

RESEARCH PAPER

Temperature-mediated trade-off between development and performance in larval wood frogs (*Rana sylvatica*)

Kaija Gahm¹  | A. Z. Andis Arietta²  | David K. Skelly² 

¹Department of Ecology & Evolutionary Biology, Yale University, New Haven, Connecticut, USA

²School of the Environment, Yale University, New Haven, Connecticut, USA

Correspondence

Kaija Gahm, 370 Prospect Street, New Haven, CT 06511, USA.

Email: Kaija.gahm@aya.yale.edu

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Abstract

Countergradient variation has been detected in diverse taxa. In a common manifestation, individuals from colder environments develop faster than conspecifics from warmer environments when placed in a common garden. Where such a pattern exists, it implies a trade-off: Individuals from warmer environments have intrinsic rates of development lower than those demonstrated by other individuals of the same species. We explored a trade-off between development rate and locomotor performance in the wood frog (*Rana sylvatica*), an amphibian for which countergradient variation has been well documented. We reared wood frogs from 10 populations under two temperature regimes, bracketing the temperatures observed in local natural ponds. Individuals reared under warmer conditions developed more rapidly but exhibited burst speeds 20% lower than individuals reared under colder conditions. The slope of the reaction norm was consistent across the 10 populations and thus, we found no evidence of countergradient variation in performance. Burst speed assays of wild-caught tadpoles from the same populations showed a similar but nonsignificant trend, with greater variability among ponds. Overall, our findings support the existence of a development–performance trade-off that may be of broad importance and which may help explain the widespread occurrence of countergradient variation.

KEYWORDS

amphibian, burst speed, countergradient, development, developmental plasticity, locomotion, morphometrics, performance, swimming, thermal physiology

1 | INTRODUCTION

Conover and Schultz (1995) define countergradient variation as “a geographical pattern of genotypes (with respect to environments) in which genetic influences on a trait oppose environmental influences, thereby minimizing phenotypic change along the gradient.” In the first documented example, an altitudinal cline in fruit fly size was reversed when the populations were reared under identical conditions in the laboratory (Levins, 1969). It is not easy to observe countergradient variation because, in the wild, it tends to diminish phenotypic difference and thus obscure its own existence. A number of instances have been discovered inadvertently during experiments

designed to investigate other questions (e.g., Conover & Schultz, 1995; Levins, 1969). In the last decade or so, the number of examples has increased more rapidly as research on countergradient patterns has gained wider notice (Richardson et al., 2014).

In spite of this increased interest in countergradient variation, critical aspects of the phenomenon remain poorly understood. Countergradient variation implies a trade-off. In ectotherms, higher temperatures are associated with more rapid development (Gillooly et al., 2002). However, in a typical example of countergradient variation, wherein individuals originating from cold and warm environments are reared in a common garden, those from cold environments develop more rapidly. The implication is that cold environment

populations have locally adapted faster intrinsic rates of development, helping them to cope with their challenging thermal conditions. However, it is harder to understand why intrinsic development rates are depressed in populations from warmer environments. Because organisms develop under seasonal and other time constraints, rapid development should confer advantages to all populations, regardless of thermal conditions. Yet, common garden experiments frequently reveal populations with decreased intrinsic development rates (e.g., Arendt, 1997; Laugen et al., 2003; Skelly, 2004). This widely observed pattern implies an equally widespread mechanism driving decreases in intrinsic rates.

Physiological trade-offs between thermally-dependent traits may constrain the adaptive evolution of thermal performance curves. While the maximum and minimum bounds of thermal performance curves seem to be relatively evolutionarily conserved, many amphibian species exhibit lability of thermal performance between critical thermal limits (reviewed in Bodensteiner et al., 2020). Nevertheless, the countergradient patterns common among temperate ectotherms indicate that the ability to balance performance and development is not limitless (Conover et al., 2009). The goal of the current study is to evaluate the potential for a trade-off between development rate and performance that may drive the formation of countergradient variation in development rate. We hypothesize that higher rates of development will be associated with decreased locomotor performance, as has been found in several previous studies (e.g., Arendt, 2003; Arnett et al., 2006; Watkins & Vraspir, 2006). We depart from previous literature in testing for parallel response across many populations and by comparing experimental results to wild cohort-mates. We additionally consider whether burst speed performance itself varies in a countergradient fashion.

In this study, we focus on the wood frog (*Rana sylvatica*). Wood frogs breed in a wide variety of wetlands that vary in thermal conditions (Halverson et al., 2003; Skelly, 2004), variation that is at least partially driven by differences in canopy cover (Skelly et al., 2014). On a microgeographic scale, development rates of both embryos and larvae (i.e., tadpoles) vary in countergradient fashion among populations—individuals from colder natal environments develop more rapidly than those from warmer environments when reared under common conditions (Ligon & Skelly, 2009; Skelly, 2004). Here, we study the same populations in which countergradient variation in development rate has previously been observed. We ask the following questions: (1) Is burst speed performance negatively associated with development rate (which we experimentally manipulate through differences in rearing temperature)? (2) Does burst speed differ between pond populations when raised at a common temperature? If so, is this variation itself countergradient to natal pond temperatures? In a parallel analysis, we compare the results from tadpoles reared in our common garden to cohort-mates collected from the wild to ask: (3) Do wild-caught tadpoles show a congruent trade-off between environmentally determined development rate and performance? (4) Do wild-caught tadpoles from the same set of ponds show countergradient variation in their burst speed performance?

2 | METHODS

2.1 | Study species

Wood frogs are the most widespread amphibian in North America and have the most northerly range (Lee-Yaw et al., 2008). Breeding occurs once per year in the early spring, just after ponds are clear of ice (reviewed in Dodd, 2013). Each female lays one “mass” of eggs, which can be distinguished from adjacent masses. Generally, all egg masses in a pond are deposited in a single aggregation within a few days. Eggs in a single mass are at least half-siblings, originating from the same female with a low occurrence of multiple paternity (Halverson et al., 2006). Oviposition is concurrent among ponds within metapopulations (Petranka et al., 2004). In 2019, oviposition among all 61 ponds at our field site occurred within 6 days beginning on April 4, and 90% of populations laid within a span of 4 days. Larvae mature and metamorph to the terrestrial life stage within a single summer, before the desiccation of their ephemeral breeding ponds.

2.2 | Study site

We collected wood frog embryos during the 2019 breeding season from 10 breeding ponds at Yale Myers Forest (YMF; 3213 ha, northeastern Connecticut, USA). Eggs were collected between April 4 and April 8, within 24 h of oviposition. Ponds were selected to represent a gradient of local water temperatures. We recorded water temperature in natal ponds over the course of the season by placing submersible loggers (HOBO 8K Pendant; Onset Computer Corporation) 10 cm below the water surface at the point of maximum depth. Loggers were placed in the ponds before breeding began. We estimated long-term pond temperatures from historic logger data. On days when temperature measurements were unavailable (~44% of days between day of year 111 and 181, years 2001–2018, across all ponds), we predicted them using a random forest including 500 regression trees implemented in the *randomForest* R package (v4.6.14; Liaw & Wiener, 2002).

2.3 | Animal collection and housing

In each pond, we collected approximately 25 embryos (roughly 3%–9% of an egg mass) from each of five egg masses (i.e., clutches) and stocked these across two temperature treatments in a split-clutch design. To induce a difference in development rates, we used incubators (I-36VL; Percival Scientific Inc.) to create two temperature treatments. Incubators were kept on a 12:12 h light:dark cycle. The high- and low-temperature incubators were initially set to 12°C and 6°C, respectively. We increased incubator temperatures gradually over the course of the developmental period, approximating the temperature trajectories that wood frog tadpoles experience in the warmest and coolest natal ponds at YMF (Figure 1). Every 14 days,

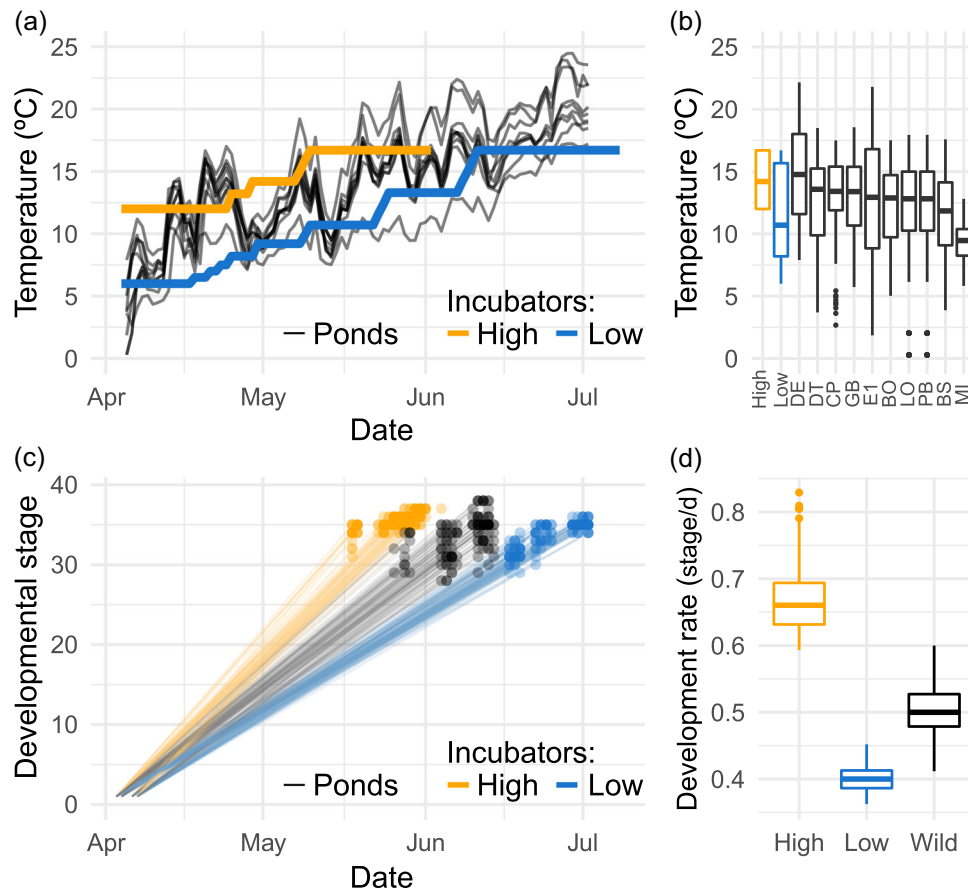


FIGURE 1 (a,b) Temperatures in incubators and natal ponds during the 2019 season. 'High' and 'Low' refer to the corresponding temperature treatments in the lab. Two-letter codes are abbreviations for the names of individual ponds. (c,d) Development rates of warm treatment, cold treatment, and wild tadpoles [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jez.2434)]

we ramped the incubator temperatures, ensuring no more than a 1°C increase each day. We ceased to ramp temperatures when they reached 17°C.

Upon hatching, tadpoles were stocked individually into glass jars (four per treatment per clutch) containing 500 ml of reconstituted distilled (RD) water (0.06-g aquarium salt; API Aquarium Pharmaceuticals, per 1 L of distilled water [final conductivity ~120 μ S]). We stocked each incubator with 200 tadpoles (10 natal ponds; five clutches per pond; four individuals per clutch). We blocked tadpoles by clutch across five shelves in each incubator, with individuals randomized on each shelf. We cleaned jars and replaced water every three or four days. At the same time, we fed each tadpole approximately 10% of body mass (3:1 ratio of powdered Kaytee Rabbit Chow; Kaytee Products, Inc. and TetraPro Goldfish Food; Tetra GmbH). We rotated jars within blocks after each cleaning. The day before conducting burst speed assays, we removed tadpoles from the incubators and fasted them for 24 h while allowing them to acclimate to the conditions in a temperature-controlled animal room. The animal room was maintained at the final incubator temperature (17°C), with a 12:12 h light:dark cycle.

We revisited the natal ponds at YMF every 2 weeks. Once wild tadpoles reached Gosner (1960) stage 30 or greater, we collected

15–20 individuals and stocked them in the animal room in 500-ml glass jars (one tadpole per jar), feeding them approximately 10% of body mass every 3 days. We maintained wild tadpoles in the lab for 1–5 days before performance assays to acclimate them to experimental temperatures (Brattstrom, 1968). Like the lab-reared tadpoles, wild tadpoles were fasted for 24 h immediately before their burst speed assays. In two natal ponds, E1 and MI, we were not able to recover any wild-caught tadpoles, despite several attempts. For the ponds from which we did collect wild tadpoles, the median number of tadpoles analyzed was 18 (minimum = 9; maximum = 20).

2.4 | Burst speed performance

To evaluate performance, we measured the “burst” swimming speed of a tadpole's startle response to a simulated predator attack. We conducted burst speed assays on both lab-reared and wild-caught tadpoles in a custom-built arena setup, over the period between May 18 and July 2. Arenas consisted of two 45 × 65 cm white, shallow trays filled with RD water to 1.5 cm depth to confine tadpoles to a horizontal swimming plane, following Arendt (2003). Arenas were illuminated using light-emitting diode light strips and overhead

lamps. A camera (Hero 4; GoPro, Inc.; 1080p, 60 f/s, narrow field of view) was fixed above each arena.

After transferring a tadpole to the arena, we placed a translucent acrylic cylinder over the tadpole to confine it to the center of the arena for a 45-s acclimation period, plus an additional 15-s motionless period. If the tadpole moved during the latter period, the 15-s count was restarted. Following the 15-s motionless period, we lifted the cylinder and tapped the tadpole's tail from behind with a blunt probe to induce a startle response (Arendt, 2010). Once the tadpole reached the edge of the arena or stopped swimming, we recaptured it in the cylinder and returned it to the center of the arena. If the tadpole bolted after the cylinder had been lifted but before its tail had been tapped, it was returned to the center and allowed an additional 30-s motionless rest period before initiating another startle response.

We conducted at least three burst speed trials for each tadpole, allowing a 15-s motionless rest period between trials. If, during a trial, the tadpole reacted minimally to a tap from the probe, we returned it to the center and conducted an additional trial after a rest period. We measured the temperature of the water in the arena, using an infrared probe, at the beginning of the sequence of trials for each tadpole. We maintained water temperature in the arenas at a mean of 17.0°C (range = 15.6°C–18.1°C, $SD = 0.55^\circ\text{C}$). Overall, our dataset included an average of 2.88 burst speed trials per tadpole for 307 lab-reared tadpoles ($N_{\text{High}} = 164$ and $N_{\text{Low}} = 143$) and 128 wild-caught tadpoles, totaling 1245 observations.

We used Adobe Premiere Pro to edit the videos of performance assays into separate trials. Video sequences were corrected to account for lens distortion from the cameras that might otherwise have affected measurements of distance and speed, especially near the edges of the arena. We used a custom script in MATLAB to identify the position of the tadpole's centroid in each video frame and track its trajectory through each video clip. We extracted burst speeds as the straight-line distance covered by the tadpole in the initial half-second of the startle response, measured from the first frame in which the tadpole moved from its starting position. Consistent with Arendt (2003), paired t tests between the first and second half second showed that tadpoles began to slow after the first half second ($t(1611) = 13.48$; $p < 0.001$).

2.5 | Development rate

We estimated development rates as the difference in developmental stage from oviposition (Stage 1) to the time of the performance assay, divided by the number of days since oviposition. Because the temperature treatments we imposed in the lab roughly bracketed the temperatures that wood frog tadpoles were exposed to in wild ponds (Figure 1) and because developmental temperature should impact developmental rates in ectotherms (Gillooly et al., 2002), we expected that high-treatment

tadpoles should develop more rapidly than low-treatment tadpoles. Therefore, the development rates of the two laboratory groups should roughly bracket those of the wild-caught tadpoles.

To test these predictions, we used a single ANOVA to compare mean development rates between the three groups: lab-reared, low-treatment tadpoles; lab-reared, high-treatment tadpoles; and wild-caught tadpoles. For this and other analyses, we visually examined residual and normal quantile plots to verify that our data met the assumptions of the test being performed. As predicted, development rates differed significantly between groups ($F_{2, 1251} = 5373$; $R^2 = 0.90$; $p < 0.001$), and rates for wild-caught tadpoles (0.50 stage/day) fell between those of the two lab-reared treatments (high: 0.67 stage/day; low: 0.40 stage/day). We further tested the proximate effect of average incubator or pond temperature on development rates (for lab-reared and wild tadpoles, respectively) using ordinary least squares regression. In the lab, development rates were higher by 0.09 stage/day per degree of difference in rearing temperatures ($F_{1, 305} = 3501$; $R^2 = 0.92$; $p < 0.001$). In the wild, development rates were higher by 0.02 stage/day per degree of difference in the average pond temperature ($F_{1, 126} = 32.18$; $R^2 = 0.20$; $p < 0.001$).

2.6 | Morphometrics

We euthanized tadpoles within 24 h after their burst speed trials and recorded tadpole wet mass (to 0.001 g). All groups (wild-caught tadpoles, and the two lab-reared temperature treatments) had similar ranges of mass (high: mean = 0.62, $SD = 0.10$; low: mean = 0.48, $SD = 0.13$; wild: mean = 0.58, $SD = 0.19$; Figure S2). We used a dissecting microscope to determine developmental stages. Tadpoles were of similar developmental stage across both lab treatment groups (high: median = 35, range = 31–37; low: median = 34, range = 29–36, Figure S2) and wild-caught tadpoles (median = 34, range = 28–38).

We captured lateral photographs of each tadpole for morphometric analysis. We used 26 morphometric landmarks (Figure 2) to estimate each tadpole's body shape, following Arendt (2010), Johansson et al. (2010), and Urban et al. (2017). Landmarks were digitized from the photographs, using tpsDig (v2.31). We used the *geomorph* package (Adams & Otárola-Castillo, 2013) to perform a generalized procrustes analysis on the landmarks and to generate principal components of lateral body and tail shape variables for further analysis (Adams et al., 2020). We considered the first two principal components generated from the morphometric landmarks, which together explained 66.4% of the variation in tadpole shape, for inclusion in the model. PC1 roughly corresponded to the ratio of body length to total length, and PC2 was an approximate measure of the ratio of total length to body depth (Figure S3). Of these two, PC2 was a stronger predictor of burst speed in a univariate regression, so we selected it for inclusion in the model (Figure 2).

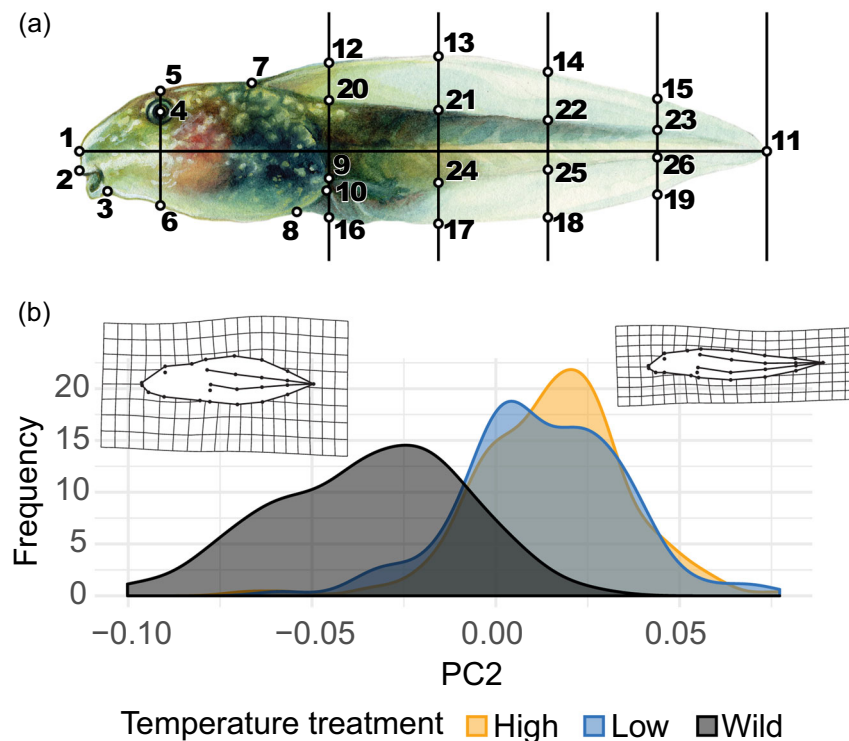


FIGURE 2 (a) Geometric morphometric landmarks. Landmarks 1–11 were treated as true landmarks because they represented homologous body parts between specimens. Landmarks 12–15 (upper edge of the tail fin), 16–19 (lower edge of the tail fin), 20–23 (upper edge of the tail muscle), and 24–26 (lower edge of the tail muscle) were digitized based on their placement relative to other landmarks (e.g., landmarks 14, 18, 22, and 25 are located along a vertical line at the halfway point between the base and tip of the tail). Therefore, these landmarks were treated as semilandmarks and allowed to “slide” along their respective curves (Adams et al., 2020). (b) Density plot of principal component (PC) scores for wild and lab-reared tadpoles along the second size-independent principal component constructed from the landmarks shown in (a). Warps represent minimum and maximum scores along the PC2 axis, respectively [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jez.2444)]

2.7 | Performance/development rate trade-off

To estimate the relationship between development rate and performance, we fit a linear mixed-effects model predicting performance from individual tadpoles' development rates, while accounting for potential confounding variables and avoiding pseudoreplication. Mixed models were fit in *lme4* (v1.1.21; Bates et al., 2015). Based on existing literature, we hypothesized that tadpole burst speeds would be affected by developmental stage, shape, size-at-stage (allocation), and the water temperature of the experimental arena (Goldstein et al., 2017; Van Buskirk & McCollum, 2000). Accordingly, we included developmental stage, size-at-stage, arena temperature, and one principal component of body/tail shape from our morphometric analysis as additive covariates in our model (Figure S2). We treated pond, clutch, and individual identity as nested random intercepts to account for our hierarchical sample structure and repeated measures. This analysis, and all others in the present study, were performed in R (v3.6.2; R Core Team, 2018).

Ectotherm growth and development proceed interactively and are affected by many environmental stimuli (Kingsolver & Huey, 2008). As a result, the allocation of resources to growth or development is variable across tadpole ontogeny in different environments (Feder & Burggen, 1992). Because allocation rates may impact

the trade-off between performance and development rates, we also included the interaction between size-at-stage and development rates in our mixed models. We estimated allocation (size-at-stage) as deviance from an average mass at a given stage. To obtain allocation values, we fit one linear model each for lab-reared and wild tadpoles, predicting mass by stage, including a categorical covariate for temperature treatment in the lab-reared model (an interaction term between temperature treatment and stage was not significant, so we did not include it). We extracted residuals from the models for each tadpole and incorporated them into subsequent models of performance as an allocation covariate.

We calculated 95% confidence intervals and *p* values for the main effect coefficients from 1000 bootstrap iterations, using the *parameters* package (v0.5.0; Makowski et al., 2019). We estimated conditional and marginal R^2 values using Nakagawa and Schielzeth's (2013) method implemented in the *MuMIn* package (v1.43.15; Bartón, 2019). We calculated 95% confidence intervals for random-effect coefficients from 1000 bootstrap iterations using *lme4* (v1.1.21; Bates et al., 2015).

After fitting the mixed-effects model, we computed conditional partial regression estimates of burst speed on development rate for each individual tadpole, while holding all other variables constant at their mean (or median, in the case of stage) values. We use these

conditional partial regression estimates (hereafter, adjusted burst speed) in subsequent analyses. We used the random-effect coefficients from our mixed models to estimate repeatability (estimated as the proportion of total variation due to individual differences (Bell et al., 2009) and overall variance of our corrected burst speed performance metric.

To evaluate the relationship between development rate and burst speed in wild-caught tadpoles, we fit a linear mixed-effects model and carried out partial regressions for wild tadpoles, following the methods described above for lab-reared tadpoles. Models for lab-reared and wild-caught tadpoles were identical, with the exception that clutch affiliation was unknown for wild tadpoles, so the random-effect term for the wild model included only the individual tadpole identifier nested within pond. As described above for the lab-reared tadpoles, we estimated repeatability and overall variance using the random-effect estimates from our model.

2.8 | Countergradient variation

To test for countergradient variation in lab-reared tadpoles' performance with respect to their natal pond temperatures, we fit a

linear mixed-effects model predicting adjusted burst speed by average long-term pond temperature over the period from 2001 to 2018, with a random effect for pond. Pond average temperatures were computed from daily pond temperature measurements. We included treatment group (low/high) as a categorical covariate in the pond temperature regression.

As described above for lab-reared tadpoles, we tested for countergradient variation in performance using a linear regression of adjusted burst speed (the partial regression coefficient derived from the mixed model) on average pond temperature over the period from 2001 to 2019, as described above. This regression differed from the method described for lab-reared tadpoles only in the absence of a covariate term for the temperature incubators.

3 | RESULTS

3.1 | Performance/development rate trade-off

Among lab-reared tadpoles, performance was negatively associated with development rate, with a reduction of 4.6 mm/s in burst speed per 0.1 stage/day increase in development rate (Table 1, Figures 3

TABLE 1 Linear mixed-effect models of swimming performance (burst speed) for lab-reared and wild-caught tadpoles by development rate, Gosner stage, tadpole shape, size-at-stage, and arena temperature as fixed effects

Fixed effects	Lab-reared			Wild-caught		
	Estimate	95% CI ^a	<i>p</i> ^a	Estimate	95% CI ^a	<i>p</i> ^a
Intercept	−96.659	−151.739 to −46.651	<0.001	48.806	−67.157 to 171.715	0.480
Size at stage	83.038	−5.826 to 182.536	0.082	422.223	−17.812 to 858.335	0.064
Development rate	−45.704	−57.821 to −33.573	<0.001	−63.064	−183.852 to 47.149	0.296
Gosner stage	5.167	4.133 to 6.283	<0.001	1.408	−0.503 to 3.224	0.130
Shape PC2	72.834	−6.087 to 152.037	0.073	36.109	−122.168 to 196.574	0.653
Arena temperature	0.235	−2.481 to 3.046	0.855	−0.182	−6.533 to 6.173	0.995
Size at stage: Development rate	−131.747	−308.008 to 27.322	0.128	−786.560	−1678.603 to 70.338	0.076
Random effects	σ	95% CI ^c		σ	95% CI ^c	
Individual: (Clutch:Pond)	11.22	9.862 to 12.399				
Individual: Pond				17.140	14.680 to 19.810	
Clutch: Pond	0.00	0.000 to 3.573				
Pond	0.00	0.000 to 2.637		4.998	0.000 to 9.930	
Residual	10.93	10.287 to 11.517		10.325	9.348 to 11.252	
Marginal R^2	0.237 ^b			0.080 ^b		
Conditional R^2	0.629 ^b			0.769 ^b		

Note: The model of lab-reared tadpoles, includes nested random intercepts for each pond, clutch, and individual tadpole ($n = 887$). The model of wild-caught tadpoles included nested random intercepts for each pond and individual tadpole ($n = 367$). Burst speed is measured in mm/s for both models. Abbreviation: CI, confidence interval.

^aThe 95% CIs and p values for main effects were estimated from 1000 bootstrap iterations, implemented in the *parameters* package (v0.5.0; Makowski et al., 2019).

^bMarginal and conditional R^2 values were estimated with Nakagawa and Schielzeth (2013) method, implemented in the *MuMIn* package (v1.43.15; Bartón, 2019).

^cThe 95% CIs for random effects were estimated from 1000 bootstrap iterations, implemented in the *lme4* package (v1.1.21; Bates et al., 2015).

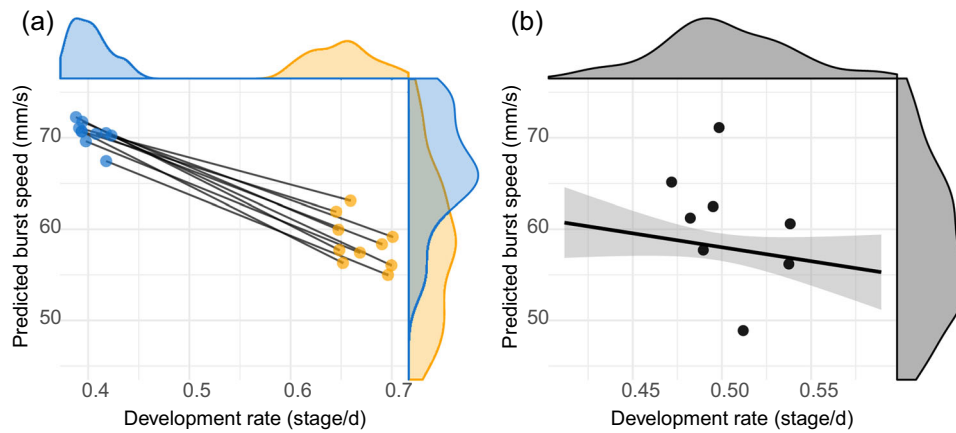


FIGURE 3 Relationship between development rate and burst speed for (a) lab tadpoles and (b) wild tadpoles. Dots represent pond-wise means, and in (a), lines connect means from the same pond. Marginal density plots are based on individual tadpoles rather than pond-wise means. Orange and blue represent tadpoles reared in the high- and low-temperature incubators, respectively [Color figure can be viewed at wileyonlinelibrary.com]

and S1). This negative relationship is consistent with a trade-off between development and performance. Our models (Table 1) suggest a similar performance trade-off in wild-caught tadpoles to that found in lab-reared tadpoles (Figure 3b). For wild-caught tadpoles, burst speed was 6.31 mm/s faster for every additional 0.1 stage/day in development rate; however, confidence intervals for the slope coefficient included 0 (Table 1).

3.2 | Countergradient variation

We found no evidence of countergradient variation in performance (adjusted burst speed) with long-term temperatures of natal ponds for lab-reared tadpoles (-0.009 mm/s/°C; $p = 0.98$; Table 2). The pond-level random-effect coefficient in our mixed model for lab-reared tadpoles confirms the absence of performance variation between ponds ($\sigma = 0.00$; 95% confidence interval [CI] = 0.00–2.64; Table 1 and Figure S5). The mean variation in performance between pond populations for wild-caught tadpoles was 5.00, although the confidence interval of the random-effect coefficient includes zero (95% CI: 0.00–9.93; Table 1). There was a slight negative relationship between performance and long-term average natal pond temperature of natal ponds for wild-caught tadpoles (-3.97 mm/s/°C; $p = 0.05$; Table 2). Although marginally significant, this relationship is in the direction that would be expected in the case of countergradient variation (Figure S4).

3.3 | Covariates of performance

For both wild-caught and lab-reared tadpoles, slope coefficients for performance were positively associated with arena temperature,

size-at-stage, and developmental stage, although all coefficients with the exception of developmental stage in the model of lab-reared tadpole performance had confidence intervals including 0 (Table 1).

Morphology was also weakly associated with performance (Table 1). Body shape varied considerably between wild and lab-reared tadpoles (Figures 2b and S2). PC2 primarily differentiated wild-caught tadpoles, which had a high ratio of tail surface area to body size and a low ratio of tail surface area of tail muscle depth, from lab-reared tadpoles, which tended to have smaller tails but deeper tail muscles (Figure 2b). More “lab-like” morphology tended to confer faster burst speeds (Table 1).

3.4 | Repeatability and variance

Repeatability of burst speeds was similarly high for measurements of both wild (0.81) and lab-reared tadpole (0.73) burst speeds. After accounting for variation in performance among measurements for an individual tadpole, within-pond variation of performance of wild-caught tadpoles was much higher ($\sigma = 17.14$; 95% CI: 14.69–19.69) than between-pond variation ($\sigma = 5.00$; 95% CI: 0.00–9.53; Table 1). For lab-reared tadpoles, there was no discernable variation between ponds ($\sigma = 0.00$; 95% CI: 0.00–2.64), nor between clutches within-ponds ($\sigma^2 = 0.00$; 95% CI: 0.00–3.57), indicating low heritability of performance traits in these populations. Likewise, we did not find a strong indication of divergence in performance among populations (Table 1). The total variance in performance in lab-reared tadpoles was driven by variation among siblings ($\sigma = 11.22$; 95% CI: 9.86–12.40; Table 1). In general, the total variation in performance was 2.3 times greater in the wild than in the lab, indicating strong environmentally-induced plasticity of performance among tadpoles from wild ponds.

TABLE 2 Linear mixed-effect models of adjusted burst speed by average pond temperature for lab-reared and wild-caught tadpoles

Fixed effects	Lab-reared			Wild-caught		
	Estimate	95% CI ^a	<i>p</i> ^a	Estimate	95% CI ^a	<i>p</i> ^a
Intercept	58.900	48.920 to 70.617	<0.001	121.687	73.894 to 170.812	0.003
Average pond temperature	-0.009	-0.771 to 0.662	0.981	-3.973	-7.193 to -0.850	0.046
Temperature treatment (low)	12.125	9.920 to 14.399	<0.001			
Random effects	σ	95% CI ^c		σ	95% CI ^c	
Pond	0.489	0.000 to 2.178		2.886	0.000 to 6.816	
Residual	10.135	9.348 to 10.967		16.028	13.865 to 18.004	
Marginal <i>R</i> ²	0.263 ^b			0.067 ^b		
Conditional <i>R</i> ²	0.264 ^b			0.097 ^b		

Note: Pond temperatures were averaged over the period 2001–2018 between day of year (DOY) 111 and DOY 181. Each model includes a pond-level random intercept term.

Abbreviation: CI, confidence interval.

^aThe 95% CIs and *p* values for main effects were estimated from 1000 bootstrap iterations, implemented in the *parameters* package (v0.5.0; Makowski et al., 2019).

^bMarginal and conditional *R*² values were estimated with Nakagawa and Schielzeth (2013) method, implemented in the *MuMIn* package (v1.43.15; Bartón, 2019).

^cThe 95% CIs for random effects were estimated from 1000 bootstrap iterations, implemented in the *lme4* package (v1.1.21, Bates et al., 2015).

4 | DISCUSSION

Countergradient variation in physiological rates such as growth and development is commonly observed in ectotherms along temperature gradients. It is often easy to explain the benefits of such adaptive rates at one extreme of the gradient (e.g., developing faster in colder environments). However, it is harder to understand why the same trait is selected against at the other end of the gradient (e.g., why should populations from warmer environments evolve a slower temperature-specific development rate?) Wood frog populations in our study area show a well-established pattern of countergradient variation in development rate along a temperature gradient. In this study, we ask whether this countergradient pattern could be explained by a fundamental trade-off between development and burst speed performance. We find that temperature-mediated development rate does, in fact, trade off with swimming performance in wood frog tadpoles. Tadpoles reared at higher temperatures develop more rapidly and swim 20% more slowly than their slow-developing (low-temperature) counterparts, a difference in burst speed of 12.1 mm/s (4.03 mm/s/°C). Ours is not the first study to detect a development/performance trade-off in wood frogs (see Watkins & Vraspir, 2006). Yet, we additionally find that the direction of the reaction norm is consistent across 10 pond populations when individuals are reared at a common temperature, and we investigate wild-caught tadpoles as well as lab-reared individuals.

It is reasonable to consider whether performance itself exhibits a countergradient pattern with respect to natal pond temperatures, especially given that individual burst speed varies among tadpoles and shows high within-subject repeatability. Notably, we find no evidence of divergence in burst speed among pond populations. Mean swimming performance does not vary among lab-reared

tadpoles originating from different ponds (Table 1). Studies of this wood frog metapopulation have consistently found microgeographic divergence in other traits, including thermal preference (Friedenburg & Skelly, 2004) and critical thermal maximum (Skelly & Friedenburg, 2000), in addition to embryonic and larval development rates (Ligon & Skelly, 2009; Skelly, 2004). That burst speed alone does not differ among populations suggests that it may be a driver of the countergradient pattern in development rates.

Rapid development rates are generally advantageous for pond breeding amphibians, whose larvae must navigate waters filled with gape-limited predators and reach metamorphosis before their pond dries. In cold habitats, it is intuitive that an accelerated intrinsic development rate would counteract the environmental influence that slows development. However, despite the strong incentives for maximizing development rates, which also apply to warm habitats, larval amphibians from warmer ponds tend to develop more slowly than their cold habitat counterparts when reared at a common temperature. Independent studies of wood frogs have found this countergradient effect in embryonic (Skelly, 2004) and larval (Ligon & Skelly, 2009) development rates. Similar findings are known in other species (Berven et al., 1979; Laugen et al., 2003; Rödin-Mörch et al., 2019). The fact that populations in warmer ponds counteract extrinsic factors through depressed intrinsic development rates implies that there is a cost to rapid development in these habitats.

Our results suggest that in wood frogs, this cost comes, at least partly, in the form of a detriment to locomotor performance. Indeed, environmentally-mediated acceleration of growth has been shown to compromise performance in a range of ectothermic vertebrates (Álvarez & Metcalfe, 2007; Arendt, 2003; D. Li et al., 2007; Parichy &

Kaplan, 1995; Watkins, 2000; Watkins & Vraspir, 2006). Additionally, a growing body of literature has examined how performance trades off with genetically mediated growth rate (Arendt, 1997; Billerbeck et al., 2001; Gregory et al., 1998; Kolok & Oris, 1995). Among potential implications, rapid development that impairs swimming performance could compromise the ability of tadpoles to evade capture by predators—a potential direction for future study. Other aspects of performance, not included in our study, could also be compromised, including terrestrial locomotion: Several studies in anurans have indicated that costs of rapid development persist after the metamorphic transition (Álvarez & Nicieza, 2003; Ficetola & De Bernardi, 2006). These costs may exert a selection pressure toward slower intrinsic growth rates to mitigate the performance disadvantage.

In amphibians, development rates tend to increase with temperature, up to the point of lethality (i.e., strongly left-skewed thermal performance curve; reviewed in Feder & Burggen, 1992). Our results suggest that locomotor performance is strongly, negatively influenced by developmental rate, but while the thermal performance curve of development is evolutionarily labile, the association with locomotor performance is not. Thus, if the covariance between these traits remains relatively fixed, but intrinsic development rates evolve more readily, then selection would favor development rates that counteract decreases in swimming performance in either direction away from the optimum. Such decreases could be caused, for example, by environmental conditions that extrinsically elevate or depress development rates away from the rate that confers optimal swimming performance (Angilletta, 2009; Conover & Schultz, 1995). The result would be a countergradient pattern of intrinsic development: rapid development in colder environments and depressed development in warmer environments.

What could be the proximate mechanism for the development/performance trade-off? Burst swimming integrates complex interactions of biophysical processes, including neuromuscular recruitment of muscle fibers and the timing of contraction and release of bilateral muscles, all of which are developmentally dependent (Feder & Burggen, 1992). The aerobic properties of the muscles may also differ between treatment groups. Arnott et al. (2006) proposed that disparity in swimming speeds may result from competing metabolic demands of growth and performance. Watkins (2000) showed that ATPase activity, which is related to muscle force and contraction velocity, was elevated in *Hyla regilla* tadpoles reared at a cooler temperature. The same relationship has also been demonstrated in teleost fish (e.g., Johnson et al., 1996) and crocodilians (Seebacher & James, 2008)). While the mechanism underlying our findings remains undefined, the potential role of temperature in the development of muscle morphology and physiology deserves further study. This mechanism could prove to be more widely relevant among ectotherms and may help to explain the widespread occurrence of countergradient variation.

In magnitude, our findings are largely congruent with the few prior studies of amphibians that have detected decreased swimming

performance with more rapid development (fire-bellied toads, *Bombina orientalis* [approx. 1.34 mm/s/°C; Parichy & Kaplan, 1995], Pacific tree frogs, *Hyla regilla* [6.46 mm/s/°C; Watkins, 2000], and wood frogs, *R. sylvatica* [1.2 mm/s/°C; Watkins & Vraspir, 2006; see Seebacher & Grigaltchik (2015) for an exception]). The consistency of effect among these studies is matched, within our study, by the strong consistency of the development/performance relationship in lab-reared individuals across 10 natural populations of wood frogs.

While we observed a similar development/performance relationship among wild-caught tadpoles from the same 10 populations, measurements were more variable. Wild-caught individuals showed a weaker relationship between development rate and performance than lab-reared individuals, and variability was higher (Figure 3b). Environmental factors in the wild ponds likely account for this higher variation. Compared with their lab-reared cohort-mates, wild tadpoles experienced more variability in temperature during development. Pond temperature means were taken across several months, obscuring both diurnal temperature variability and large swings, such as those that occurred in late April and mid-May 2019 (Figure 1a). The temperature environments in our study ponds are spatially heterogeneous (Skelly et al., 2014) and tadpoles exhibit thermal preference through their behavior (Freidenburg & Skelly, 2004; Herreid & Kinney, 1967). Pond temperatures estimated from a single logger in a fixed location likely do not reflect tadpoles' experiences of the pond thermal environment. This thermal heterogeneity may contribute to the greater variation in burst speed observed relative to lab-reared individuals (Figure S6).

In addition to temperature, predation and other selection pressures in wild ponds likely affected the performance of our wild-caught tadpoles. In the lab, survival was high, conditions controlled, and predators absent. By contrast, the tadpoles that we captured from the wild were those that had survived whatever episodes of selection had whittled down the initial cohort by the time they were collected. These selective pressures almost certainly differed among ponds. Work on *Rana temporaria* has also illustrated the influence of predation pressure on physiological rates, including growth and development (Steiner & Van Buskirk, 2009), and predator communities almost certainly varied among ponds, potentially leading to different selective pressures (e.g., Urban, 2007). Finally, selection on burst speed likely affected the distribution of speeds in our sample of wild tadpoles, altering the development–performance relationship compared with that observed in their lab-reared cohort-mates.

Temperature is an external force that shapes nearly every feature of ectotherms. If thermal biology could be understood as a simple function of distinct biological reactions, we could scale up the temperature dependencies of individual processes to understand how temperature impacts the function and fitness of organisms, populations, or even species. However, physiological functions depend on temperature in different ways that are sometimes in conflict, as our study demonstrates. Understanding trade-offs like the one considered here helps us to better grasp the complex, interrelated processes involved in ectotherm

physiology. The consistency of the development–performance trade-off among populations in our study, together with similar findings across taxa, suggests that performance costs of rapid growth and development are a fundamental feature of ectotherm life history.

It is also critical to understand how climate change will affect organisms in a warming world. Amphibians are especially vulnerable to climate change effects (Y. Li et al., 2013), and ectotherms, in general, are likely to be particularly affected by temperature increases (Parmesan, 2006). In the case of pond-breeding amphibians like the wood frog, the dual pressures of warming temperatures and shortening hydroperiods should favor more rapid development. As our study shows, developing more rapidly can come with performance costs. Conceivably, organisms could counteract the costs of temperature-mediated rapid development by evolving adaptively slower intrinsic development rates, but only to an extent if the thermal dependence of performance is constrained. These results highlight the importance of looking beyond critical thermal limits to considering the (co)evolution of thermal dependencies for interacting traits. The degree to which rapid evolution will support the persistence of species facing a changing climate is a challenging but critical topic for further study.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.69p8cz8zz>.

ORCID

Kaija Gahm  <http://orcid.org/0000-0002-4612-4426>

A. Z. Andis Arietta  <https://orcid.org/0000-0002-3368-1346>

David K. Skelly  <https://orcid.org/0000-0002-5067-4535>

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SUPPORTING INFORMATION

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