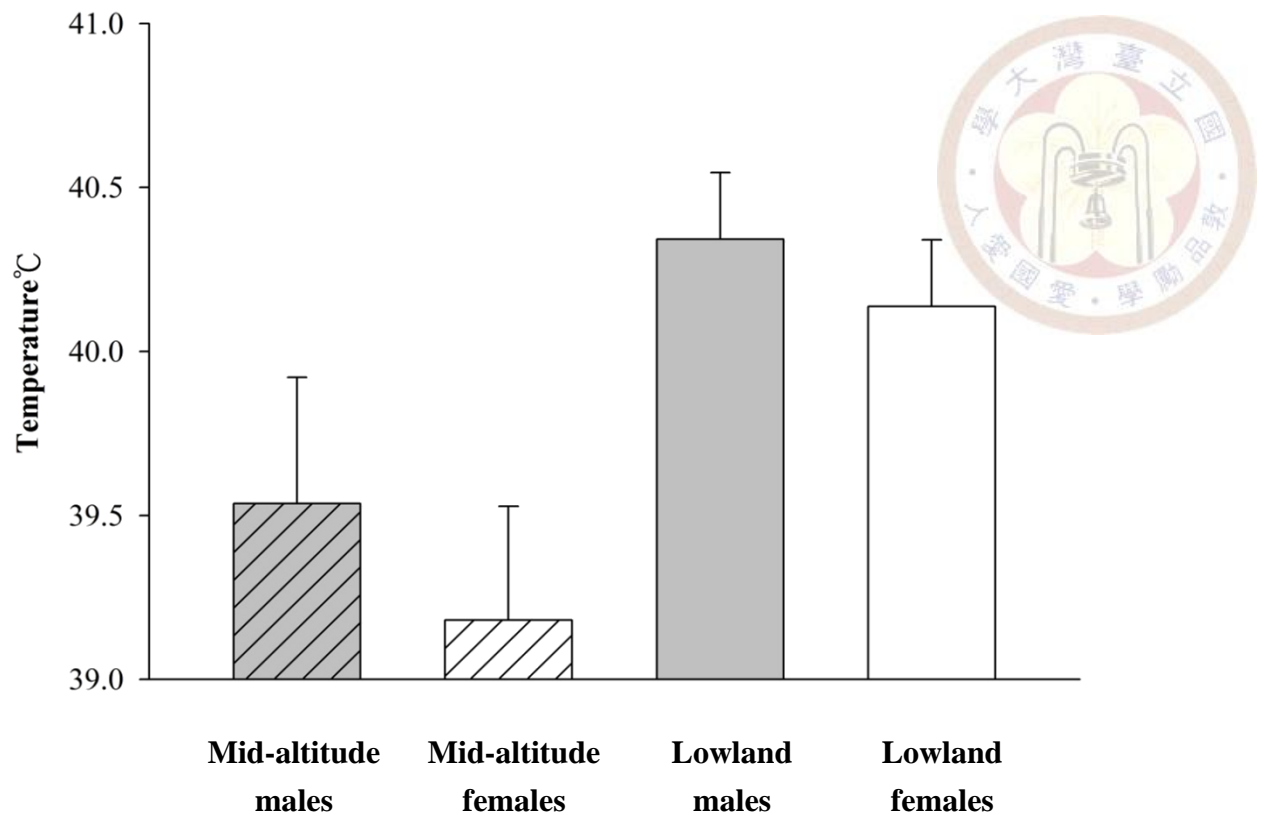


Figure 6. The critical thermal maximum of *Japalura swinhonis*. Values give mean \pm 1se.

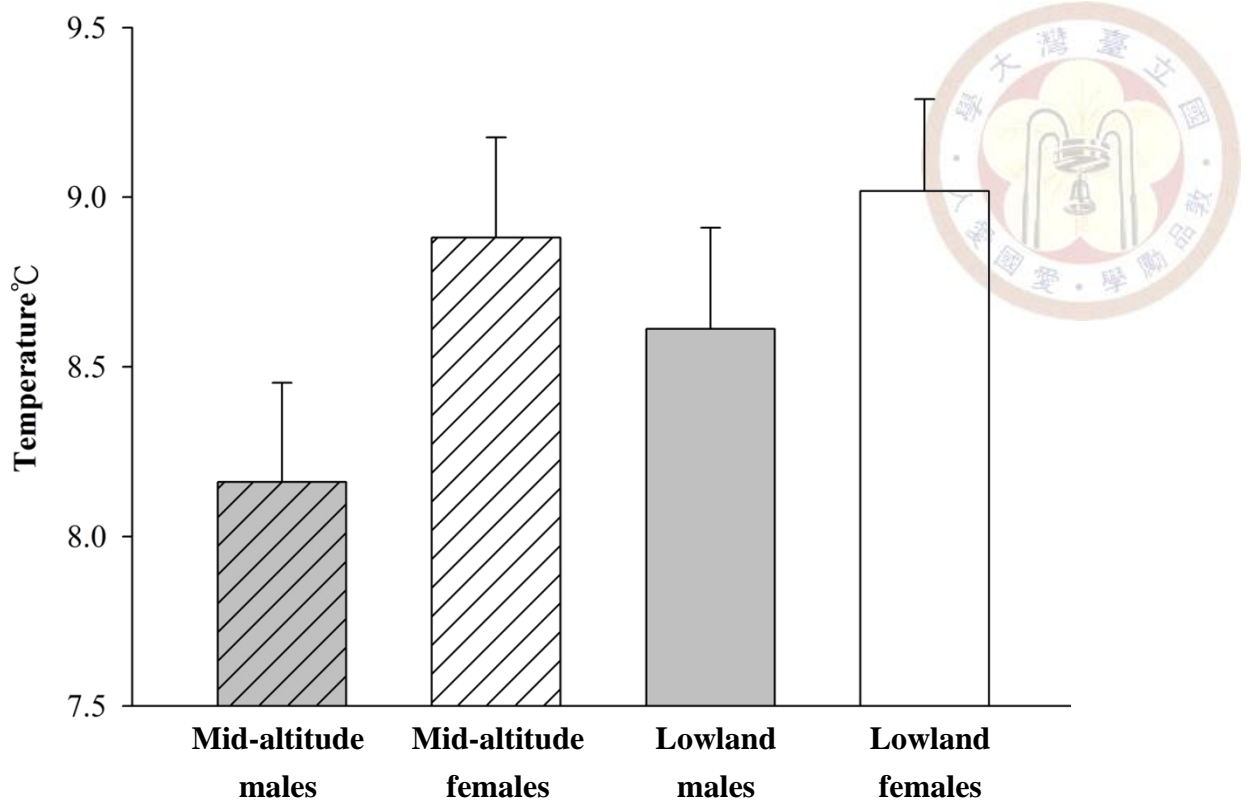


Figure 7. The critical thermal minimum of *Japalura swinhonis*. Values give mean \pm 1se.

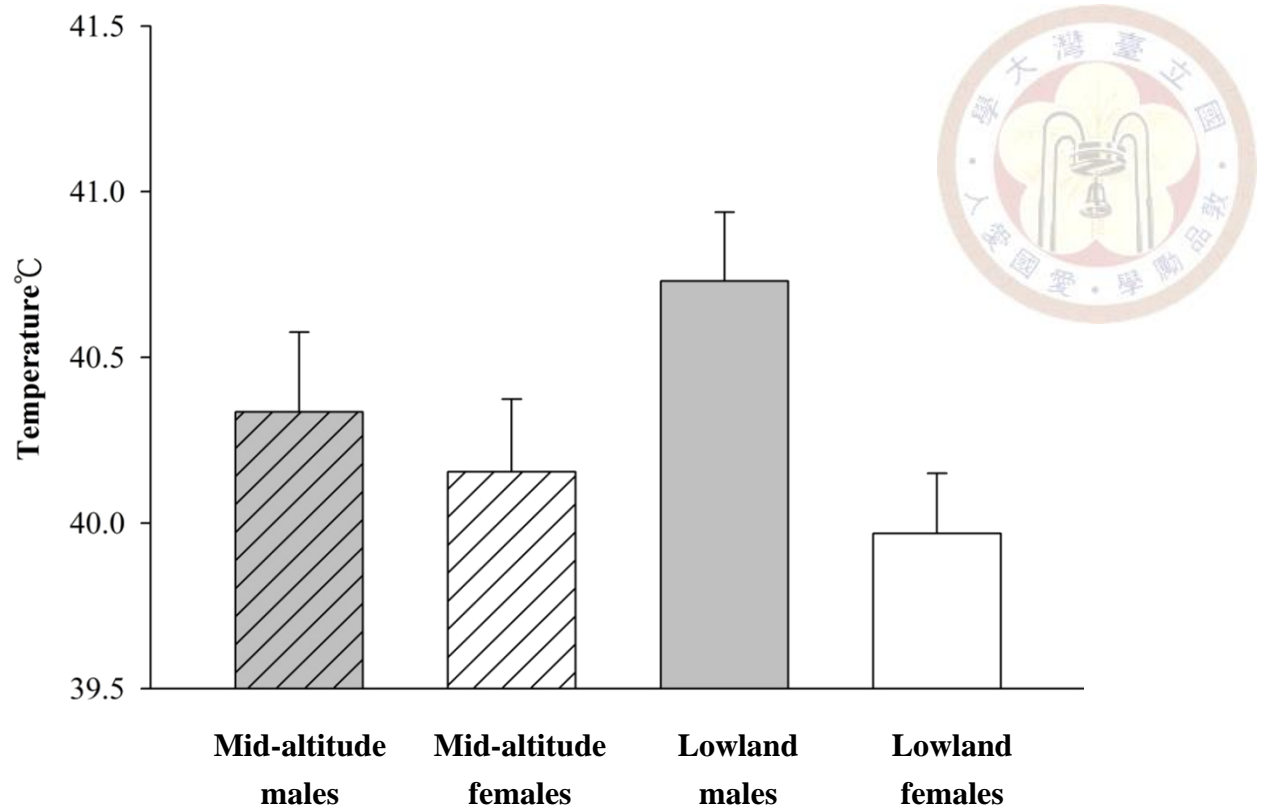


Figure 8. The critical thermal maximum of *Japalura polygonata xanthostoma*. Values give mean \pm 1se.

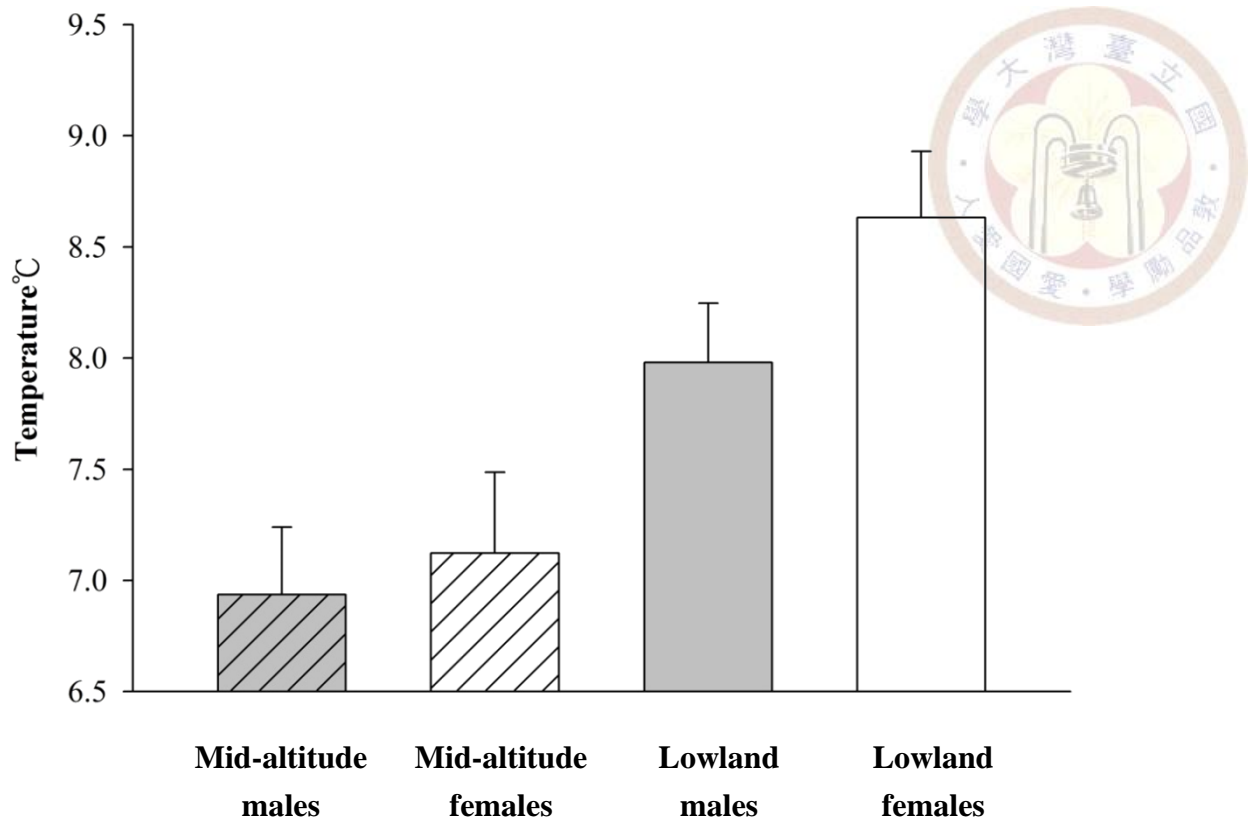


Figure 9. The critical thermal minimum of *Japalura polygonata xanthostoma*. Values give mean \pm 1se.

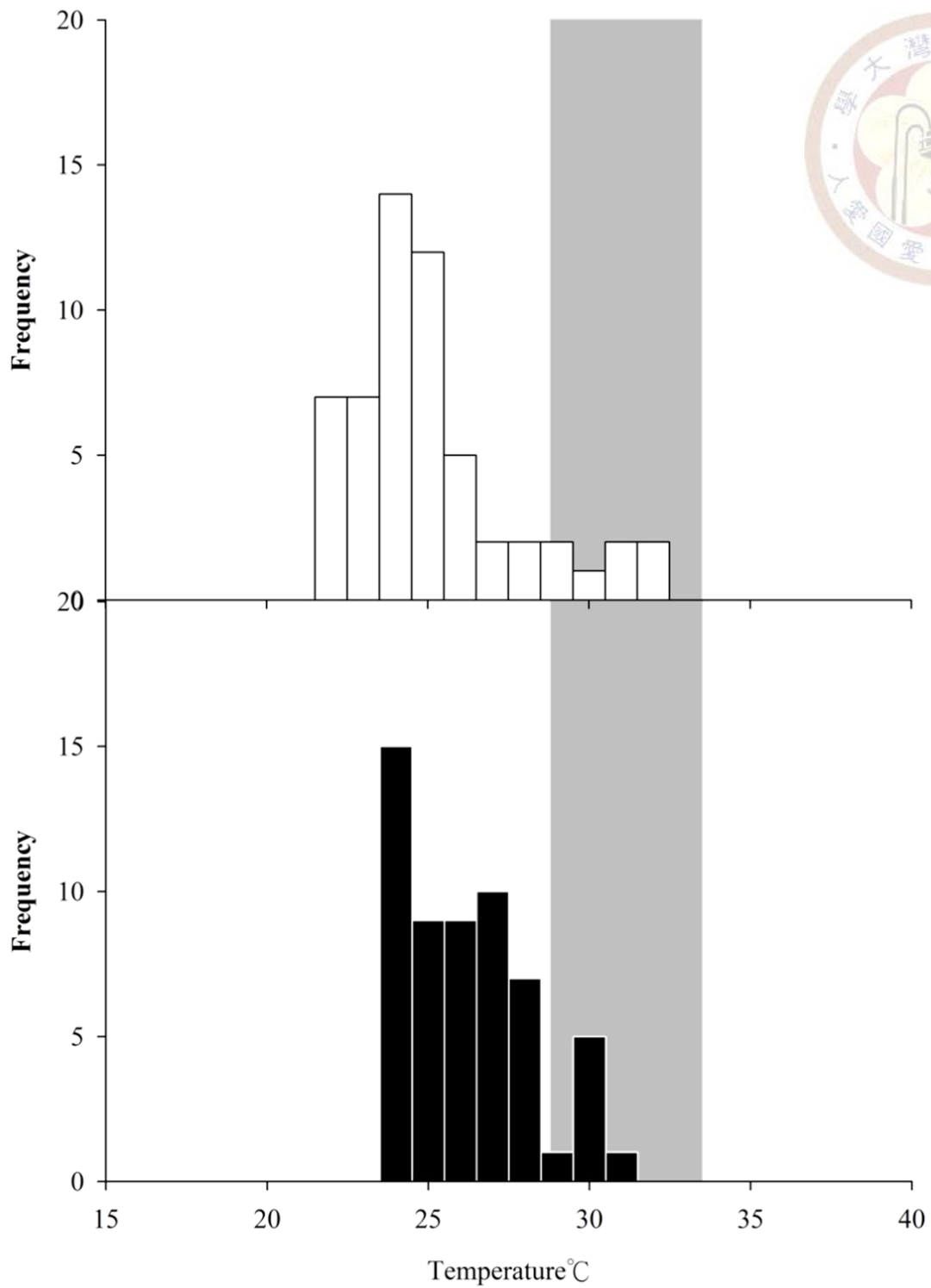


Figure 10. The thermal profiles of mid-altitude *Japalura swinhonis*. White bars are operative temperature (T_e); black bars are field body temperature (T_b). Grey area indicates the range of mean selected body temperature (T_{sel}) \pm 1SD.

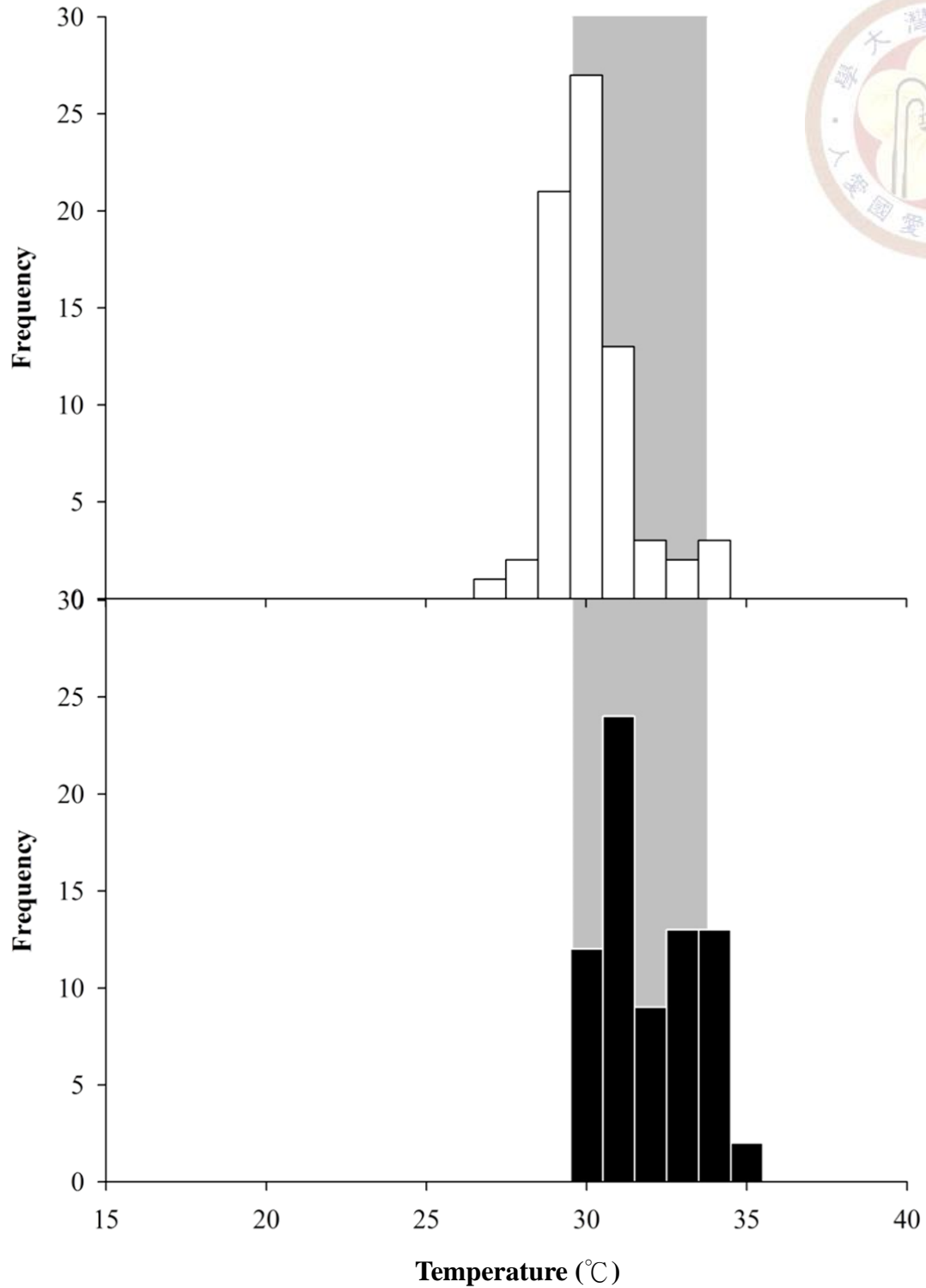


Figure 11. The thermal profiles of lowland *Japalura swinhonis*. White bars are operative temperature (T_e); black bars are field body temperature (T_b). Grey area indicates the range of mean selected body temperature ($T_{sel} \pm 1SD$).

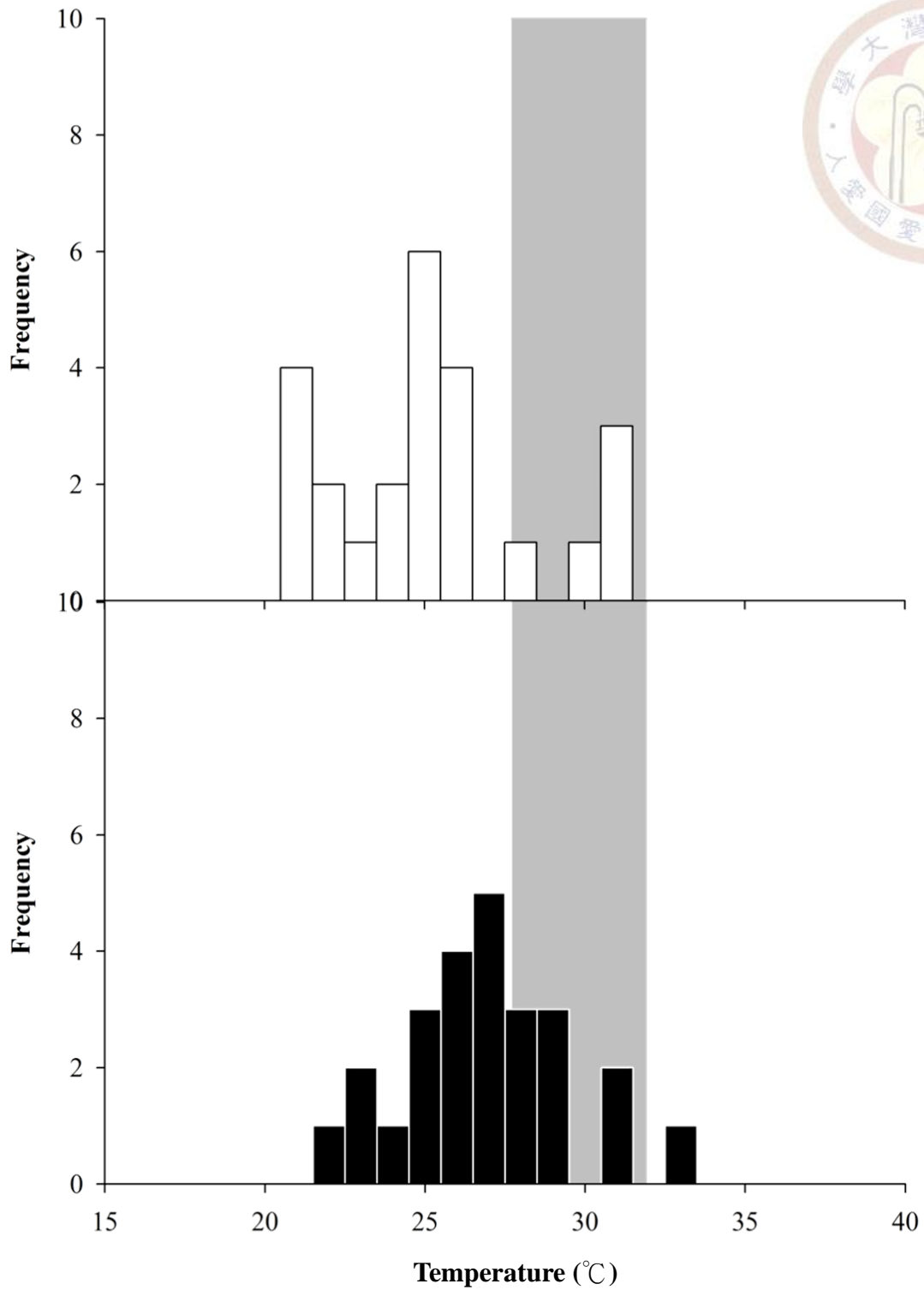


Figure 12. The thermal profiles of mid-altitude *Japalura polygonata xanthostoma*. White bars are operative temperature (T_e); black bars are field body temperature (T_b). Grey area indicate the range of mean selected body temperature (T_{sel}) \pm 1SD.

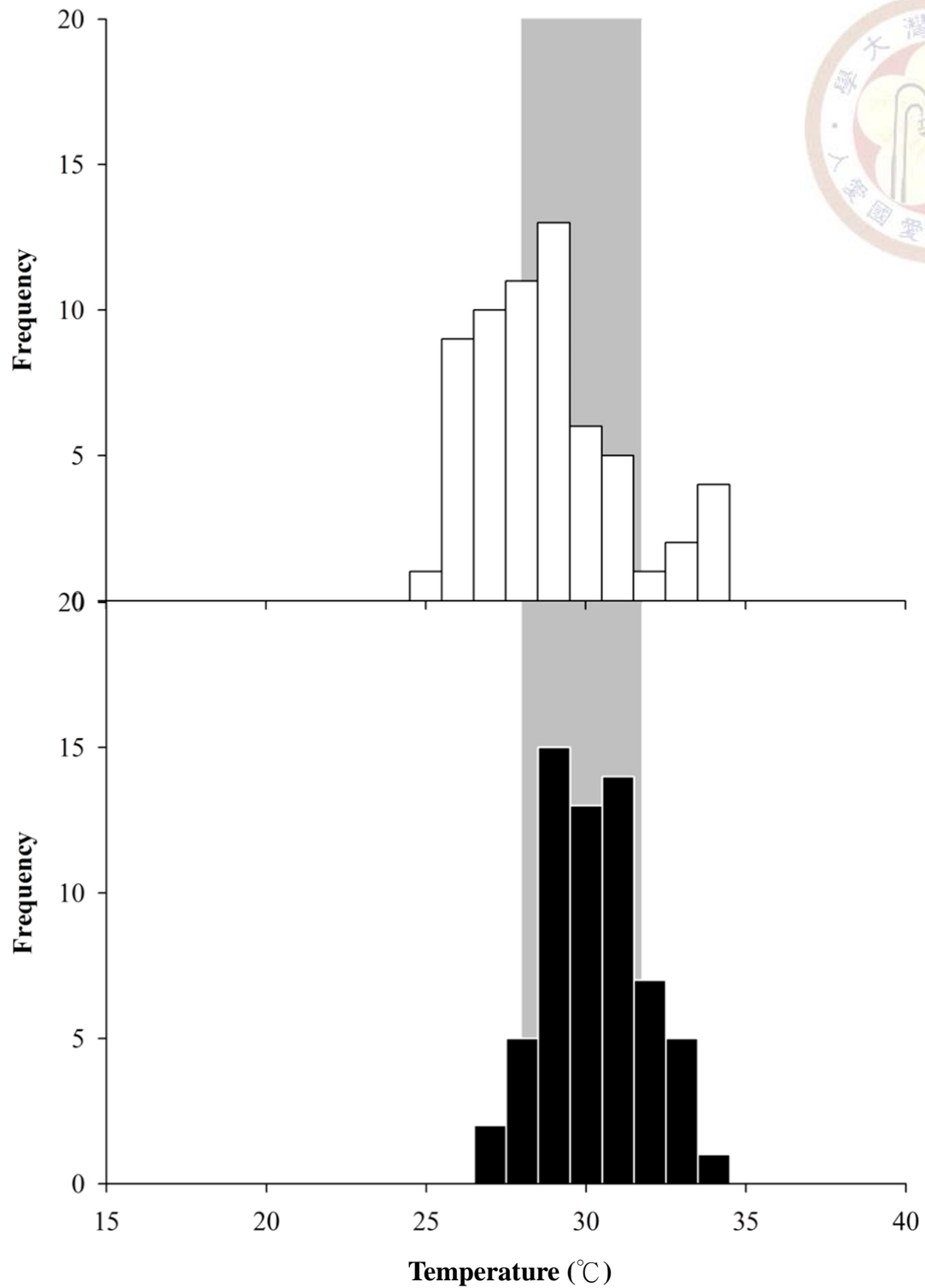


Figure 13. The thermal profiles of mid-altitude *Japalura polygonata xanthostoma*. White bars are operative temperature (T_e); black bars are field body temperature (T_b). Grey area indicates the range of mean selected body temperature (T_{sel}) \pm 1SD.

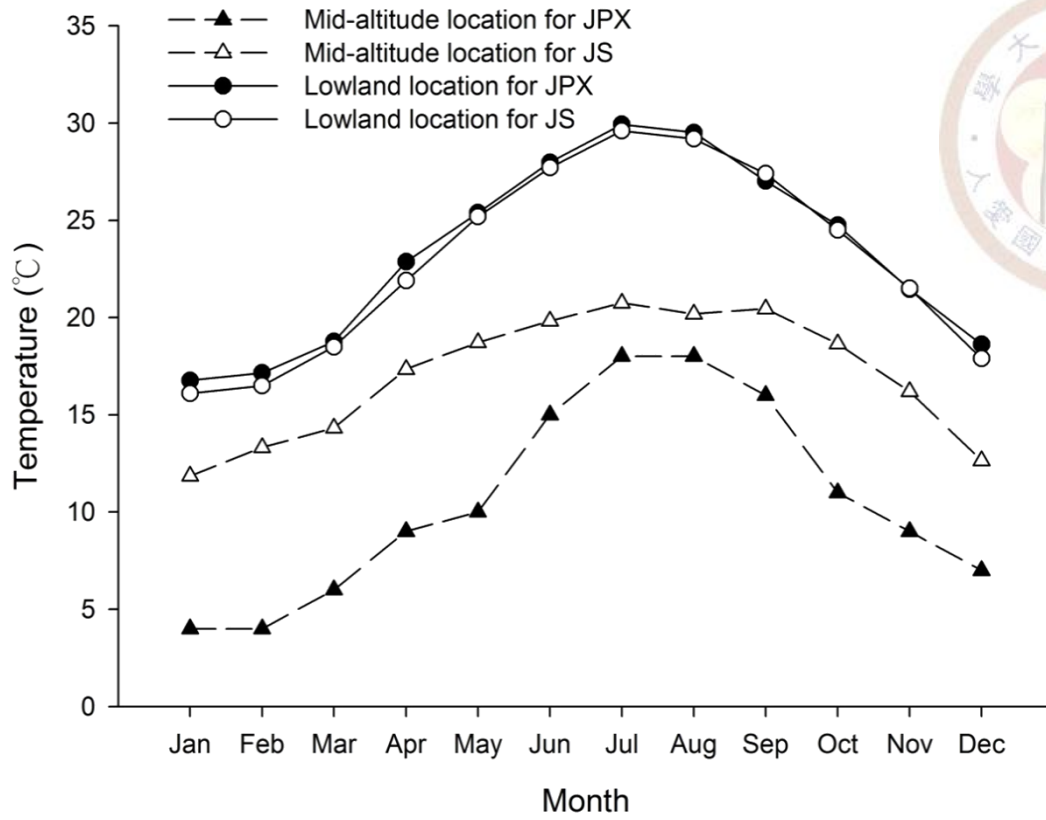


Figure 14. The monthly mean temperature at four study locations. JPX = *Japalura polygonata xanthostoma*; JS = *Japalura swinhonis*.

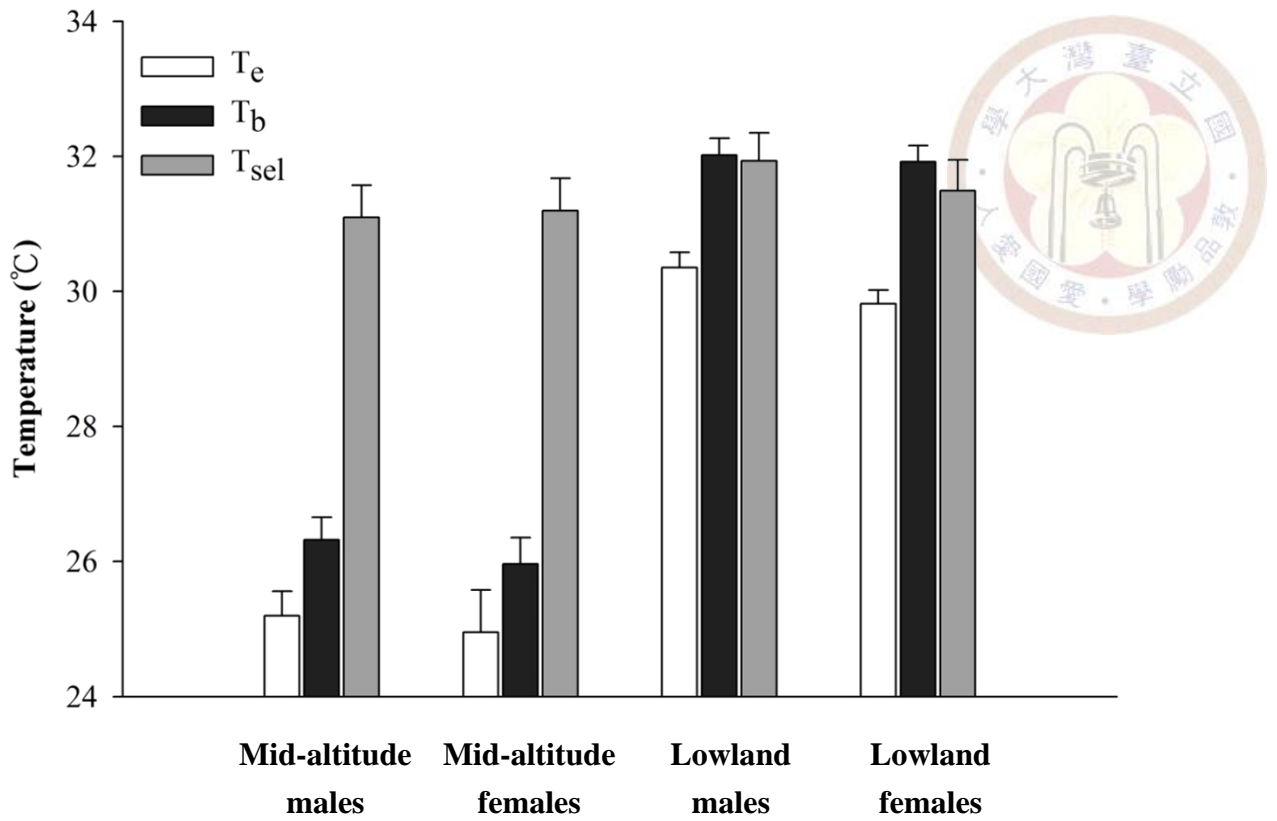


Figure 15. The thermal profiles of *Japalura swinhonis*. White bars are operative temperature (T_e); black bars are field body temperature (T_b). Grey bars are selected body temperature (T_{sel}). Values give mean \pm 1se.

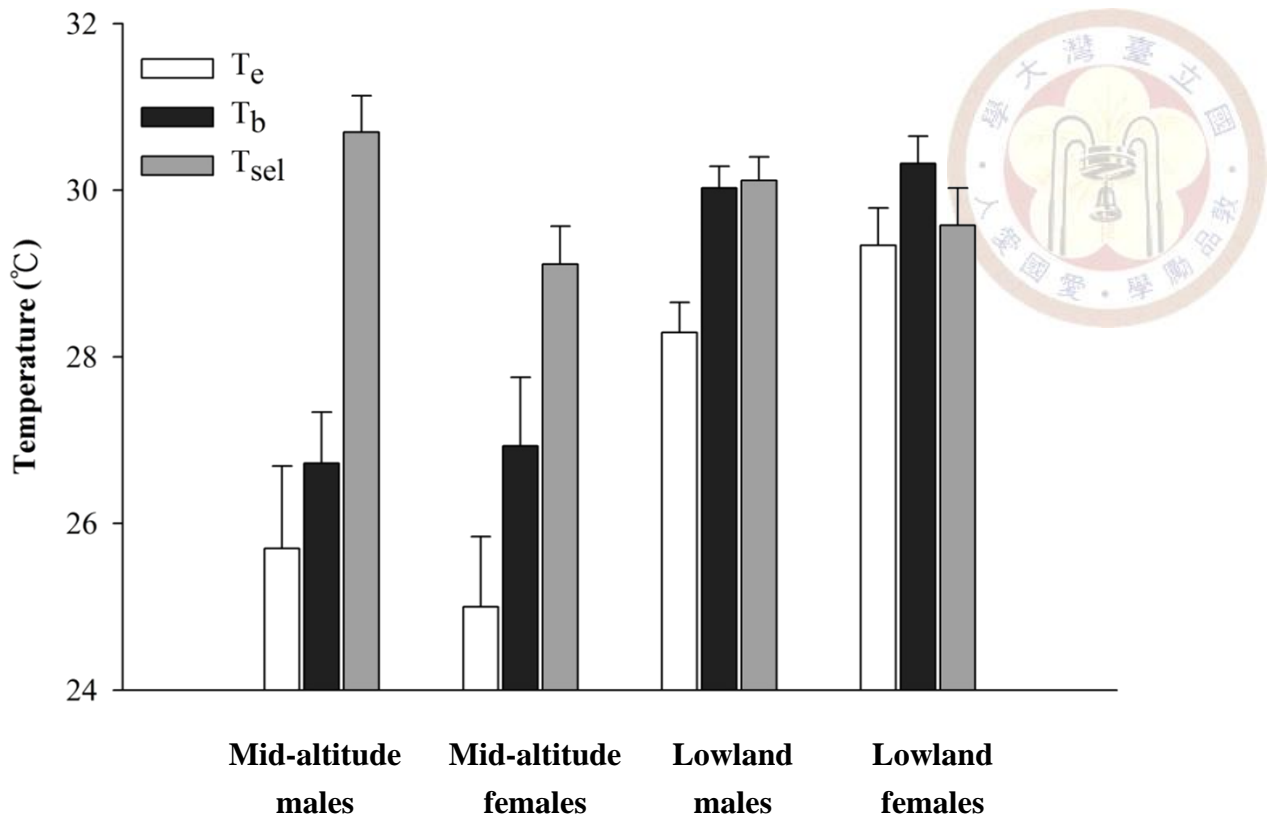
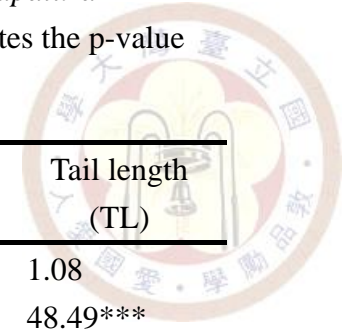


Figure 16. The thermal profiles of *Japalura polygonata xanthostoma*. White bars are operative temperature (T_e); black bars are field body temperature (T_b). Grey bars are selected body temperature (T_{sel}). Values give mean \pm 1se.



Figure 17. The contraption for measuring sprint speed of lizards

Table 21. The comparisons of size-independent morphological variables between two altitudinal populations and sexes in *Japalura swinhonis*. Statistical results were based on two-way ANOVAs. Values are F-value. * indicates the p-value <0.05, ** indicates the p-value <0.01, *** indicates the p-value <0.001.



	Head length (HL)	Head width (HW)	Head height (HH)	Body width (BW)	Body height (BH)	Snout-ventral length (SVL)	Tail length (TL)
Altitude	0.09	0.003	0.19	0.30	0.45	1.48	1.08
Sex	71.51***	54.28***	63.62***	5.56*	64.40***	48.64***	48.49***
Altitude*Sex	0.313	0.38	0.25	1.54	4.03	0.001	0.70

	Forelimb length (Flimb)	Forelimb palm length (Fpalm)	Length of the longest toe of forelimb (Ftoe)	Hindlimb length (Hlimb)	Hindlimb palm length (Hpalm)	Length of the longest toe of hindlimb (Htoe)
Altitude	0.007	0.16	16.44***	2.68	0.17	17.62***
Sex	74.67***	17.45***	79.64***	47.89***	46.71***	98.54***
Altitude*Sex	1.19	0.29	2.11	2.18	0.17	0.09

Table 22. The comparisons of size-independent morphological variables between two altitudinal populations and sexes in *Japalura polygonata xanthostoma*. Statistical results were based on two-way ANOVAs. Values are F-value. * indicates the p-value <0.05, ** indicates the p-value <0.01, *** indicates the p-value <0.001.



	Head length (HL)	Head width (HW)	Head height (HH)	Body width (BW)	Body height (BH)	Snout-ventral length (SVL)	Tail length (TL)
Altitude	0.04	0.20	10.84**	0.21	4.53*	7.44**	8.20*
Sex	26.40***	13.4***	22.26***	0.07	4.65*	8.50**	27.16***
Altitude*Sex	0.13	0.01	0.24	7.99**	0.47	0.12	2.02

	Forelimb length (Flimb)	Forelimb palm length (Fpalm)	Length of the longest toe of forelimb (Ftoe)	Hindlimb length (Hlimb)	Hindlimb palm length (Hpalm)	Length of the longest toe of hindlimb (Htoe)
Altitude	2.81	2.02	0.01	7.39**	0.13	2.71
Sex	10.69**	17.49***	40.60***	8.99**	7.43**	22.93***
Altitude*Sex	0.38	2.85	0.72	0.04	4.67*	1.10

Table 23. The comparisons of thermal sensitivity and thermal profiles between *Japalura swinhonis* (JS) and *Japalura polygonata xanthostom* (JPX) in mid-altitude males. Statistical results were based on permutation t-test. Values are temperature (°C).

Parameter		JS	JPX	p value
Thermal sensitivity of sprint speed	H ₉₅	32.98	32.26	0.11
	L ₉₅	29.10	28.40	0.15
	H ₈₀	34.90	35.01	0.37
	L ₈₀	24.94	25.10	0.38
	B ₈₀	9.96	9.91	0.47
	B ₉₅	3.88	3.86	0.49
	T ₀	31.04	30.33	0.07
Thermal sensitivity of jump distance	H ₉₅	32.73	33.20	0.22
	L ₉₅	27.98	28.69	0.24
	H ₈₀	34.70	35.33	<0.05
	L ₈₀	23.71	23.14	0.27
	B ₈₀	10.99	12.19	0.09
	B ₉₅	4.75	4.51	0.38
	T ₀	30.35	30.59	0.11
Thermal tolerance	CT _{max}	39.54	40.34	0.07
	CT _{min}	8.16	6.94	<0.01
	Thermal tolerance	31.36	33.40	<0.01
Thermal profiles	Field T _b	26.32	26.73	0.27
	T _e	25.19	25.70	0.26
	T _{sel}	31.10	30.70	0.28

Table 24. The comparisons of thermal sensitivity and thermal profiles between *Japalura swinhonis* (JS) and *Japalura polygonata xanthostom* (JPX) in mid-altitude females. Statistical results were based on permutation t-test. Values are temperature (°C).

Parameter		JS	JPX	p value
Thermal sensitivity of sprint speed	H ₉₅	32.43	34.32	<0.01
	L ₉₅	27.40	31.01	<0.001
	H ₈₀	34.76	35.71	<0.001
	L ₈₀	23.54	26.57	<0.001
	B ₈₀	11.23	9.14	<0.001
	B ₉₅	5.03	3.31	<0.001
	T ₀	29.91	32.66	<0.001
Thermal sensitivity of jump distance	H ₉₅	33.08	34.42	<0.01
	L ₉₅	28.40	29.09	0.19
	H ₈₀	34.84	35.74	<0.001
	L ₈₀	23.53	23.43	0.44
	B ₈₀	11.31	5.33	0.10
	B ₉₅	4.68	12.31	0.16
	T ₀	30.74	31.76	<0.05
Thermal tolerance	CT _{max}	39.18	40.15	0.01
	CT _{min}	8.88	7.12	<0.001
	Thermal tolerance	30.30	33.03	<0.001
Thermal profiles	Field T _b	25.96	26.93	0.12
	T _e	24.95	25.00	0.23
	T _{set}	31.19	29.11	<0.01

Table 25. The comparisons of thermal sensitivity and thermal profiles between *Japalura swinhonis* (JS) and *Japalura polygonata xanthostom* (JPX) in lowland males. Statistical results were based on permutation t-test. Values are temperature (°C).

Parameter		JS	JPX	p value
Thermal sensitivity of sprint speed	H ₉₅	33.85	34.57	<0.05
	L ₉₅	30.95	30.10	0.11
	H ₈₀	35.55	35.77	0.09
	L ₈₀	26.79	26.35	0.29
	B ₈₀	8.76	9.42	0.18
	B ₉₅	2.90	4.47	<0.01
	T ₀	32.40	32.34	0.45
Thermal sensitivity of jump distance	H ₉₅	34.16	34.73	0.11
	L ₉₅	30.38	30.13	0.37
	H ₈₀	35.52	35.74	0.19
	L ₈₀	25.31	24.06	0.08
	B ₈₀	10.21	11.68	0.05
	B ₉₅	3.77	4.60	0.11
	T ₀	32.27	32.43	0.36
Thermal tolerance	CT _{max}	40.34	40.73	0.10
	CT _{min}	8.63	7.98	0.06
	Thermal tolerance	31.73	32.75	<0.05
Thermal profiles	Field T _b	32.02	30.02	<0.001
	T _e	30.35	28.29	<0.001
	T _{sel}	31.93	30.12	<0.001

Table 26. The comparisons of thermal sensitivity and thermal profiles between *Japalura swinhonis* (JS) and *Japalura polygonata xanthostom* (JPX) in lowland females. Statistical results were based on permutation t-test. Values are temperature (°C).

Parameter		JS	JPX	p value
Thermal sensitivity of sprint speed	H ₉₅	34.17	34.14	0.47
	L ₉₅	30.33	30.88	0.18
	H ₈₀	35.66	35.62	0.38
	L ₈₀	26.44	27.35	0.08
	B ₈₀	9.28	8.28	0.06
	B ₉₅	3.84	3.26	0.13
	T ₀	32.25	32.51	0.26
Thermal sensitivity of jump distance	H ₉₅	34.44	34.65	0.26
	L ₉₅	29.65	31.52	<0.01
	H ₈₀	35.68	35.82	0.08
	L ₈₀	25.32	26.17	0.17
	B ₈₀	10.35	9.65	0.22
	B ₉₅	4.79	3.13	<0.01
	T ₀	32.05	33.08	<0.001
Thermal tolerance	CT _{max}	40.14	39.97	0.27
	CT _{min}	9.02	8.63	0.18
	Thermal tolerance	31.12	31.34	0.35
Thermal profiles	Field T _b	31.92	30.32	<0.001
	T _e	29.82	29.34	0.14
	T _{sel}	31.49	29.58	<0.01

Table 27. The comparisons of thermal sensitivity between two types of locomotion in *Japalura swinhonis*. Statistical results were based on permutation t-test. Values are temperature (°C).

	Parameter	Sprint speed	Jump distance	p value
Mid-altitude males	H ₉₅	32.98	32.73	0.32
	L ₉₅	29.10	27.98	0.07
	H ₈₀	34.90	34.70	0.25
	L ₈₀	24.94	23.71	<0.05
	B ₈₀	9.96	10.99	0.09
	B ₉₅	3.88	4.75	0.07
	T ₀	31.04	30.35	0.11
Mid-altitude females	H ₉₅	32.43	33.08	0.15
	L ₉₅	27.40	28.40	0.08
	H ₈₀	34.76	34.84	0.42
	L ₈₀	23.54	23.53	0.50
	B ₈₀	11.23	11.31	0.46
	B ₉₅	5.03	4.68	0.30
	T ₀	29.91	30.74	0.08
Lowland males	H ₉₅	33.85	34.16	0.28
	L ₉₅	30.95	30.38	0.22
	H ₈₀	35.55	35.52	0.46
	L ₈₀	26.79	25.31	<0.05
	B ₈₀	8.76	10.21	<0.05
	B ₉₅	2.90	3.77	<0.05
	T ₀	32.40	32.27	0.41
Lowland females	H ₉₅	34.17	34.44	0.20
	L ₉₅	30.33	29.65	0.13
	H ₈₀	35.66	35.68	0.45
	L ₈₀	26.44	25.32	0.06
	B ₈₀	9.28	10.35	0.06
	B ₉₅	3.84	4.79	0.06
	T ₀	32.25	32.05	0.31

Table 28. The comparisons of thermal sensitivity between two types of locomotion in *Japalura polygonata xanthostom*. Statistical results were based on permutation t-test. Values are temperature (°C).

	Parameter	Sprint speed	Jump distance	p value
Mid-altitude males	H ₉₅	32.26	33.20	0.08
	L ₉₅	28.40	28.69	0.38
	H ₈₀	35.01	35.33	0.15
	L ₈₀	25.10	23.14	<0.01
	B ₈₀	9.91	12.19	<0.001
	B ₉₅	3.86	4.51	0.19
	T ₀	30.33	30.59	0.21
Mid-altitude females	H ₉₅	34.32	34.42	0.41
	L ₉₅	31.01	29.09	<0.01
	H ₈₀	35.71	35.74	0.41
	L ₈₀	26.57	23.43	<0.001
	B ₈₀	9.14	5.33	<0.001
	B ₉₅	3.31	12.31	<0.01
	T ₀	32.66	31.76	0.05
Lowland males	H ₉₅	34.57	34.73	0.33
	L ₉₅	30.10	30.13	0.49
	H ₈₀	35.77	35.74	0.44
	L ₈₀	26.35	24.06	<0.01
	B ₈₀	9.42	11.68	<0.01
	B ₉₅	4.47	4.60	0.42
	T ₀	32.34	32.43	0.41
Lowland females	H ₉₅	34.14	34.65	0.08
	L ₉₅	30.88	31.52	0.15
	H ₈₀	35.62	35.82	<0.05
	L ₈₀	27.35	26.17	0.08
	B ₈₀	8.28	9.65	<0.05
	B ₉₅	3.26	3.13	0.41
	T ₀	32.51	33.08	0.09