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Domesticated and wild fathead minnows differ in growth and thermal tolerance

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ABSTRACT

Many populations have evolved in response to laboratory environments (lack of predators, continual food availability, etc.). Another potential agent of selection in the lab is exposure to constant thermal environments. Here, we examined changes in growth, critical thermal maximum (CT_{max}), and food consumption under constant (25 °C) and fluctuating (22–28 °C and 19–31 °C) conditions in two populations of fathead minnows, *Pimephales promelas*: one that has been kept in a laboratory setting for over 120 generations (~40 years) and a corresponding wild one. We found that under thermal fluctuations, domesticated fathead minnows grew faster than their wild counterparts, but also exhibited lower thermal tolerance. Food consumption was significantly higher in the lab population under the constant and large fluctuation thermal treatments. Our results suggest that the lab population has adjusted to the stable conditions in the laboratory and that we should carefully apply lessons learned in the lab to wild populations.

1. Introduction

Laboratory conditions inevitably create an environment that differs from the wild (Sterken et al., 2015). It is not surprising, then, that many populations reared in the lab have, over time, become behaviorally and physiologically different from those in the wild (e.g., Alvarez and Nicieza, 2003; Calisi and Bentley, 2009; Frankham, 2008; Huntingford, 2004; Krebs et al., 2001; Robison and Rowland, 2005; Wright et al., 2006; Yamamoto and Reinhardt, 2003). Selective pressures that may be common under captivity include lack of predators or competitors, different diets, increased handling-related stress, and reduction in mate competition and choice (reviewed in Gering et al., 2019). The evolution of traits in response to the lab *thermal* environment, however, has received comparatively less attention (but see, e.g., Kingsolver et al., 2009; Morgan et al., 2019).

Keeping study animals at a constant temperature is a common feature in the large majority of physiology and life history studies, primarily to control for temperature. However, constant thermal regimes, when compared to fluctuating treatments, can lead to plastic changes in growth rate (e.g., Morash et al., 2018), upper thermal tolerance limit (e.g., Salachan and Sørensen, 2017), fecundity (e.g., Carrington et al., 2013), and lifespan (e.g., Carroll and Quiring, 1993). Importantly, prolonged exposure to a stable thermal environment could select for 'thermal specialists', organisms whose thermal reaction norms are narrower but with higher performance at the optimal temperature (Foray et al., 2014; Gilchrist, 1995; but see, Ketola et al., 2013). For example, brown trout, brook trout, and rainbow trout from the wild showed a 0.5–1.6 °C higher critical thermal maximum when compared to domesticated strains from hatcheries (Carline and Machung, 2001).

Thermal lab domestication could be particularly pervasive in model systems (Matos et al., 2002; Sterken et al., 2015), and some of these may be used to generate predictions of the effects of climate change on physiology and life history. Given the recent popularity of physiology experiments hoping to predict responses to climate change (Chown et al., 2010; Fuller et al., 2010), we need to understand the impacts of thermal lab domestication.

Here, we examined life history consequences of exposure to a constant thermal laboratory environment for over 120 generations (~40 years) in a population of fathead minnows, *Pimephales promelas*, compared to their wild counterparts. We raised the two populations at a constant temperature and at two levels of daily thermal fluctuations and quantified growth, critical thermal maximum, and food consumption.

The fathead minnow, *Pimephales promelas*, is a small-bodied member of the Cyprinidae family found in freshwater bodies throughout North America (Ankley and Villeneuve, 2006). Its large geographic range is partly due to its eurythermal physiology (can withstand temperatures

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above 40°C; Beitinger et al., 2000) and ability to tolerate salinity (Hoover et al., 2013) and pH (Mount, 1973) variation. They typically inhabit boggy lakes, ponds, and streams, and their diet consists mostly of insect larvae and algae (Becker, 1983). Because they can reproduce in large numbers, these minnows have a marked influence on the macroinvertebrate community (Zimmer et al., 2002). Spawning season typically begins in late May and lasts until the middle of August in the northern part of its range (Becker, 1983). Eggs hatch within three to five days and, under optimal conditions, larvae can reach maturity in four months (Ankley and Villeneuve, 2006). The fathead minnow's small body size (7–10 cm), rapid development, and tolerance makes them an ideal laboratory model system.

2. Methods

2.1. Fish sources

We obtained laboratory domesticated fish from the Environmental Protection Agency (EPA)'s Mid-continent Ecology Division laboratory in Duluth, Minnesota. The EPA lab population was established using fathead minnows from Cincinnati, Ohio, United States in the 1960s, but was supplemented with Duluth, Minnesota, United States minnows in the 1980s and with a small sample from a commercial source (Aquatic Research Organisms, Inc., Hampton, New Hampshire, United States) in 1997 to avoid potential inbreeding issues (K. Jensen, Great Lakes Toxicology and Ecology Division, US EPA, personal communication). These locations share a similar thermal profile (Fig. S1). Throughout the ~120 generations (3-4 generations per year; U.S. Environmental Protection Agency, 2006), fathead minnows were maintained at a constant temperature of 25 °C (K. Jensen, personal communication).

From the EPA lab, we received 27 adult male and 27 adult female fathead minnows (P generation) in 2018. These fish produced offspring (F1) that were grown for a year in our laboratory at Kalamazoo College. A subset of ~50 F1 fish were spawned to obtain the experimental fish (F2). During the year, they were kept in 190-L tanks under constant thermal conditions (25 ± 0.5 °C), a 16:8 light:dark photoperiod, and were fed Tetramin flake food (Tetra, Blackburn, VA, USA) twice and frozen adult brine shrimp, *Artemia* spp., once per day. Water chemistry (ammonia, nitrate, and nitrite levels) was monitored routinely to maintain optimal conditions. pH and hardness were 8.1 and 325 ppm, respectively, at the beginning of the experiment.

Wild fish were caught by local fishermen in Clitherall, Minnesota (46.152338, −95.608560). At this site, water temperatures fluctuate between 6 and 29 °C during the summer (similar temperatures are found in similar ponds and lakes in Duluth and Cincinnati; Fig. S1). Upon collection, we transported wild-caught fathead minnows to our laboratory in Kalamazoo College. They were placed in 190-L tanks in identical conditions to the lab stock (25 ± 0.5 °C, 16:8 photoperiod, three feedings per day). The wild population was maintained under laboratory conditions for a month before spawning to minimize parental effects.

We placed 8 polyvinyl chloride (PVC) pipe pieces (10.2 cm diameter pipe cut in half lengthwise, each piece 15 cm long) to obtain eggs from both wild and lab populations - fathead minnows spawn on the underside of logs, rocks, and other debris (Becker, 1983). The adults spawned under a constant temperature of 25 ± 0.5 °C, and the eggs were transferred within 3 h to their randomly assigned temperature treatment. We treated eggs with methylene blue (3 ppm concentration; Fritz Aquatics, Mesquite, TX, USA) for 60 s to prevent infection and raised the larvae in Marina net breeders (Hagen Inc., Montreal, QC, Canada; 16.5 cm × 13 cm x 13 cm, L x W x H) for 16 days. We then transferred larvae to their own individual growth chambers (cylindrical mini-tanks with mesh sides to facilitate water exchange with the tank, 8 cm diameter x 25 cm length). All fish were grown for 85 days.

2.2. Experimental treatments

We set up three different temperature treatments: constant 25 °C (25 ± 0.5 °C), small fluctuations (25 ± 3 °C; min 22 °C, max 28 °C), and large fluctuations (25 ± 6 °C; min 19 °C, max 31 °C). The temperature fluctuations exhibited daily periodicity, with the warmest temperature at 12:00 (noon) and the coldest at 00:00 (midnight). Note that these treatments represent realistic diel fluctuations during the summer season (Fig. S1; see Fig. S2 for a schematic of the experimental design). Each temperature treatment was replicated in two 190-L (153 × 61 × 26 cm) tanks, with larvae from the lab and wild sharing tanks in their individual growth chambers made of mesh for complete water exchange between tank and growth chambers. To ensure appropriate water quality, each 190-L tank was fitted with an Eheim Classic 600 filter (Eheim GmbH; Deizisau, Germany) and ~20% of the water replaced weekly. The temperatures were maintained via tank-specific APEX Jr. controllers (Neptune Systems Inc.; Morgan Hill, CA, USA) connected to titanium heaters (Finnex, Chicago, IL, USA) and chillers (Your Choice Aquatics, Guangzhou, China). Each temperature treatment consisted of 104 fish (52 per tank, i.e., 52 individual growth chambers of which 26 had wild fish and 26 lab-adapted fish), for a total of 312 fish in the experiment. The photoperiod was maintained at 16:8 L:D.

Temperatures were logged automatically by the controllers and monitored daily throughout the day. At the beginning of each week, we also checked temperature time series for the previous week to confirm that water temperatures were following our preestablished treatments (Fig. S3). Other than brief deviations of 1–2 °C during water changes, treatments followed the protocols described.

During the first 16 days, spent in net breeders placed in the experimental tanks (Fig. S2), the fathead minnow larvae were fed Hikari First Bites (Kyorin Food Industries, Japan) and 1-day-old brine shrimp nauplii 3x a day at ~09:00, 12:30, and 17:30 (~3500 nauplii per feed per net breeder). After 16 days, when larvae were moved into individual growth chambers, we fed them Tetramin flake food *ad libitum* 3x day; our protocol was to feed each individual chamber a small amount of flake food and spend at least 30 s away from the tank, and we only fed a chamber again if food was gone after this period of time. Water chemistry was monitored at least every three days to maintain optimal water quality. All protocols were approved by the Institutional Animal Care and Use Committee at Kalamazoo College.

2.3. Length measurements

Starting with 16-day-old larvae, we measured each fish's length weekly (a minority [17%] of larvae were moved when they were 20–26 days old because of logistical constraints). The procedure consisted of photographing each individual using a copy stand and a Nikon D7200 camera fitted with an AF-S Micro NIKKOR 105 mm f/2.8 macro lens (Nikon Co., Tokyo, Japan) stationed at a 90° angle. The fish was suspended in 1 cm of water, within its individual chamber, to prevent stress (see Fig. S4). We then used ImageJ (Schneider et al., 2012) to measure each fish. Fish length during these early stages in fathead minnows is linear (Salinas et al., 2019 and corroborated here); therefore, we chose to calculate growth by using the first and last length measurements divided by the number of days elapsed.

2.4. CTmax assay

We quantified each fish's upper thermal tolerance limit at 70-days-old in a separate apparatus fitted with heaters and a water pump to recirculate water and ensure homogenous heating rate. We raised the temperature by 0.5 °C every minute (Lutterschmidt and Hutchison, 1997) until onset of uncoordinated movement. Fish from each treatment were assayed starting at their peak temperature (i.e., 25 °C for constant, 28 °C and 31 °C for the fluctuating treatments). Immediately after visually detecting uncoordinated movements, the individual growth

chamber was removed from the CT_{max} apparatus and placed back into the experimental tank.

2.5. Food consumption

To compare food consumption across treatments, we counted how many individual thawed adult brine shrimp fathead minnows could consume to satiation (until they could not consume any for 30 s) during one feeding. We did this with 20 fish from each treatment (i.e., population of origin x temperature) when the fish were 80 days old and all trials were run concurrently. This was considered their 'normal' food consumption. Thereafter, we did not feed the fish for two days and repeated the protocol to quantify food consumption after the period of starvation. All food consumption trials were conducted at 14:00–15:00.

2.6. Statistical analysis

To compare wild vs. lab populations under each treatment, we quantified effect size differences via estimation statistics instead of relying on standard significance tests – the emphasis is thus on the magnitude and the precision of the experimental manipulation. An estimation plot displays all observed values along with the effect size and confidence interval, allowing for robust visualization (Ho et al., 2019). We calculated 95% confidence intervals by bootstrapping (5000 resamples); the confidence intervals were bias-corrected (Ho et al., 2019).

We also ran significance testing statistics. We analyzed growth, CT_{max}, and food consumption (under 'normal', pre-starvation conditions) via general linear models with population (lab, wild), temperature treatment (25 °C, 22–28 °C, 19–31 °C), and their interaction as independent variables. Because all interaction terms in those models were significant (Tables S1–3) and precluded us from interpreting main effects, we also conducted t-tests (after Bonferroni correction, $\alpha = 0.006$) to compare the effect of population, under each temperature treatment, on each of the three traits. To evaluate how each population responded to the three temperature treatments, we analyzed the three traits via general linear models for each population separately, followed by post-hoc tests (and Tukey's HSD corrections) for pairwise comparisons. Additionally, for food consumption, we used paired t-tests to test for differences between 'normal' and post-starvation consumption within each population x temperature treatment.

3. Results

3.1. Growth

Lab and wild fish grew at the same rate under constant 25 °C ($t_{97} = 0.25$, $p = 0.80$). Under thermal fluctuations, however, lab-adapted fish grew more rapidly than wild-caught fish (22–28 °C: $t_{90} = 5.10$, $p < 0.001$; 19–31 °C: $t_{99} = 6.15$, $p < 0.001$; Fig. 1). In terms of differences within each population across temperature treatments, lab fish under small fluctuations grew statistically more rapidly than under constant or large fluctuation conditions (Table S4). Wild fish growth was significantly different in each of the three treatments, with growth being fastest at constant 25 °C and slowest under large fluctuations (Table S5).

3.2. CT_{max}

CT_{max} exhibited the opposite pattern as growth: fluctuations led wild fish to have higher CT_{max} values compared to lab fish as the level of thermal fluctuations increased (constant 25 °C: $t_{97} = 3.74$, $p < 0.001$; 22–28 °C: $t_{84} = 1.43$, $p = 0.156$; 19–31 °C: $t_{100} = 5.93$, $p < 0.001$; Fig. 2). In both the lab and wild populations, all pairwise comparisons between temperature treatments (for, e.g., lab fish, constant 25 °C vs. 22–28 °C, constant 25 °C vs. 19–31 °C, etc.) were highly significant (Table S5).

3.3. Food consumption

Food consumption under 'normal' (non-starved) conditions was higher for lab fish under large thermal fluctuations ($t_{38} = 5.36$, $p < 0.001$); under constant ($t_{38} = 2.47$, $p = 0.018$) and small fluctuating ($t_{38} = 0.08$, $p = 0.939$) conditions, however, no difference was detected (Fig. 3). In the lab population, the only pairwise difference in food consumption was between constant 25 °C and small fluctuation fish (Table S6). For the wild population, the significant differences were between fish in the constant and large fluctuating treatments and between small and large fluctuating treatments (Table S6).

After two days of starvation, the lab fish ate more food under constant temperature (paired t-test comparison of 'normal' and starved consumption $p = 0.009$; Fig. S5) and small thermal fluctuations ($p = 0.003$; Fig. S5) but not under large ones ($p = 0.100$; Fig. S5).

3.4. Mortality rates

The lab and wild populations both had evenly distributed and similar mortality rates across all temperature treatments; no single population x temperature treatment lost more than 3 fish throughout the experiment

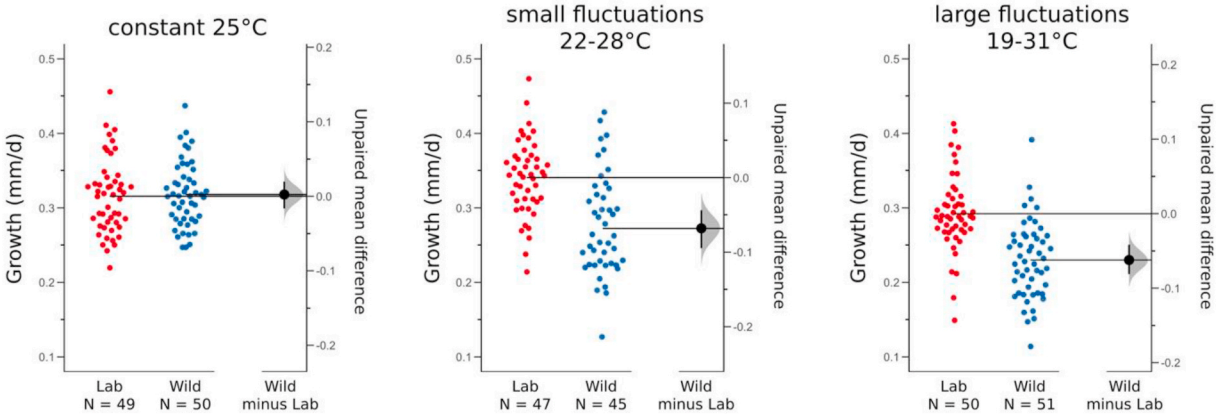

Fig. 1. Growth differences between lab (red) and wild (blue) fathead minnows, *Pimephales promelas*, under the three temperature regimes (each point represents an individual fish). On the right of each plot, the mean difference between groups is denoted by the point, along with the 95% CI as a vertical black line and a bootstrap sampling distribution in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

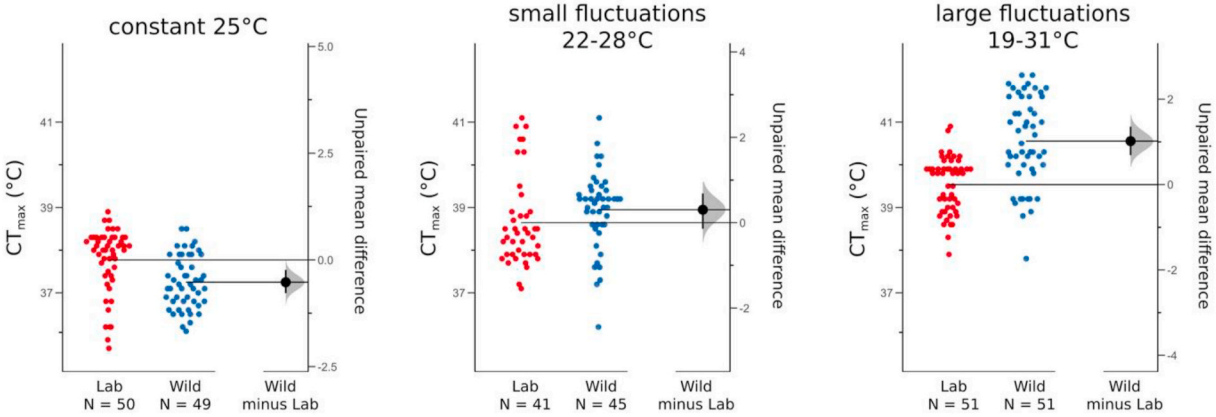

Fig. 2. CT_{max} differences between lab (red) and wild (blue) fathead minnows, *Pimephales promelas*, under the three temperature regimes (each point represents an individual fish). On the right of each plot, the mean difference between groups is denoted by the point, along with the 95% CI as a vertical black line and a bootstrap sampling distribution in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

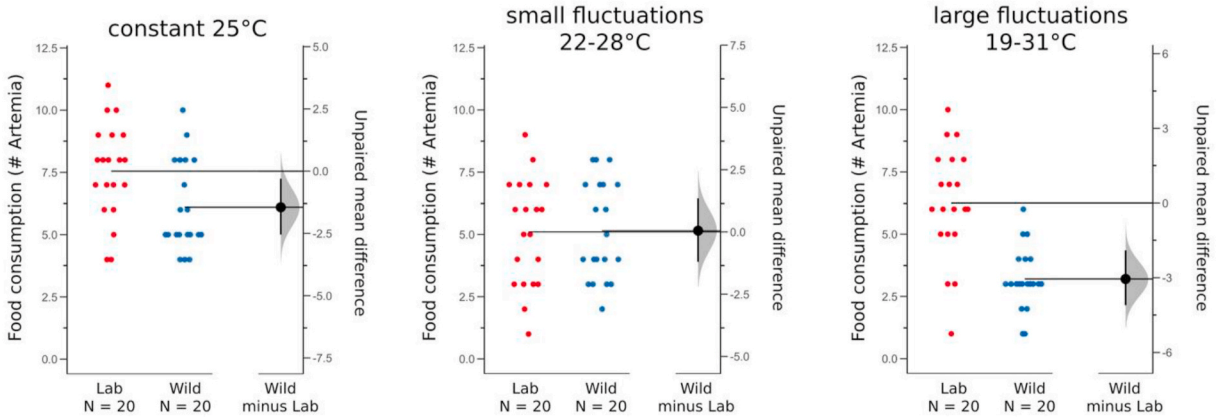

Fig. 3. Food consumption differences between lab (red) and wild (blue) fathead minnows, *Pimephales promelas*, under the three temperature regimes (each point represents an individual fish). On the right of each plot, the mean difference between groups is denoted by the point, along with the 95% CI as a vertical black line and a bootstrap sampling distribution in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Table S7).

4. Discussion

Under fluctuating thermal conditions, fathead minnows from the domesticated population grew faster than their wild counterparts but also exhibited lower thermal tolerance (CT_{max}). Wild fish may grow sub-maximally when exposed to diel fluctuations to invest energy in thermal tolerance or other stress-tolerance traits. Trade-offs between growth and other traits tied to fitness appear to be common among fishes (Lee et al., 2003; Munch and Conover, 2004). Food consumption under normal, non-starved conditions was higher in lab fish under both constant 25 °C and 19–31 °C treatments, mostly driven by a lower consumption of *Artemia* in the wild populations. This pattern differs from what we observed for growth, suggesting that consumption alone cannot explain the difference in growth across treatments. We also observed a higher increase in food consumption after starvation in the lab population when compared to the wild fish (only statistically significantly so under constant and small fluctuations). This is consistent with other studies that observed changes in the resistance to starvation and foraging decisions after domestication (Alvarez and Nicieza, 2003; Huntingford, 2004; Simões et al., 2009; Troxell-Smith et al., 2016).

The apparent loss of plasticity observed (i.e., the shallowing of the reaction norms as the thermal environment increased in temperature variability; see Fig. S6) is suggestive of genetic assimilation (Kelly, 2019; Pigliucci et al., 2006). Maintaining thermal tolerance is energetically costly, as is made clear when comparing stenotherms and eurytherms (Somero et al., 1996; Somero, 2002). A laboratory population living under a constant environment would then be predicted to lose the ability to tolerate thermal deviations (see, e.g., Sikkink et al., 2014), much like thermophilic cyanobacteria did in response to stable, high temperature environments (Miller et al., 2020). More careful experimentation is needed to confirm this phenomenon.

Within lab and wild populations, larger thermal fluctuations led to decreased growth, an effect that has been well documented (see examples in Morash et al., 2018), and increased upper thermal tolerance, also commonly observed (reviewed in Colinet et al., 2015). Daily temperature cycles could allow organisms to recover after a short period of stressful temperatures, possibly due to differences in gene expression of heat shock proteins under constant vs fluctuating conditions (Podrabsky and Somero, 2004).

Wernberg et al. (2012) found, in a review of climate change studies on marine organisms, that ~90% were done in lab settings, and the vast majority of these experiments used constant temperatures. If animals tested are adapted or acclimated to constant conditions, then results could be biased, especially in studies of extreme environmental change. The concern is therefore two-fold: (1) constant temperatures may not reflect an organism's true physiology and (2) if organisms are held in

constant conditions for extended periods, this effect would be exacerbated. For some traits, like CT_{max}, using lab-adapted fish represents a conservative approach that errs on the side of over-predicting the impact of a climate-driven scenario, as it is clear that wild fish under more realistic conditions can tolerate higher temperatures. For others, like growth, it may be the complete opposite. It is not clear how often organisms are held in the lab for a considerable period of time ("considerable" clearly depends on the species) before the experiment, so we suggest biologists take this issue into account, report it in the methods, and we caution about projecting lab findings to wild organisms. Such extrapolations also ignore local adaptation by focusing on a single population, or issues of limited genetic diversity or transgenerational effects. Careful consideration of experimental design and reporting are necessary for accurate predictions of climate change effects (Baumann, 2019).

Lab domestication could prove a valuable system in which to study parallel evolution, similar to the direction urban ecology and evolution studies are taking (Johnson and Munshi-South, 2017; Rivkin et al., 2019), by leveraging all the populations that have been kept in the lab over extended periods of time. Evolution to thermal lab conditions has been found in a phylogenetically varied group of organisms already (fishes: (Carline and Machung, 2001; Fleming and Einum, 1997; Vincent, 1960); insects: (James and Partridge, 1995; Kingsolver et al., 2009; Kingsolver and Nagle, 2007; Mudavanhu et al., 2014), bacteria (Cooper et al., 2001):). There are also compelling cases that found no differences between wild and captive populations (Morgan et al., 2019; Pintanel et al., 2020). Lab populations could thus provide novel insights into thermal evolution at the genetic, genomic, and transcriptomic levels.

Author contributions

Kento Hirakawa: Methodology, Investigation, Data Curation, Writing – Original Draft; Santiago Salinas: Conceptualization, Methodology, Validation, Formal Analysis, Resources, Data Curation, Writing – Review & Editing, Visualization, Supervision, Project Administration.

Declaration of competing interest

The authors declare no competing or financial interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2020.102784.

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