BRIEF COMMUNICATION

Sex-Specific Population Differences in Resting Metabolism Are Associated with Intraspecific Variation in Sexual Size Dimorphism of Brown Anoles

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ABSTRACT

Sexual size dimorphism can vary in direction and magnitude across populations, but the extent to which such intraspecific variation is associated with sex and population differences in underlying metabolic processes is unclear. We compared resting metabolic rates (RMRs) of brown anole lizards (*Anolis sagrei*) from two island populations in the Bahamas (Eleuthera and Great Exuma) that differ in the magnitude of male-biased sexual size dimorphism. Whereas females from each population exhibit similar growth rates and body sizes, males from Great Exuma grow more quickly and attain larger body sizes than males from Eleuthera. We found that these population differences in growth of males persisted in captivity. Therefore, we predicted that males from each population would differ in RMR, whereas females would not. Consistent with this prediction, we found that RMR of males from Eleuthera was higher than that of males from Great Exuma, particularly at higher temperatures. As predicted, RMR of females did not differ between populations. Despite this apparent sex-specific trade-off between growth rate and RMR at the population level, we found a positive relationship between growth rate and RMR at the individual level. The fact that Great Exuma males maintain lower RMR than Eleuthera males, despite their greater absolute growth rates and the positive relationship between RMR and growth rate across individuals, suggests that Great Exuma males may have lower baseline metabolic demands and/or greater growth efficiency than Eleuthera males. Our results call attention to sex-specific divergence in metabolism as a potential mechanism for intraspecific divergence in sexual size dimorphism.

Keywords: Anolis sagrei, growth rate, life history, resting metabolic rate, pace of life.

Introduction

Sexual dimorphism is ubiquitous and evolves despite the fact that males and females share an autosomal genome (Lande 1980; Chenoweth et al. 2008; Mank 2008; Cox and Calsbeek 2009). Consequently, the evolution of sexual dimorphism requires not only genetic change but also intermediate physiological mechanisms that allow this change to be expressed in sex-specific fashion. Sex differences in body size often result from sex differences in the regulation of growth and underlying gene networks (Badyaev 2002; Cox et al. 2017; Cox 2020), but less is known about the evolution of organismal metabolism as it relates to sex differences in growth and body size (Henderson et al. 2003; Cox et al. 2005; Rennie et al. 2008). One way to address this issue is to compare metabolic physiology between populations that have diverged in patterns of growth and sexual size dimorphism, particularly those for which intraspecific differences reflect genetic divergence (Garland and Adolph 1991). Although many studies have linked interpopulation divergence in life history to associated differences in basal, standard, or resting metabolic rate (RMR; e.g., Angilletta 2001; Lahti et al. 2002; Lardies et al. 2004; Sears 2005; Arnott et al. 2006; Lardies and Bozinovic 2006; Bronikowski and Vleck 2010; Auer et al. 2018), few have explored whether these population differences in metabolism are sex specific (Gangloff et al. 2015) to address whether they may shape intraspecific variation in sexual dimorphism.

RMR is the minimum metabolic rate of an individual in a relatively quiescent state, which provides an estimate of baseline energy expenditure in the absence of activity and digestion (Burton et al. 2011). There are at least two distinct ways in which RMR might relate to growth and, by extension, to sexual size dimorphism. First, RMR might reflect the overall metabolic potential of an individual to support rapid growth. In this scenario, growth should be positively correlated with metabolic rate such that individuals and populations with faster growth rates should also have higher RMR for any given body size (Metcalfe et al. 1995; Millidine et al. 2009; Bronikowski and Vleck 2010). On the other

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hand, estimates of RMR are often interpreted as approximating the baseline rate of energy expenditure that is required for maintenance and essential physiological processes. To the extent that these energetic demands of maintenance trade off against allocation to growth, RMR should be negatively correlated with growth rate at both the population and individual levels (Steyermark 2002; Burton et al. 2011; Reid et al. 2011). These hypotheses predicting positive versus negative associations between RMR and growth are not mutually exclusive in terms of their underlying mechanisms, which may shift in relative importance during development or in response to changes in environmental factors, such as food availability (Burton et al. 2011; Auer et al. 2015). Moreover, relationships between RMR and growth that are observed across populations can be absent at the individual level, and vice versa (Reid et al. 2011; Handelsman et al. 2013). Additionally, the maintenance costs that contribute to RMR can change throughout ontogeny, across seasonal and circadian cycles, and in response to temperature and other biophysical variables (Bennett and Dawson 1976; Clarke 2004; Clarke and Fraser 2004; Careau et al. 2008; Burton et al. 2011).

To test whether intraspecific differences in sexual size dimorphism are associated with sex-specific differences in resting metabolism, we compared two populations of the brown anole (*Anolis sagrei*), a small lizard in which males are substantially larger than females. The extent to which males exceed females in size varies considerably across island populations in the Bahamas (Schoener and Schoener 1980; Stamps 1999). Detailed demographic studies show that males on the island of Great Exuma are 32% longer in snout-vent length (SVL) and 153% more massive than females, whereas males on the island of Eleuthera are only 22% longer in SVL and 106% more massive than females (Cox and Calsbeek 2010). Females attain similar body sizes on each island such that intraspecific variation in sexual size dimorphism is largely attributable to differences in the growth and body size of males (Cox and Calsbeek 2010). These differences in male growth and body size persist in captive-bred individuals (R. M. Cox, unpublished data), and growth and body size are also heritable within populations (Cox et al. 2017; McGlothlin et al. 2019), suggesting that population differences in growth, size, and sexual dimorphism have a genetic basis. Our goal in this study was to test whether this sex-specific (i.e., present only in males) population divergence in growth and body size is accompanied by similarly sex-specific population divergence in RMR of males. We focus on RMR in part because previous work has shown that testosterone is an important regulator of sexually dimorphic growth in this species (Cox et al. 2009, 2017) and that stimulatory effects of testosterone on growth are associated with increased RMR (Cox et al. 2015*a*).

We measured RMR in adult males and females that we collected from Great Exuma and Eleuthera and maintained in captivity for over a year under common-garden conditions. First, we characterized growth and body size in captivity to confirm that population differences in the growth rates of wild males persisted under the laboratory common-garden conditions in which we measured RMR. Second, we measured RMR across three temperatures during the normal diurnal activity period and then tested for sex and population differences in size-corrected measures of RMR. Third, we characterized the relationship between RMR and growth rate at the individual level. We predicted that population differences in RMR would be sex specific (present only in males), similar to population differences in growth and size. We also predicted that, if RMR primarily reflects the overall metabolic potential of an organism to support rapid growth, then we should see higher RMR (after correcting for body size) in Great Exuma males as well as a positive association between RMR and growth at the individual level. However, if RMR primarily represents allocation to maintenance processes that compete with growth for limited energy, then we should see higher RMR in Eleuthera males (after correcting for body size) and a negative association between RMR and growth at the individual level.

Methods

Study Populations

We collected adult brown anoles (*Anolis sagrei*) from the islands of Eleuthera (24°50′N, 76°19′W) and Great Exuma (23°29′N, 75°45′W) in the Commonwealth of the Bahamas, then maintained them in captivity at the University of Virginia. We housed lizards individually in small plastic cages (males: 40 cm × 23 cm × 32 cm; females: 30 cm × 20 cm × 20 cm; Lee's Kritter Keeper, San Marcos, CA) within a room set to maintain a constant 29°C diurnal temperature, 25°C nocturnal temperature, and 65% relative humidity. We watered cages daily and provided lizards with a diet of crickets (*Gryllus assimilis*, *Gryllodes sigillatus*; Ghann's Cricket Farm, Augusta, GA) dusted weekly with Fluker's reptile vitamin and calcium supplements (Fluker's Cricket Farms, Port Allen, LA). We marked each lizard with a subcutaneous injection of a unique combination of colored elastomer tags on the underside of the limbs to ensure reliable identification (Northwest Marine Technology, Shaw Island, WA). All metabolic data were collected from 79 adults (Eleuthera: 20 females, 20 males; Great Exuma: 20 females, 19 males) that we maintained in captivity for approximately 1 yr before measurement. We also included data on body size, growth rate, and sexual dimorphism from a larger sample of 212 captive individuals (Eleuthera: 49 females, 46 males; Great Exuma: 74 females, 43 males). For each animal, we measured SVL (to the nearest 1 mm with a ruler) after 1 mo of acclimation to captivity, before the start of metabolism trials (11 mo later), and again after metabolism trials (13 mo later). Brown anoles rarely survive beyond 2 yr of age in either population (Cox and Calsbeek 2010), so our growth measurements spanning a year of life encompass the majority of the adult life stage. We calculated growth rates for each animal in both absolute (mm d^{-1}) and relative (percent increase) units over the entire 13-mo period and the shorter 2-mo period bracketing metabolism trials. In our data set, absolute growth rate (mm d^{-1}) is highly correlated with relative measures, such as specific growth rate (Reid et al. 2011) and percent increase in SVL ($r > 0.98$ within each sex), so we focus on analyses of absolute growth rate because this measure also reflects the sex differences in growth that give rise to sexual dimorphism. Below, we show that inferences about population differences in male growth are the same with either approach (fig. 1; table 1). We present these data to confirm that population differences in male

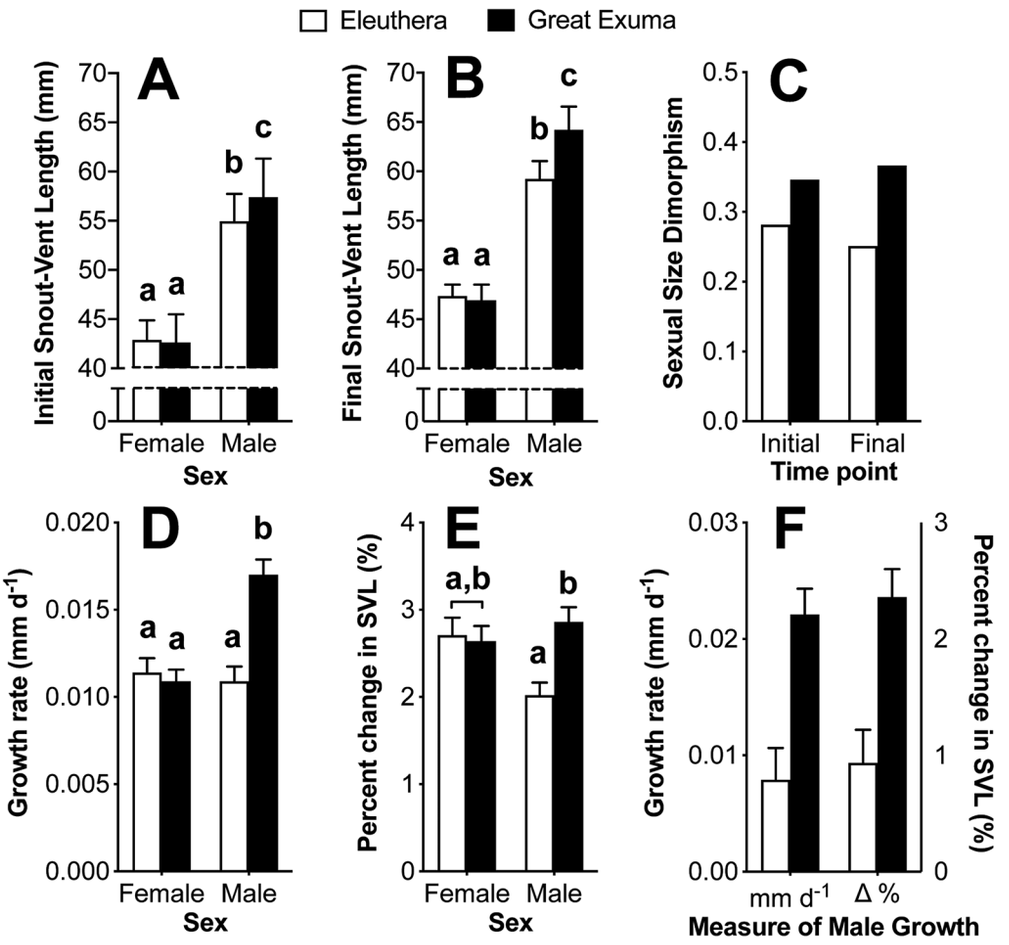

Figure 1. Population differences in size, growth, and sexual size dimorphism of 212 adults collected from Eleuthera and Great Exuma. *A*, *B*, Mean (±1 SD) snout-vent length (SVL) after 1 mo of acclimation to captivity (*A*) and 13 mo after initial measurement (*B*). *C*, Indexes of sexual size dimorphism, expressed as (male size/female size) − 1, based on means from *A* and *B*. *D*, *E*, Mean (±1 SE) growth in SVL expressed as an absolute rate (*D*) and percent change (*E*) over 13 mo in captivity. *F*, Comparable measures of growth for males over the 2-mo interval bracketing metabolism trials. Lowercase letters denote post hoc statistical separation (Tukey's honestly significant difference) based on analyses in table 1.

growth persist in captivity and were present when we measured RMR.

Metabolic Rate

We measured metabolism using stop-flow (constant-volume) respirometry with a field metabolic system (FMS; Sable Systems International, Las Vegas, NV) following previously established methods (Cox et al. 2015*a*, 2015*b*) and procedures recommended by the manufacturer (Sable Systems International 2009). We fasted lizards for 2 d before metabolic measurements, then weighed each animal to the nearest 0.01 g with a digital balance (Scout Pro, Ohaus, Parsippany, NJ) and placed it into one of eight 300-mL Plexiglass respirometry chambers (G115, Qubit Systems, Kingston, ON) housed within an incubator set for precise temperature regulation ± 0.2°C (PTC-1 cabinet and PELT-5 temperature controller, Sable Systems). Air was first drawn through a Drierite column to remove water vapor using a mass flow system sensor and pump (Sable Systems), then routed to individual chambers using an eight-channel multiplexer calibrated for stop-flow operation (RM-8, Sable Systems). Sampling occurred after each chamber had been closed for 50 min, at which point air was pushed through the chamber at 1,000 mL min^{-1} to purge the chamber and return it to ambient gas concentrations. One chamber was left empty (no animal) as a blank control for the sampling system. Excurrent chamber air was pushed into a manifold attached to the FMS, which subsampled the chamber air passing through the manifold by pulling it into the analyzer at 200 mL min^{-1}. The FMS continuously measured water vapor pressure, CO_2 concentration, and O_2 concentration as the chamber air flowed through the sensors, generating bolus traces of gas concentration versus time as the chamber was purged and returned to ambient concentrations. The areas under these curves were integrated to determine O_2 consumption. We automated sampling and data collection using ExpeData software (ver. 1.6.4; Sable Systems) and calculated O_2 consumption after accounting for barometric pressure, water vapor pressure, CO_2 concentration, flow rate through the chamber, and amount of time that the chamber was

Table 1: Tests for sex and population differences in body size and growth rate

Phenotype, effect	df	*F*	*P*
Initial SVL:			
Sex	1, 208	1,067.47	<.0001*
Population	1, 208	7.15	.0081*
Sex × population	1, 208	10.65	.0013*
Final SVL:			
Sex	1, 208	3,532.33	<.0001*
Population	1, 208	82.63	<.0001*
Sex × population	1, 208	117.48	<.0001*
Growth (mm d^{-1}):			
Sex	1, 208	12.13	.0006*
Population	1, 208	12.16	.0006*
Sex × population	1, 208	16.86	<.0001*
Growth (% change):			
Sex	1, 208	.37	.5442
Population	1, 208	6.02	.0149*
Sex × population	1, 208	7.75	.0059*

Note. Two-way ANOVA was used to test for sex and population effects. Initial snout-vent length (SVL) was measured in wild-caught adults after 1 mo of acclimation to captivity. Final SVL was measured 13 mo after initial SVL. Analyses of growth correspond to rates or percent changes measured over this 13-mo period. See figure 1 for corresponding data and statistical separation of groups based on post hoc Tukey tests.

*Statistically significant at $P < 0.05$.

closed (Lighton 2008). Before the study, we calibrated the O_2 sensor using the fixed-span mode with ambient air flowed through a Drierite column (Lighton 2008). We calibrated the CO_2 sensor with pure nitrogen (zero oxygen) and custom span gas (0.05% CO_2, 99.5% nitrogen, product no. NI CD5000C-Q, GTS-WELCO, Morrisville, PA). We calibrated the water vapor sensor using zero-humidity nitrogen and water-saturated ambient air (Lighton 2008).

We sampled each chamber hourly for 10 h (0900 hours to 1900 hours), over which time we varied the chamber temperature among three set points (25°, 30°, and 35°C), with 3 h of consecutive sampling at each temperature and the order of temperatures determined randomly each day. This range encompasses the ambient nocturnal (25°C) and diurnal (29°C) temperatures in our vivarium, the mean daily operative environmental temperatures on Great Exuma (29.8°C) and Eleuthera (32.5°C), and the mean preferred (32°–33°C) and field-active (32°–35°C) body temperatures of *A. sagrei* (Corn 1971; Logan et al. 2014, 2018).

Statistical Analyses

Our sampling protocol resulted in three measures of $\dot{V}O_2$ per temperature per animal. To avoid any disproportionate influence of relatively high or low values on resultant analyses, we used the median $\dot{V}O_2$ at each temperature as the estimate of RMR for that animal. We also excluded eight hourly $\dot{V}O_2$ measurements (~1% of 711 total measurements) with unrealistically low values (all measured in females at 25°C) before calculating these median values for each animal. Across individuals, median values were highly correlated with mean values ($0.91 < r < 0.99$ across six combinations of sex and temperature) and with minimum values ($0.73 < r < 0.93$). Although minimum values are often used to estimate RMR, we chose the median to better reflect an individual's typical RMR (given that our analyses involve repeated measures of individual RMR across temperatures and correlations between RMR and growth across individuals) rather than attempt to measure the minimum possible RMR.

Within each sex, we tested for population differences in RMR using restricted maximum likelihood (REML) linear mixed models that combined $\dot{V}O_2$ at each temperature (25°, 30°, and 35°C) and included individual ID as a random effect (i.e., random intercept). These models included fixed effects of population, temperature, and body mass and all two-way interactions between fixed effects (the three-way interaction was not significant and was excluded). To test for sex specificity of population differences, we conducted a similar analysis that included sex as a fixed effect and all two-way interactions between fixed effects and the three-way interaction of sex × population × temperature (other three- and four-way interactions were not significant and were therefore excluded). We calculated the thermal sensitivity of RMR for each individual as the temperature coefficient Q_{10} = RMR at 35°C/RMR at 25°C and tested for sex and population differences in mean Q_{10} using two-way ANOVA with interaction.

To test for statistical associations between RMR and growth, we calculated the change in SVL of each male over a 14-mo period that included our metabolism trials, then expressed this change as a rate (mm d^{-1}). We tested for an association between growth rate and measures of $\dot{V}O_2$ at 25° and 30°C (excluding 35°C), which approximate the ambient temperatures that animals experienced while growing (25°C nocturnal, 29°C diurnal). We used REML linear mixed models that included measures of RMR at each temperature; fixed effects of growth rate, body mass, population, and temperature; and a random effect of individual ID (i.e., random intercept). All two-, three-, and four-way interactions among fixed effects were nonsignificant and were hierarchically removed, with the exception of the marginally significant population × mass interaction, which we retained in the final model. For all growth analyses, we excluded one Great Exuma male with an extremely high growth rate (2.8 SD above the mean) whose Mahalanobis distance (M_i = 3.49, upper control limit = 2.42) indicated a significant bivariate outlier relative to the overall correlation structure for growth rate and mass-adjusted RMR. Statistical analyses were conducted in JMP version 9.0.2 (SAS Institute, Cary, NC).

Results

Population Differences in Size, Growth, and Sexual Dimorphism

Females from Eleuthera and Great Exuma did not differ in SVL (fig. 1*A*, 1*B*) or growth (fig. 1*D*, 1*E*; table 1). By contrast, males from Great Exuma substantially exceeded males from Eleuthera in size at the beginning and end of the study and in growth during the study (fig. 1*A*–1*E*; table 1), including during

the 2-mo period bracketing metabolism trials (fig. 1*F*). Population differences in the size and growth of males accentuated population differences in the degree of male-biased sexual size dimorphism over the course of the study (fig. 1*C*). This interpretation is supported by significant sex × population interactions for each measure of size and growth (table 1). For the subset of animals used in metabolism trials, there was no difference in mass at the time of measurement between females from Eleuthera (mean ± SD = 2.26 ± 0.34 g; range = 1.32–2.94 g) and females from Great Exuma (2.31 ± 0.36; 1.72–2.80), but males from Eleuthera (5.47 ± 0.90; 4.12–7.44) were smaller than males from Great Exuma (7.42 ± 0.99; 5.66–9.26).

Population Differences in Resting Metabolic Rate

Females from Eleuthera and Great Exuma did not differ in RMR across any of the three temperatures at which we conducted metabolism trials (fig. 2*A*; table 2). By contrast, we found a significant population × temperature interaction in males such that the extent to which Eleuthera males exceeded Great Exuma males in RMR increased with temperature (fig. 2*B*; table 2). Combining males and females, we found a significant population × temperature × sex interaction (table 2), confirming that population differences in RMR were absent across temperatures in females, whereas population differences in RMR became more pronounced as temperature increased in males. RMR increased with mass, particularly in males, and this relationship became steeper as temperature increased (table 2). Temperature was the strongest predictor of RMR in all models (table 2). The temperature coefficient for RMR was estimated as $Q_{10} = 2.091 \pm 0.087$ (mean ± SE across all individuals) and did not differ as a function of sex ($F_{1,75} = 0.80$, $P = 0.37$), population ($F_{1,75} = 1.80$, $P = 0.18$), or their interaction ($F_{1,75} < 0.01$, $P = 0.98$).

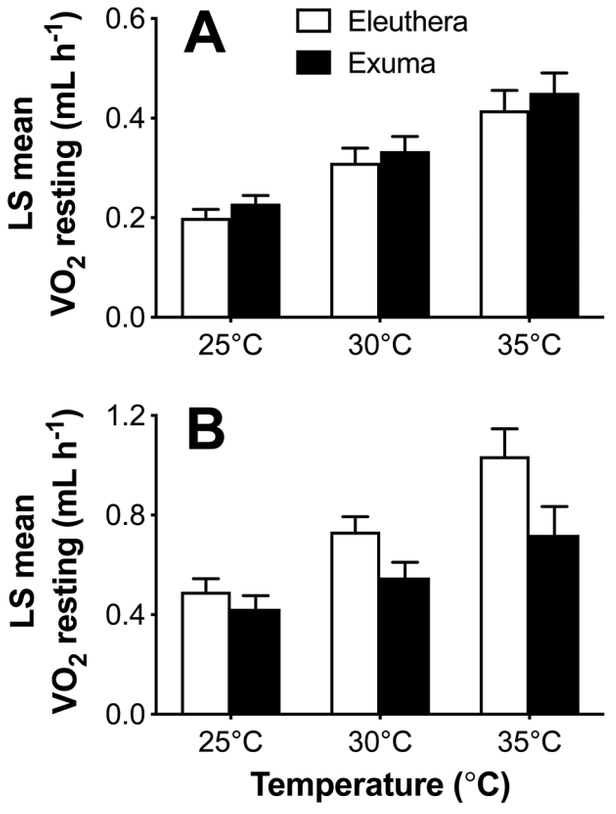

Figure 2. Resting metabolic rate (RMR; expressed as $\dot{V}O_2$ at rest) as a function of population (Eleuthera, Great Exuma) and temperature, plotted separately for females (*A*) and males (*B*). Data are least squares (LS) means (±1 SE) from analyses with body mass as a covariate, conducted separately for each sex. See table 2 for corresponding analyses showing that the population difference in RMR of males increases with temperature.

Table 2: Tests for population, mass, and temperature effects on resting metabolic rate (RMR)

Sex, fixed effects	df	*F*	*P*
Female:			
Population	1, 36	.61	.441
Body mass	1, 36	2.53	.120
Temperature	1, 77	134.06	<.0001*
Population × mass	1, 36	.01	.919
Population × temperature	1, 77	.03	.858
Mass × temperature	1, 77	3.19	.078
Male:			
Population	1, 35	2.84	.101
Body mass	1, 35	8.86	.005*
Temperature	1, 75	111.53	<.0001*
Population × mass	1, 35	.44	.511
Population × temperature	1, 75	4.42	.039*
Mass × temperature	1, 75	5.92	.017*
Both:			
Population	1, 72	2.26	.137
Body mass	1, 72	5.35	.024*
Temperature	1, 153	211.28	<.0001*
Sex	1, 72	.19	.665
Population × mass	1, 72	.60	.441
Population × temperature	1, 153	4.83	.029*
Population × sex	1, 72	.01	.937
Mass × temperature	1, 153	10.96	.001*
Mass × sex	1, 72	.17	.683
Temperature × sex	1, 153	2.85	.093
Population × temperature × sex	1, 153	5.58	.019*

Note. Analyses are from linear mixed effects models with RMR measured at 25°, 30°, and 35°C and with a random effect of individual ID (random intercept) that is not shown. For within-sex models, the three-way interaction between population, body mass, and temperature was removed because it was not significant. For the between-sex model, all nonsignificant three- and four-way interactions were removed.

*Statistically significant at $P < 0.05$.

Resting Metabolic Rate and Growth Rate

Using measures of RMR at 25° and 30°C, we found that RMR was positively associated with growth rate measured over a year in captivity (fig. 3*A*). For any given growth rate, RMR was

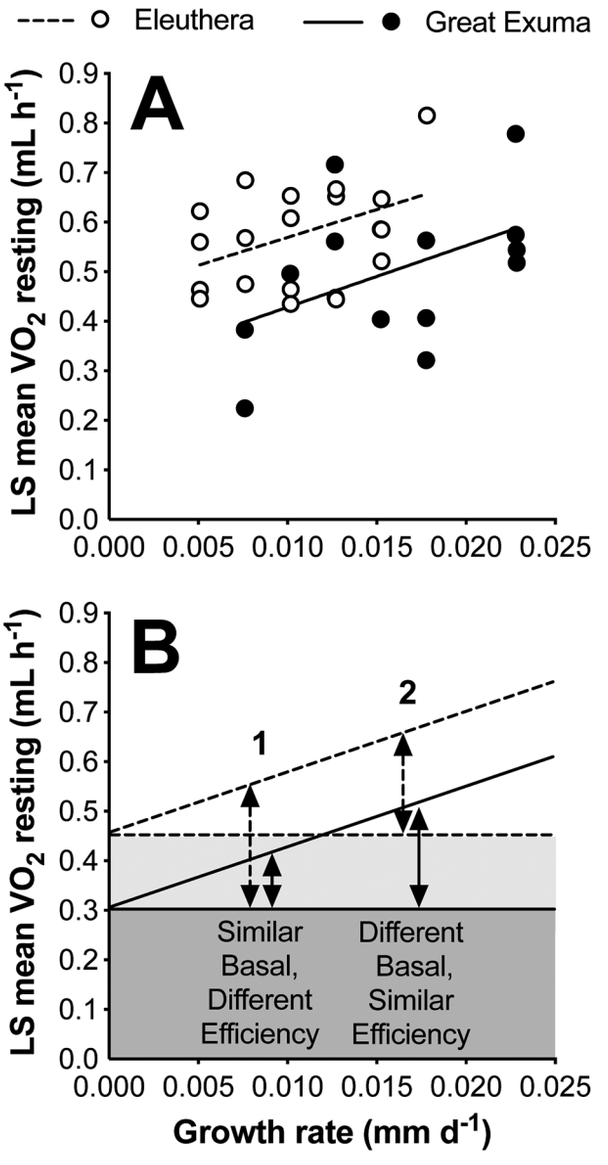

Figure 3. *A*, Resting metabolic rate (RMR) is positively associated with growth rate of males over a 13-mo period in captivity. Eleuthera males have higher RMR than Great Exuma males for any given growth rate. RMR is expressed as the least squares (LS) mean $\dot{V}O_2$ for each individual from a mixed effects model using measures at 25° and 30°C, temperature as a fixed effect, body mass as a covariate, and individual ID as a random effect. These LS mean values are analogous to modeling individual as a fixed effect and are based on the best linear unbiased predictors from the restricted maximum likelihood mixed effects model. Population was excluded to preserve the mean difference in RMR between Eleuthera and Great Exuma males for illustrative purposes but was included in corresponding analyses in table 3. Regression lines are estimated separately for each population but are nearly identical in slope. *B*, Population-specific trend lines from *A* are replotted to illustrate two hypothetical scenarios consistent with faster growth and lower RMR of Great Exuma males in light of the positive association between RMR and growth across individuals: (1) populations have similar baseline metabolic demands, but Eleuthera males are less efficient at translating increased metabolic expenditure into growth and (2) populations have similar growth efficiency per unit metabolic expenditure, but Eleuthera males have greater baseline metabolic demands that must be met before positive growth is possible.

higher in Eleuthera males than in Great Exuma males (fig. 3*A*), and RMR was positively associated with both body mass and temperature (table 3).

Discussion

We found that sex-specific population differences in the growth and size of brown anoles are accompanied by sex-specific population differences in RMR. Males from a population with highly male-biased sexual size dimorphism (Great Exuma) grew more quickly than males from a population with more modest sexual size dimorphism (Eleuthera), even after a year under common-garden conditions in captivity (fig. 1). For any given growth rate, males from Eleuthera had higher mass-adjusted RMR than males from Great Exuma when measured at temperatures approximating those under which growth occurred (25°–30°C; fig. 3), and population differences in RMR of males were most pronounced at warmer temperatures bracketing preferred and field-active body temperatures (30°–35°C; fig. 2). Although this pattern evokes a trade-off between growth and RMR at the population level (i.e., fast growth and slow metabolism in Great Exuma males, slow growth and fast metabolism in Eleuthera males), growth rate was positively correlated with RMR at the individual level after accounting for population differences in RMR and growth (fig. 3). In contrast to males, females from each population did not differ in any measure of size, growth, or resting metabolism (figs. 1, 2). Although males and females may differ in mass-adjusted RMR in some sexually dimorphic species (Ducret et al. 2020), we did not detect an overall sex difference in RMR of brown anoles after correcting for pronounced sex differences in size (table 2; also see Cox et al. 2015*a*), similar to studies of other sexual dimorphic species (Finkler et al. 2014).

The sex-specific population differences in size and growth that we observed in captivity are consistent with those previously observed in the wild on Great Exuma and Eleuthera (Cox and Calsbeek 2010), albeit with the caveat that growth rates in captivity at 25°–29°C were lower than typically observed during the warmest parts of the active season, when body temperatures of field-active anoles average 33°–34°C (Logan et al. 2014, 2018). Nonetheless, our measures of growth in captivity captured the key element of population divergence in males (fig. 1*D*–1*F*) and correlated with individual measures of RMR at corresponding temperatures of 25°–30°C (fig. 3). Therefore, population differences in the metabolic physiology of males may underlie natural differences in sexual size dimorphism, although the strength of this inference is tempered by the nature of our two-point comparison (Garland and Adolph 1991, 1994). Definitively linking sex-specific divergence in RMR to intraspecific variation in sexual size dimorphism will require measures of RMR from a larger sample of populations in which variation in sexual size dimorphism is at least partly independent of phylogenetic relationships (Garland and Adolph 1994). Despite this limitation of a two-point comparison, our study establishes a key prediction to guide future tests: the slower growth of males in populations with reduced sexual dimorphism will be associated with higher RMR across populations, despite positive associations

Table 3: Test for an association between resting metabolic rate (RMR) and growth rate

Fixed effects	df	*F*	*P*
Growth rate	1, 28	8.47	.007*
Population	1, 28	6.37	.018*
Body mass	1, 28	7.15	.012*
Temperature	1, 32	45.56	<.0001*
Population × mass	1, 28	3.66	.066

Note. A linear mixed effects model was used to test for an association between RMR and growth rate while accounting for fixed effects of population and body mass on RMR. The model includes measures of RMR at 25° and 30°C for each individual and a random effect of individual ID (random intercept) that is not shown. Nonsignificant two-, three-, and four-way interactions were removed from the final model. The interaction between population and mass was retained because it approached statistical significance.

*Statistically significant at $P < 0.05$.

between individual growth and RMR within populations. Althoughmany previous studies have linked intraspecific variation in life-history traits to variation in metabolic rate in other ectotherms (e.g., Garland and Adolph 1991; Angilletta 2001; Lahti et al. 2002; Lardies et al. 2004; Sears 2005; Arnott et al. 2006; Lardies and Bozinovic 2006; Bronikowski and Vleck 2010; Auer et al. 2018), our study extends this literature by showing that intraspecific variation in metabolism can be sex specific, thereby contributing to intraspecific variation in sexual dimorphism.

Intraspecific comparisons of ectotherm populations that differ in growth and body size have found both positive and negative associations between growth rate and RMR. For example, the large and fast-growing ecotype of the western terrestrial garter snake (*Thamnophis elegans*) has a higher mass-specific RMR than the relatively small and slow-growing ecotype (Bronikowski and Vleck 2010), suggesting that a higher resting metabolism may support rapid growth and a faster pace of life. By contrast, sagebrush lizards (*Sceloporus graciosus*) from high-elevation populations grow faster and have lower RMR than those from nearby low-elevation populations, suggesting that a reduction in baseline metabolic demands may instead permit greater allocation to growth (Sears 2005). At the population level, our results are similar to this example from sagebrush lizards in that fast-growing male anoles from Great Exuma have lower size-adjusted RMR than slow-growing males from Eleuthera (fig. 2). However, at the individual level, male anoles that grow more quickly tend to have higher RMR after controlling for effects of body size and population (fig. 3). Other studies have reported population-level associations between standard metabolic rate and growth rate that are absent at the individual level (Handelsman et al. 2013) or individual-level correlations that are absent at the population level (Reid et al. 2011). Moreover, studies conducted within populations have reported both positive and negative correlations between individual measures of growth and standard metabolic rate or RMR (Steyermark 2002; Burton et al. 2011; Reid et al. 2011; Handelsman et al. 2013). This raises the question of how to reconcile the apparent trade-off between growth rate and RMR at the population level with the observation that growth rate is positively correlated with RMR at the individual level (fig. 3).

At both the population and individual levels, negative correlations between growth and standard metabolic rate or RMR have been interpreted as consistent with the idea that the basal metabolic demands of self-maintenance trade off against allocation to growth (Steyermark 2002; Sears 2005; Burton et al. 2011; Reid et al. 2011). By contrast, positive associations could indicate that individuals with "faster" metabolic machinery are generally more capable of sustaining rapid growth (Arnott et al. 2006; Burton et al. 2011). These opposing views are roughly analogous to the compensation and increased intake models proposed by Careau and Garland (2012), with the substitution of growth and RMR in place of their focus on physical activity and basal metabolic rate. Although we cannot distinguish between these possibilities, the bigger question is why Eleuthera males tend to have a higher RMR than Great Exuma males of similar size (fig. 2*B*) or similar growth rates (fig. 3*A*). One possible explanation is that baseline metabolic demands are similar in both populations, but males from Great Exuma are more efficient at converting additional metabolic expenditure into growth (fig. 3*B*, scenario 1). Although speculative, this could occur if Eleuthera males allocate fractionally more energy toward metabolic costs of reproduction or if they exhibit lower mitochondrial efficiency. Another possibility is that males from both populations are similarly efficient at converting metabolic expenditure into growth, but males from Great Exuma have lower per-gram metabolic demands associated with self-maintenance such that they meet these baseline demands and begin converting metabolic expenditure into growth at a lower overall value of mass-specific RMR (fig. 3*B*, scenario 2). Males from Great Exuma could also exhibit a combination of lower baseline metabolic demands and greater growth efficiency. For example, individual garter snakes (*Thamnophis elegans*) with lower RMR also have greater growth efficiency per unit food consumption (Gangloff et al. 2015).

The ecological and evolutionary factors that drive differences in metabolic rate, growth, and sexual size dimorphism between Eleuthera and Great Exuma are only partially understood. Natural selection arising through differential adult survival favors large size in males of each population, perhaps even more strongly and consistently on Eleuthera than on Great Exuma (Cox and Calsbeek 2010). Therefore, population differences in growth and metabolism of males are not associated with population differences in selection for large size. The local environment on Eleuthera is hotter and harsher than that on Great Exuma, with less vegetative cover and a less diverse floral assemblage (Logan et al. 2014, 2018), suggesting conditions that may limit growth and activity. Wild males and females from Eleuthera weigh significantly less than those from Great Exuma for any given SVL, suggesting that population differences in male size may result from reduced energy availability on Eleuthera, coupled with the tendency for this energetic limitation to constrain the growth of males more strongly than that of females (Cox and Calsbeek 2010). However, subsequent studies of captive-bred F_1 animals have shown that, despite their similar growth rates as juveniles, males from Eleuthera and Great Exuma eventually diverge in growth rate and body size as adults, whereas females from each population exhibit similar patterns of growth and body size throughout ontogeny (R. M. Cox,

unpublished data). These additional studies on captive-bred anoles partially address the concern that the population differences in male growth that we report here are merely environmental effects that persisted long after wild-caught animals were acclimated to captivity, although captive-bred F_1 progeny can still exhibit maternal effects carried over from the original parental environment (Garland and Adolph 1991). Nonetheless, population differences in male growth and in sexual size dimorphism appear to have a genetic basis and cannot be explained solely by proximate environmental effects of energy availability on growth. Similar differences between captive-bred F_1 anoles from Great Exuma and Eleuthera have also been observed for thermal performance curves (Logan et al. 2018), suggesting that other aspects of physiology and performance have diverged genetically between populations.

Although direct energetic constraints are unlikely to fully explain population differences in male growth and body size, differences in energy availability and other environmental factors could indirectly lead to selection for divergent growth phenotypes. For example, survival of both sexes is higher on Eleuthera than on Great Exuma, and population demographics are broadly consistent with the idea that anoles from Great Exuma, and males in particular, are shifted toward a "live fast, die young" life-history strategy (Cox and Calsbeek 2010). Although attempts to link the evolution of life history or pace of life with metabolic rate have had mixed success (Trevelyan et al. 1990; Harvey et al. 1991; White and Seymour 2004; Lovegrove 2009; Bech et al. 2016), one predicted aspect of a live fast, die young strategy is a reduction in allocation to self-maintenance, which could manifest as lower RMR (Burton et al. 2011). Although speculative, this interpretation would be consistent with the second scenario illustrated in figure 3*B*. However, the predominant expectation is that the evolution of a faster life history involving rapid growth and low survival should generally be associated with a relatively higher metabolic rate, as has been found in a variety of systems (Arnott et al. 2006; Wiersma et al. 2007; Okada et al. 2011; Auer et al. 2018; Scholer et al. 2019). This expectation is opposite the trend we observed, so it is unclear precisely how to interpret our metabolism results in light of inferred population differences in survival and pace of life.

Our study is noteworthy in that population differences in growth and metabolic rate are evident only in male anoles, which raises the question of how intraspecific divergence has been achieved in sex-specific fashion. Treatment of juvenile brown anoles with testosterone, which typically circulates at high levels only in adult males, stimulates growth, increases RMR, and shifts energy away from storage in both sexes (Cox et al. 2015*a*). Likewise, treatment of juvenile females with testosterone induces male-like patterns of transcription in hepatic gene networks associated with growth, metabolism, and cell proliferation (Cox et al. 2017). These hormone manipulations have been conducted only on stock from Great Exuma, so it is unknown whether the magnitudes of any such androgenic effects on growth and metabolism are reduced in Eleuthera animals or whether circulating androgen levels naturally differ between males from each population. Nonetheless, these findings suggest that the sex specificity of population divergence in body size is likely to have arisen, at least in part, through changes in aspects of growth, metabolism, and gene expression that are regulated by testosterone. Although many aspects of growth, reproduction, and sexually dimorphic morphology have been found to exhibit condition dependence in this and other anole species (Kahrl and Cox 2015; Curlis et al. 2017), our results from a laboratory common garden suggest that population differences in adult growth and metabolism are either genetically determined or canalized by environmental conditions before adulthood. Collectively, our results suggest that intraspecific divergence in growth, body size, and sexual dimorphism is associated with sex-specific divergence in metabolic rate, a hypothesis that could be further tested by characterizing RMR throughout ontogeny and across a larger and phylogenetically informed selection of populations that vary in sexual dimorphism.

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