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Integration of Genotype, Physiological Performance, and Survival in a Lizard (*Uta stansburiana*) with Alternative Mating Strategies

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ABSTRACT

Covariation among behavioral and physiological traits is thought to enhance reproductive success and Darwinian fitness. Species that exhibit alternative mating strategies provide excellent opportunities to assess the relative contributions of physiological and behavioral traits to fitness. Male side-blotched lizards (*Uta stansburiana*) exhibit three heritable throat color morphs that are associated with alternative mating behaviors. The three morphs differ in resource holding potential, mate attraction, mate defense, and physiological performance. We examined interrelationships of body mass, stamina, field metabolic rate, growth rate, and survival to the second capture (a fitness proxy). Relationships among variables were complex, and mass, stamina, and throat color interacted to predict male survival. Our analyses suggest that male side-blotched lizards exhibit trade-offs among physiological traits related to reproductive success and survival and that differential survival for different combinations of traits has caused correlational selection, leading to adaptive integration of phenotypic traits associated with alternative mating strategies.

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Introduction

The integration of genotype, phenotype, physiological performance, and Darwinian fitness has a central position in research in evolutionary physiology (Feder et al. 2000). Currently, there is considerable interest in the genetic basis of individual variation in physiology (Garland et al. 1990*a*; Watt 1991; Dohm et al. 2001; Careau and Garland 2012; Lailvaux and Husak 2014). Two key components of the genetic architecture of physiological traits are the trade-offs between various functional modules (e.g., maintenance vs. activity metabolism) and functional integration of multiple traits (Garland and Huey 1987; Sinervo et al. 2008; Armbruster et al. 2014; Garland et al. 2016). For example, performance capacity and aggression need to be matched to body size and energy metabolism; otherwise, the individual will suffer negative selective consequences in either a social context, the ecological context of competition or predation (Lancaster et al. 2010), or owing to other abiotic factors affecting survival. Furthermore, the energetic costs of activity metabolism are thought to involve trade-offs with maintenance metabolism (Costa and Sinervo 2004; Kilpimaa et al. 2004; Ahtiainen et al. 2005; Husak and Lailvaux 2014; Gangloff et al. 2015; Husak et al. 2016).

Alternative mating strategies are genetic polymorphisms that result in different behavioral phenotypes with equal average fitnesses; the strategies are maintained in the population through frequency-dependent selection (Dominey 1984; Gross 1996). These systems provide evolutionary physiologists with model systems to explore the integration of physiology and behavior (Miles et al. 2007; Noble et al. 2013). Discrete behavioral phenotypes facilitate study of the causes and correlates of variation in physiological traits associated with fitness differences. This is because functional integration in these systems can be resolved as the outcome of correlational selection; phenotypic differences associated with each strategy are the result of multivariate selection, which reflect alternative fitness optima and different adaptive solutions to the same ecological problems (Sinervo and Svensson 2002). The existence of two or sometimes three discrete behavioral types implies that two or three possible adaptive solutions exist (e.g., Martin 2016). Correspondingly, one would expect to find combinations of two or three traits that each enhances a different strategy (Sinervo et al. 2008).

One such model system of alternative behaviors can be found in side-blotched lizards (*Uta stansburiana* Baird and Girard 1852)

in the Central Valley of California. This population exhibits alternative reproductive behaviors that have been termed a rock-paper-scissors game (Sinervo and Lively 1996), which is widespread across animal, plant, and prokaryote taxa (Sinervo and Calsbeek 2006; Sinervo et al. 2007). The lizards have three distinct throat color morphs, each associated with a different mating behavior (dominant, mate guarding, and sneaker). Orange-throated males are ultradominant and maintain large territories with many females but cannot keep yellow-throated males (female mimics) from sneaking in to mate (Zamudio and Sinervo 2000). Blue-throated males cooperatively guard their females (Sinervo and Clobert 2003; Sinervo et al. 2006b), which prevents sneaky yellow-throated males from invading, but they are less able to defend against the more aggressive orange-throated males. Each male morph has a reproductive advantage when rare, and morph frequencies in the population cycle over a 4-yr period (Sinervo 2001; Sinervo et al. 2007).

Color morphs are genetically determined (Sinervo and Zamudio 2001), and on the basis of laboratory crosses with field release of progeny (Sinervo et al. 2001), linkage mapping studies (Sinervo et al. 2006a), and theoretical models (Sinervo 2001), inheritance behaves as a simple single-locus three-allele system (o, b, y), the OBY locus (Sinervo et al. 2006a). Thus, the males can be readily categorized into homozygous (oo, bb, yy) and heterozygous combinations (bo, by, yo) of the three alleles. Correlational selection of throat morph with other traits has resulted in a number of physiological and behavioral traits differing among morphs (Sinervo and Svensson 2002). The OBY locus also governs alternative reproductive strategies of females, and this has been the focus of all previous correlational selection studies on the species (Sinervo et al. 2000b, 2001; Sinervo and Svensson 2002; Svensson et al. 2001a, 2001b, 2002). Here we consider the impacts of correlational selection on male behavior and physiology and partition this analysis into functional integration on three components of energy use (storage, activity metabolism, and performance capacity) and their influence on male survival.

Field metabolic rate (FMR) is a measure of the total energy expenditure of free-living animals under natural conditions (Nagy 1983). As such, it is determined by the many factors influencing energy use, including body mass, ambient temperature, and foraging, breeding, and antipredator activities. Animals with greater physiological capacities would be predicted to have higher activity levels (e.g., for territory defense) and thus a potentially higher FMR.

Stamina, here measured as time to exhaustion on a treadmill (as indexed by the loss of the righting response), gives a reasonable measure of whole-animal physiological capacity (Sinervo and Huey 1990; Garland and Losos 1994) linked to components of activity metabolism, such as the maximum rate of oxygen consumption (John-Alder et al. 1986). Higher stamina is presumed to be important for energetically intensive activities, such as territory defense (Brandt 2003). Stamina in *Uta stansburiana* has been found to be correlated with plasma testosterone, which is itself correlated with male morph; orange-throated males have higher testosterone and higher stamina than blue-throated or yellow-throated males but also lower rates of survival during the breeding season (Sinervo et al. 2000a).

Growth rate directly reflects energy allocation to storage rather than activity or maintenance metabolism. Because larger males may have higher stamina (Braña and Ji 2000) and are better able to defend territories and compete with other males for mates (Calsbeek and Sinervo 2002, 2004), growth rate is an additional component of fitness that acts through size at maturity, which enhances the usurpation ability of orange males (Calsbeek and Sinervo 2002). Alternatively, low growth and/or small body size might be expected to enhance the sneaker male strategy that could more effectively mimic female lizards, which have a smaller body size at maturity than males and exhibit different optima for body size based on hatchling survival to maturity (Calsbeek and Sinervo 2004).

Here we describe the relationships among alternative mating behaviors (as indicated by throat color morph), FMR, stamina, growth rate, and survival (a component of Darwinian fitness) for male side-blotched lizards in a natural population during the breeding season. Growth reflects the storage component of metabolism, and FMR and stamina should contribute more strongly to the activity component of metabolism. Thus, we explore the functional links among traits to explore trade-offs expressed as cascading effects on survival of males from one reproductive period to the next. We predicted that ultradominant orange-throated males would have higher FMR and stamina than blue or yellow-throated males, that larger blue and orange-throated males would have faster growth rates than yellow-throated males, and that FMR, stamina, and growth rate would interact with throat color to influence survival.

Material and Methods

Side-blotched lizards in California's Central Valley are found primarily on sandstone outcrops surrounded by grassland. There is little movement of lizards between outcrops (Svensson and Sinervo 2004). We studied four isolated populations of lizards near Los Baños, California, during the 2002 breeding season. One population was an unmanipulated control plot, while the others had previously had population frequencies of the color morphs manipulated in 1999 such that each population had a higher frequency of one of the morphs (Sinervo et al. 2001, 2006a). This ensured that in any given year we would have sufficient numbers of each morph to study and determine selection acting on the morphs across all phases of the rock-paper-scissors cycle. This is particularly challenging in genetic systems in which homozygotes (e.g., oo and yy in the lizards) are often quite rare owing to cyclical gene frequency dynamics (Sinervo 2001).

Throat color develops gradually over the course of the breeding season, and throat phenotypes were scored visually several times during the season. Lizards were assigned throat genotypes (bb, bo, by, oo, yo, yy) on the basis of throat color phenotype (Sinervo and Lively 1996; Sinervo et al. 2000a, 2006a); all six genotypes are visibly distinguishable from one another. Genotype was scored as three variables: number of blue alleles ($B = 0$, 1, or 2), number of orange alleles ($O = 0$, 1, or 2), or number of yellow alleles ($Y = 0$, 1, or 2). Only the O and B variables were

Table 1: Summary data for body mass, field metabolic rate (FMR), stamina, growth rate, and survival of male side-blotched lizards

Throat color genotype	Mass (g)	FMR (kJ/d)	Stamina (s)	Growth rate $((\ln \text{mass}_2 - \ln \text{mass}_1)/\text{day})$	Survival	
					Initial to first recapture	First to second recapture
bb	7.32 ± .23 (29)[B]	1.21 ± .06 (24)	268 ± 23 (19)	−.00042 ± .0005 (25)	80 (16/20)	63 (10/16)
bo	7.16 ± .27 (17)[AB]	1.07 ± .07 (11)	378 ± 35 (13)	.00176 ± .00085 (13)	69 (9/13)	33 (3/9)
by	6.89 ± .11 (139)[AB]	1.16 ± .03 (55)	319 ± 16 (92)	.00016 ± .00046 (56)	33 (42/126)	60 (25/42)
oo	7.29 ± .29 (14)[B]	.99 ± .1 (8)	327 ± 46 (10)	−.00163 ± .00154 (8)	45 (5/11)	60 (3/5)
yo	7.38 ± .34 (10)[AB]	1.19 ± .09 (7)	294 ± 51 (9)	−.00171 ± .00073 (8)	78 (7/9)	29 (2/7)
yy	6.19 ± .17 (28)[A]	1 ± .06 (17)	250 ± 16 (21)	.000378 ± .00093 (17)	52 (12/23)	58 (7/12)
All data	6.92 ± .08 (237)	1.13 ± .02 (122)	308 ± 11 (164)	.00001 ± .0003 (127)	45 (91/202)	55 (50/91)

Note. Data are means ± SE (*N*). Survival indicates the percent surviving (number surviving/total number). FMR data include multiple measurements for some animals measured during both measurement periods. For body mass, similar letters indicate that means did not differ significantly.
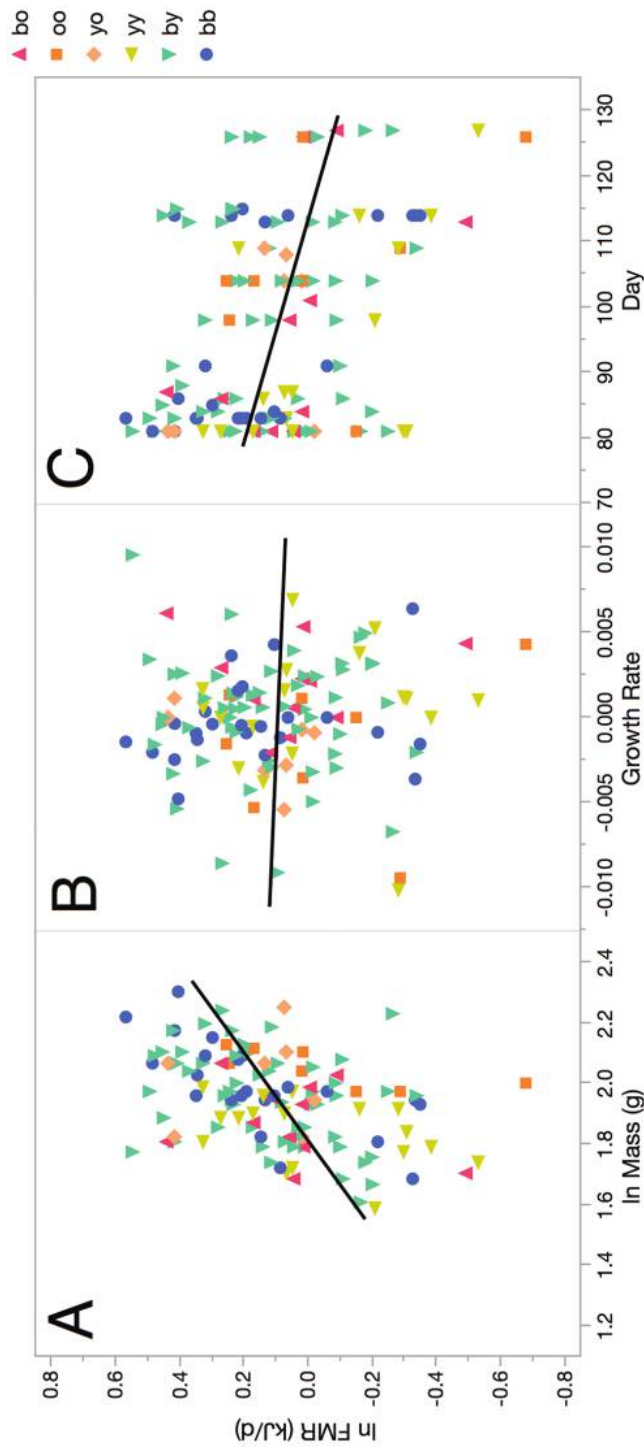
Figure 1. Effects of body mass, growth rate, and season (Julian day) on field metabolic rate (FMR) of male side-blotched lizards. Univariate regression lines and throat color genotypes are presented for informational purposes; full statistical model is provided in table 2. *A,* FMR (ln kJ/d) versus body mass (ln initial mass [g]): $y = -1.25 + 0.689x$ ($F_{1,120} = 25.45$, $P < 0.0001$, $R^2 = 0.175$). *B,* FMR (ln kJ/d) versus growth rate (($\ln \text{mass}_2 - \ln \text{mass}_1$)/day): $y = 0.091 - 2.29x$ ($F_{1,120} = 0.11$, $P = 0.737$, $R^2 = 0.001$). *C,* FMR (ln kJ/d) versus season (Julian day): $y = 0.663 - 0.00588x$ ($F_{1,120} = 19.08$, $P < 0.0001$, $R^2 = 0.137$). Symbols indicate throat color genotypes.

Table 2: Effect of throat color genotype on field metabolic rate of male side-blotched lizards

Effect	Slope estimate	SE	P
Covariates:			
ln mass (g)	.48	.215	.026*
Growth rate			
$((\ln mass_2 - \ln mass_1)/day)$	14.5	5.92	.016*
Day	−.007	.001	<.0001*
Genotype:			
o	.09	.075	.221
$o \times o$	−.24	.081	.004*
Interactions:			
$o \times$ mass	−1.46	.53	.007*
$o \times o \times$ mass	2.13	.65	.001*

Note. Mass, growth rate, and Julian day were included as covariates. Lizard identification was included as a random effect to control for multiple field metabolic rate measurements made on some animals and accounted for 15.1% of the total variance ($N = 122$, $R^2 = 0.62$). There was no effect of number of blue alleles, stamina, or other interaction terms, and these variables were dropped from the model. o = number of orange alleles. Significant $o \times o$ interactions indicate a nonlinear relationship between o and FMR.

*Indicates statistical significance.

used for analysis, since the value of Y is automatically determined by the values of O and B.

To enhance statistical power, we used covariates for the number of o alleles and for the number of b alleles (Sinervo et al. 2000b; Svensson et al. 2009), which allows one to estimate the additive genetic effect of alleles on a particular trait as well as dominance effects that can be estimated by $o \times o$ and $b \times b$ and overdominance or underdominance effects ($b \times o$). Effects of these terms for color alleles on other physiological traits are indicative of correlational selection if the dependent variable is fitness or physiological epistasis (e.g., for an example of endocrine epistasis, see Lancaster et al. 2007) if the dependent variable is another phenotypic trait (Sinervo et al. 2008). We also evaluated genotype effects (*oo*, *bo*, *yo*, *bb*, *by*, *yy*) for body mass and FMR.

Lizards were toe clipped for permanent identification, and temporary numbers or letters were painted on their backs with colored correction fluid so that manipulated animals could be identified at a distance in the field. Side-blotched lizards at this site show strong site fidelity, remaining within territories/home ranges during the breeding season, and thorough collecting at each site over several days ensured that we recaptured nearly every lizard present (Sinervo et al. 2006a). Lizards not recaptured or observed by the end of the study were presumed to have died, and intensive recapture effort indicates that the probability of capturing males is 0.97 across the three census periods conducted each spring (Sinervo et al. 2006b).

Male lizards ($n = 209$) were captured early in the breeding season (mid-March through late April) and brought to the University of California, Santa Cruz, for stamina measurements and injection of doubly labeled water. Mass was measured shortly after capture to the nearest 0.1 g with a 10-g capacity Pesola hanging

scale, and snout-vent length was measured to the nearest 1 mm. We then measured endurance once for each animal at 36°C (preferred body temperature; Paranjpe et al. 2014) as time to exhaustion (loss of righting response) on a canvas treadmill running at 0.5 km/h. Following a recovery period of at least 24 h, lizards were injected with 0.10 mL of doubly labeled water (30 atom percent [18]O and 0.7 mCi tritium/mL). Lizards were allowed an equilibrium period of at least 1 h after injection before we collected initial blood samples. We collected blood from the postorbital sinus using heparinized capillary tubes, which were flame sealed and refrigerated until analysis. Lizards were kept at room temperature overnight and released the following morning at their sites of capture. We recaptured lizards during two subsequent recapture periods, and blood samples were taken within 5 min of capture. Lizards were weighed and released after sampling.

Blood samples for FMR were transported on ice to the University of California, Los Angeles, and refrigerated until analysis. Distilled samples were analyzed for tritium using liquid scintillation spectrometry (Nagy and Costa 1980) and for [18]O by cyclotron-generated proton activation (Wood et al. 1975). Total body water was calculated from initial dilution of injected isotopes in body water. Water turnover and CO_2 production were calculated from changes in blood isotope concentrations using the equation previously determined for reptiles (Nagy 1980). Carbon dioxide production was converted to energy use (FMR) assuming 26 J/mL CO_2 (Nagy 1983); this estimate was based on *Uta stansburiana* eating mealworm (*Tenebrio*) larvae, which may have a higher fat content than the arthropods eaten in the field, but the error is likely no more than 2%–5%.

Mass was measured at each capture, and values were used to calculate mass-specific growth rate ($(\ln mass_2 - \ln mass_1)/day$; Brody 1945; Sinervo 1990). Statistical tests were conducted using JMP 11.0 for Mac OS X (SAS Institute). Values of $P \leq 0.05$ were considered to be significant. Where necessary, variables were log transformed to meet the assumptions of each statistical test (e.g., for allometric models of mass and FMR). For FMR, for which there were multiple measurements for some animals, lizard identification (ID) was included as a random effect. Survival was classified as a binary variable (survival from initial for first recapture and from first to second recapture) and was analyzed using logistic regression. For all tests, a full factorial model with four or more effect variables often led to loss of statistical power,

Table 3: Factors affecting stamina (ln stamina [s]) of male side-blotched lizards

Effect	Slope estimate	SE	P
ln mass (g)	.76	.33	.026*
Growth rate			
$((\ln mass_2 - \ln mass_1)/day)$	47.0	18.8	.014*
Day	.015	.006	.025*
Day × day	−.0017	.00055	.002*

Note. Overall ANOVA: $F_{4, 85} = 6.67$, $P < 0.0001$, $R^2 = 0.24$.
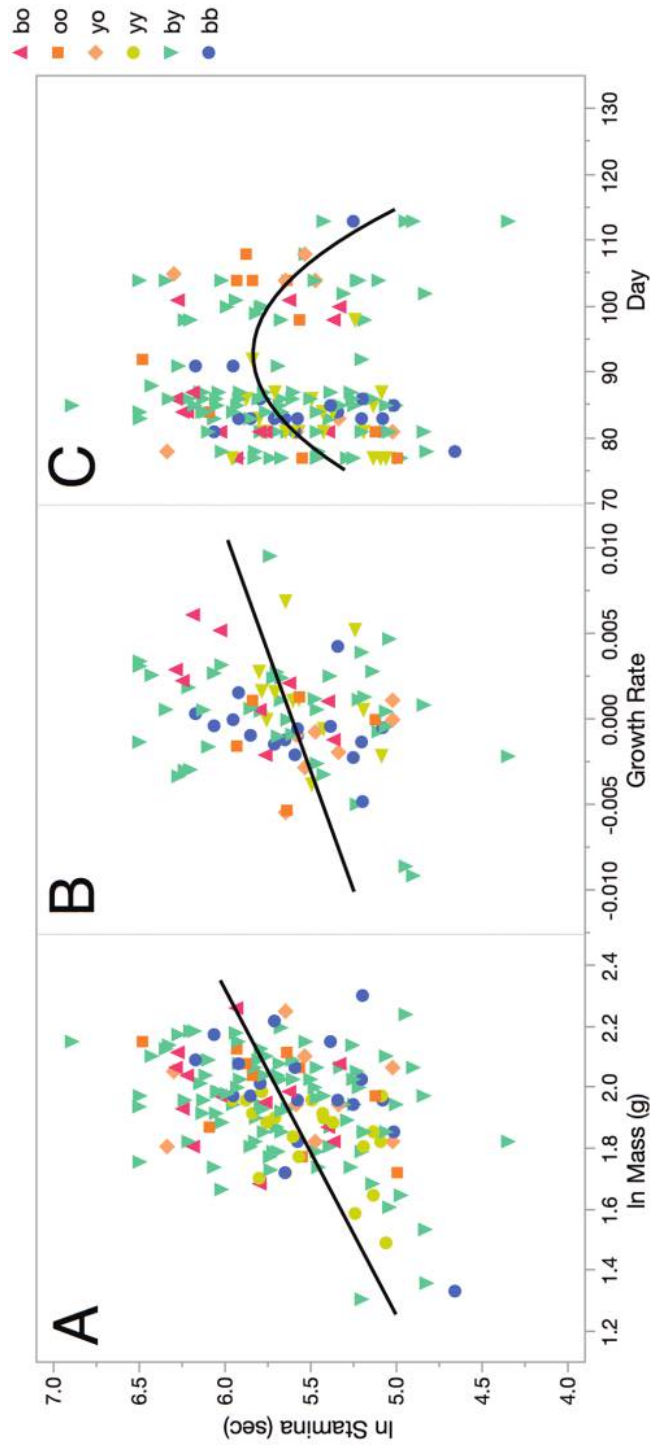
*Indicates statistical significance.

Figure 2. Effects of body mass, growth rate, and season on stamina of male side-blotched lizards. Univariate regression lines and throat color genotypes are presented for informational purposes; full statistical model is provided in table 3. A, Stamina (ln s) versus body mass (ln initial mass [g]): $y = 3.82 + 0.937x$ ($F_{1, 162} = 25.77$, $P < 0.0001$, $R^2 = 0.137$). B, Stamina (ln s) versus growth rate (($\ln \text{mass}_2 - \ln \text{mass}_1$)/day): $y = 5.603 + 35.9x$ ($F_{1, 88} = 5.77$, $P = 0.0184$, $R^2 = 0.062$). C, Stamina (ln s) versus season (Julian day): $y = -8.96 + 0.319x - 0.00172x^2$ ($F_{2, 61} = 10.64$, $P < 0.0001$, $R^2 = 0.117$). Symbols indicate throat color genotypes.
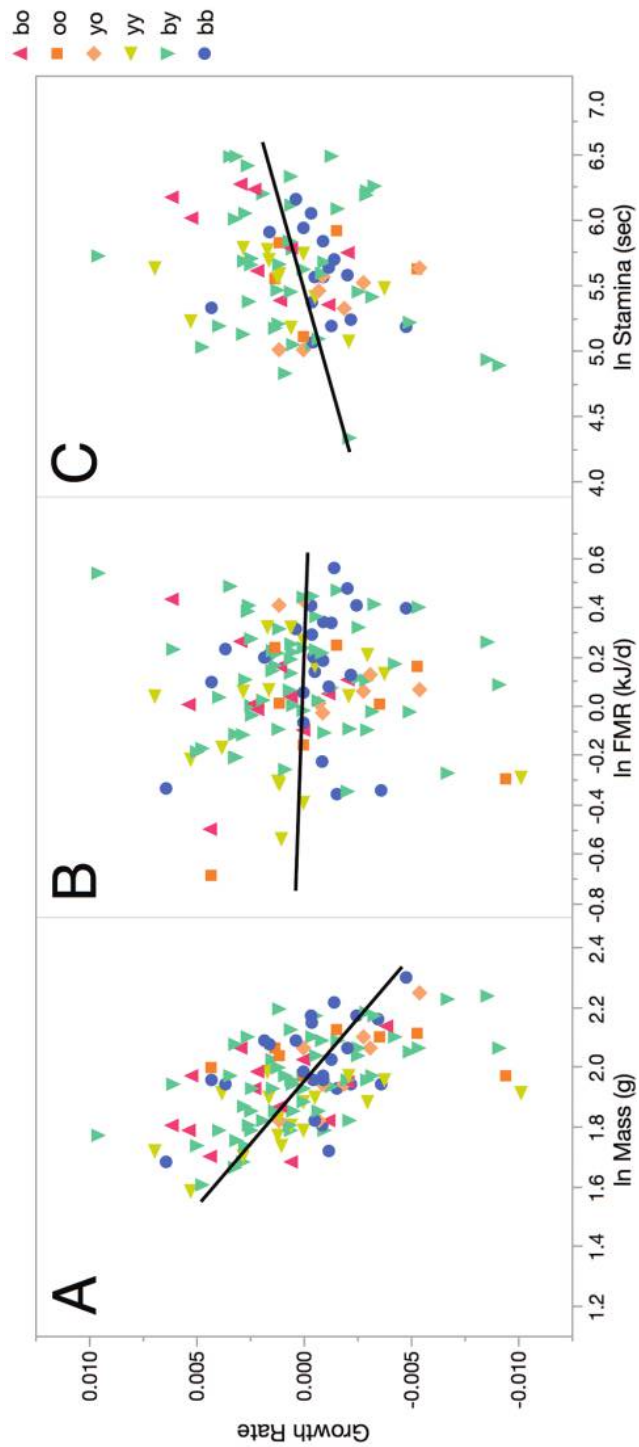
308

Figure 3. Effects of body mass, field metabolic rate (FMR), and stamina on growth rate of male side-blotched lizards. Univariate regression lines and throat color genotypes are presented for informational purposes; full statistical model is provided in table 4. A, Growth rate $((\ln \text{mass}_2 - \ln \text{mass}_1)/\text{day})$ versus body mass $(\ln \text{initial mass} [g])$: $y = 0.0233 - 0.0119x$ $(F_{1, 125} = 50.44, P < 0.0001, R^2 = 0.287)$. B, Growth rate $((\ln \text{mass}_2 - \ln \text{mass}_1)/\text{day})$ versus FMR $(\ln kJ/d)$: $y = 0.000059 - 0.000412x$ $(F_{1, 120} = 0.11, P = 0.737, R^2 = 0.001)$. C, Growth rate $((\ln \text{mass}_2 - \ln \text{mass}_1)/\text{day})$ versus stamina $(\ln \text{stamina} [s])$: $y = -0.0094 + 0.00172x$ $(F_{1, 88} = 5.77, P = 0.0184, R^2 = 0.062)$. Symbols indicate throat color genotypes.

309

and nonsignificant variables and higher interaction terms were therefore dropped.

Results

We recaptured 89 of the 209 lizards (43%) after 28 ± 5 d (range: 13–39 d), which is a typical recovery rate for unmanipulated control males (Zamudio and Sinervo 2000). About 19 ± 2 d after the first recapture period (range: 16–22 d), we recaptured 48 lizards for a third blood sample (22.9% of original sample). Fourteen of these were animals that were not located during the first recapture period, and their FMR measurements span both measurement periods (mean: 48 ± 5 d; range: 39–61 d). We continued the censuses on a fourth recapture round, but no additional new males were recovered. Summary data for body mass, FMR, stamina, growth rate, and survival are presented for reference (table 1); statistical analyses are described below.

Body mass at initial capture differed with respect to throat color (table 1); yellow (yy) males were smaller than blue (bb) or orange (oo) males, while heterozygotes did not differ from the other genotypes. Total body water (measured by tritium dilution) averaged 70.1% of total body mass ($N = 76, R^2 = 0.88$, $P < 0.0001$) and was directly proportional to body mass (slope of log-transformed data = $1.036 \pm 0.044, P < 0.0001$).

FMR increased with increasing body mass, following an allometric relationship (ln FMR = 0.689(ln mass) − 1.25; $R^2 = 0.175, P < 0.0001, N = 122$; fig. 1A). FMR was also influenced by growth rate (fig. 1B; not significant in univariate analysis) and Julian day (fig. 1C); these plus body mass were included as covariates when throat color genotype was evaluated (table 2). Lizard ID was included as a random effect to account for repeated measures of FMR on some individuals; ID contributed 15.1% of the total variance. Number of blue alleles and stamina did not have a significant effect on FMR, and these factors were dropped from the statistical model. Number of orange alleles had a nonlinear effect on metabolic rate, with a significant interaction between orange alleles and body mass (table 2). The relationship between mass and FMR was greatly exaggerated for homozygous orange males. Small orange males had relatively low FMR for their size compared with the other morphs (fig. 1A); the regression had a slope of 3.70 compared with the overall slope of 0.689 (ln FMR = 3.70(ln mass) − 7.65; $R^2 = 0.542, P \leq 0.037, N = 8$).

Stamina increased with increasing body mass and with faster growth rate (table 3; fig. 2A, 2B). Stamina also increased early in the breeding season, peaking at about Julian day 94 and then declining (table 3; fig. 2C). There were no significant interaction terms (other than the quadratic day × day term), and those effects were dropped from the model. There was no direct effect of throat color on stamina, regardless of whether genotype or number of blue or orange alleles was incorporated into the model. Thus, any apparent effects of throat color are likely due to the differences in body mass and growth rate for the different genotypes.

The factors influencing growth rate were complex. Growth rate was negatively related to body mass; smaller lizards grew

faster than larger ones (growth rate = 0.0233 − 0.0119 (ln mass); $F_{1, 125} = 50.4, P < 0.0001, R^2 = 0.29$; fig. 3A), an experimentally verified allometric effect (Sinervo 1990). Growth rate was also negatively associated with Julian day; lizards grew faster earlier in the breeding season. However, lizards were also smaller earlier in the season, and the effect of day disappeared when mass-corrected growth rates were used (residuals of the regression of growth rate on ln mass; analysis not shown). Julian day was therefore not included in the final statistical model. Higher stamina and FMR were associated with higher growth rate (table 4; fig. 3B, 3C; no effect of FMR in univariate analysis). There were also significant interactions of orange and blue alleles with body mass. Smaller orange males had higher growth rates than larger ones, and orange males had higher growth rates at a given body mass than males lacking orange alleles. For lizards with no blue alleles (oo, yo, and yy genotypes), smaller males grew faster than larger male lizards, whereas for lizards with two blue alleles, larger males grew faster than smaller males (table 4).

Survival from initial capture to the first recapture period was significantly affected by throat color (both number of orange and number of blue alleles), body mass, and stamina, with significant interactions among these factors (table 5; fig. 4). In particular, there was a significant interaction between mass and stamina. Across genotypes, for smaller animals lower stamina resulted in higher probability of survival, while higher stamina decreased the probability of survival; the opposite was true for larger animals. This relationship shifted depending on genotype. The general trend was the same regardless of number of blue alleles, but for animals with one or two orange alleles (oo, oy, bo), higher stamina led to lower survival regardless of body mass. Effects of FMR on survival could not be evaluated because no data on FMR were available for animals that were not recaptured.

Survival from the first recapture to the second recapture was significantly predicted by throat color, stamina, and mass, with interactions among some of these terms (table 5). Again, there was an interaction between mass and stamina but only in con-

Table 4: Factors influencing growth rate
(($\ln \text{mass}_2 - \ln \text{mass}_1$)/day) of male *Uta stansburiana*

Term	Slope estimate	SE	t ratio	P
Intercept	.00638	.00623	1.02	.3092
Mass	−.00942	.00273	−3.45	.0009*
FMR	.00464	.0014	3.40	.0011*
Stamina	.00191	.00053	3.60	.0006*
o	−.000286	.00106	−.27	.7884
$o \times o$	.00194	.00129	1.50	.1370
b	.000231	.00041	.56	.5756
$o \times$ mass	.0212	.00777	2.73	.0078*
$o \times o \times$ mass	−.0220	.00967	−2.28	.0257*
$b \times$ mass	.00669	.00257	2.61	.0109*

Note. Overall model: $F_{9, 77} = 10.56, P < 0.0001, R^2 = 0.553$. o = number of orange alleles; b = number of blue alleles; stamina = stamina (ln stamina [s]); FMR = field metabolic rate (ln FMR [kJ/d]). Nonsignificant higher interaction terms were dropped from the model.

*Indicates statistical significance.

Table 5: Effects of stamina, body mass, and throat color on survivorship of male side-blotched lizards from initial capture to first recapture and from first to second recapture (likelihood ratio)

Source	Survival from initial capture to first recapture		Survival from first recapture to second recapture	
	χ^2	P	χ^2	P
Independent mass, stamina, and throat color effects:				
Mass	11.45	.0007*	52.96	<.0001*
Stamina	4.67	.0307*	68.62	<.0001*
o	10.48	.0012*	.00004	.9951
$o \times o$	…	…	.00013	.9908
b	7.35	.0067*	2.87	.09
$b \times b$	5.18	.0228*	…	…
$o \times b$	5.19	.0227*	3.95	.047*
Mass and throat color interactions:				
$o \times$ mass	7.84	.0051*	48.93	<.0001*
$o \times o \times$ mass	…	…	68.05	<.0001*
$b \times$ mass	4.80	.0285*	1.019	.32
$b \times b \times$ mass	1.21	.2706	…	…
$o \times b \times$ mass	25.20	<.0001*	1.31	.25
Stamina and throat color interactions:				
$o \times$ stamina	4.49	.0341*	12.79	.0003*
$o \times o \times$ stamina	…	…	21.15	<.0001*
$b \times$ stamina	2.09	.1484	2.95	.09
$b \times b \times$ stamina	.30	.5844	…	…
$o \times b \times$ stamina	2.38	.1231	2.34	.13
Mass, stamina, and throat color interactions:				
Mass $\times$ stamina	4.20	.0405*	.00017	.9895
$o \times$ mass $\times$ stamina	4.63	.0314*	.00000	.9988
$o \times o \times$ mass $\times$ stamina	…	…	.00007	.9934
$b \times$ mass $\times$ stamina	6.42	.0113*	8.05393	.0045*
$b \times b \times$ mass $\times$ stamina	5.85	.0155*	…	…
$o \times b \times$ mass $\times$ stamina	4.91	.0268*	8.87829	.0029*

Note. Logistic regression, overall model for initial to first recapture: $R^2 = 0.31$, $N = 164$, $P < 0.0001$. Logistic regression, overall model for first to second recapture: $R^2 = 0.28$, $N = 90$, $P < 0.018$. Nonsignificant interaction terms were dropped from each model. Stamina = ln stamina (s); mass = ln body mass (g); o = number of orange alleles; b = number of blue alleles.

*Indicates statistical significance.

junction with throat color (table 5). There was no effect of FMR or interactions of FMR with other variables, and this term was dropped from the model.

Discussion

We found complex relationships among physiological traits and genetically determined mating strategies. Typically, the different traits interactively affected survival in the field. FMR, stamina, growth rate, and survival were interrelated, and their effects on one another often depended on mating strategy, as measured by throat color genotype.

FMR

Body mass had the expected allometric effect on FMR: in general, larger males had higher metabolic rates, and the slope of the relationship was consistent across most genotypes. However, body size had a much more dramatic effect on FMR for

homozygous orange males than for other males, with a significantly steeper slope. Small orange males had very low FMR for their size, whereas the FMR of larger orange males was comparable to other large males (fig. 1A). On average, orange males had territories that were 2.5-fold greater than the territories of blue males (Sinervo et al. 2000a), so it is surprising that their FMR was not higher. The low FMR of small homozygous orange males suggests that these individuals spend less energy on defense, possibly because of lower resource holding potential compared with larger orange males. However, it is also possibly that lower FMR indicates a reduction in foraging effort, which could then lead to fewer resources being available for defense. Small males could also still be growing, thus devoting a greater fraction of energy intake to storage rather than metabolism, although with the small number of homozygous orange males in this study it is difficult to determine this.

In a 15-mo comprehensive study of field energetics of a Nevada population of *Uta stansburiana*, Nagy (1983) found
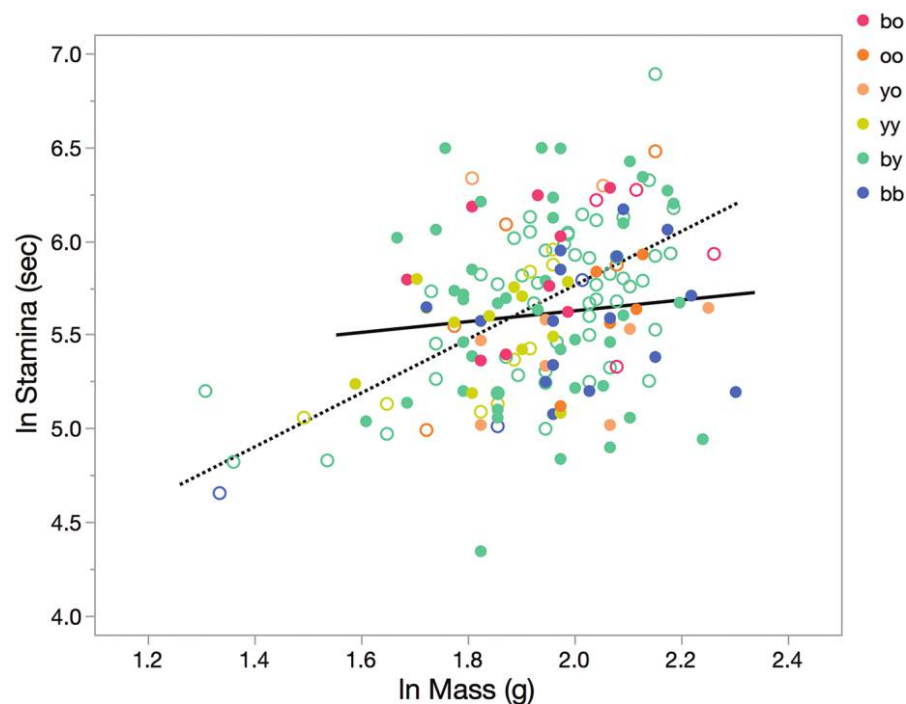
Figure 4. Effects of body mass and stamina on survival of male side-blotched lizards. Filled circles = animals that survived the first recapture period; open circles = animals that did not survive the first recapture period. Univariate regression lines and throat color genotypes are presented for informational purposes; full statistical model is provided in table 4. Stamina (ln s) versus body mass (ln g) for survivors (solid line): $y = 5.05 + 0.289x$ ($F_{1,88} = 0.94$, $P = 0.335$, $R^2 = 0.01$). Stamina (ln s) versus body mass (ln g) for nonsurvivors (dashed line): $y = 2.89 + 1.437x$ ($F_{1,72} = 0.47.29$, $P < 0.0001$, $R^2 = 0.40$). Symbols indicate throat color genotypes.

that FMR for adult males was highest in the spring (March, April, and May measurements, roughly corresponding to the measurement period for this study and the time during which males are establishing territories). Mean whole-animal FMRs for these time periods were 0.494, 0.630, and 0.645 kJ/d, respectively. These values are lower than most FMR values measured in this study (table 1). However, the Nevada population also had considerably smaller body mass (adult male mean body mass ~3.5 g compared with 5–10 g for male *Uta* in this study), and the mass-specific metabolic rates are comparable.

Stamina

Individual variation in stamina should reflect a male's capacity for territorial defense or resource holding potential (Calsbeek and Sinervo 2002). Furthermore, throat color may serve as a badge to convey the resource holding potential of a male (Whiting et al. 2003). Evidence from a variety of taxa supports the role of stamina in conveying dominance (and hence territorial) status (Garland et al. 1990b; Robson and Miles 2000; Brandt 2003; Perry et al. 2004), although in other taxa other factors such as bite force may be more relevant (Husak et al. 2006; Lailvaux and Irschick 2007). In this study, larger males had higher stamina regardless of genotype. The territorial orange and blue-throated males were larger than the non-territorial yellow-throated males and thus had higher stamina, consistent with higher resource holding potential capacity.

Stamina and activity in the wild are known to be coupled (Garland 1993; Garland and Albuquerque 2017). Therefore, high stamina of larger orange males may allow them to have higher activity levels during the breeding season but resulting higher mortality by the end of the season. Orange males gain high paternity from earlier clutches (Zamudio and Sinervo 2000). Thus, survival to later clutches is traded off against high siring success on the first clutch for orange males. In contrast, the sneaky yellow males specialize in survival to later clutches and even have higher fertility from posthumous survival of their sperm and/or because of selective sperm sorting by females (Zamudio and Sinervo 2000). The association of high growth rate with high stamina (table 3) is interesting, as one prediction might instead be a trade-off between growth and performance.

Growth Rate

As with FMR, growth rate exhibited striking mass-specific patterns that varied among genotypes. Mass-specific growth rate of orange genotypes declined with size, but mass-specific growth rates of blue males increased with size. The pattern observed for orange males is typical for mass-specific growth rate, which declines with size (Sinervo 1990), but the pattern observed for blue males is paradoxical. We suggest that this variation in body mass on growth may arise because of an interaction of the cooperative blue male strategy with the physiology of growth, if, for example, larger blue males are more likely

to secure a cooperative territorial partner, thus lowering expenditure on territorial behavior and allowing energy savings to be shunted to growth. Higher stamina and FMR were also associated with higher growth rate; lizards with higher stamina may have been able to forage for longer, leading to higher FMR and faster growth. Other studies (Gregory and Wood 1998; Clobert et al. 2000) have found similar positive relationships between stamina and growth.

Integrating Genetics, Physiological Performance, and Fitness

The throat color morphs (with their associated alternative mating behaviors) interact with other traits, such as body mass, to influence physiological traits (FMR and stamina), which in turn affect the fitness-influencing traits, growth rate and survival. Orange males have a previously identified (Calsbeek and Sinervo 2004) strategy of rapid growth off of high-quality territories immediately before the beginning of breeding, but as soon as females become receptive, they capitalize on their now large size to forcibly eject other males from high-quality rock piles. Lizard species with high levels of stamina have been shown to correlate stamina with key measures of foraging behavior (Bennett et al. 1984; Garland 1999). However, their high stamina is associated with poor survival to the end of the breeding season because of high activity and greater exposure to predators. Therefore, for this strategy to persist in the population, the orange males should have relatively high fitness early in the season, which is the case (Zamudio and Sinervo 2000). In contrast, higher stamina for the other morphs leads to a higher probability of survival.

Nagy (1983) found similar interactions among FMR, growth rate, and body mass for free-living *U. stansburiana*, as were found in this study. Increased growth rate and increased body mass were both associated with higher FMR, and the two together accounted for about three-quarters of the variation in FMR. Other studies have found similar relationships; in *Lacerta vivipara*, individuals with higher stamina also showed higher activity and growth rates but more apparent predation attempts (tail loss), leading to comparable survival rates between high- and low-stamina individuals (Clobert et al. 2000).

This study is one of the first to explicitly link genotype (the OBY locus for throat color), phenotype (mating behavior), physiological performance (FMR, stamina), and fitness correlates (growth and survival). The relationships among these traits are complex and likely would have been much more difficult to detect in the absence of the existence of discrete morphs. The different mating strategies used by the three morphs have different costs and benefits to having high performance associated with them, leading to apparent correlational selection on the physiological traits associated with them.

Acknowledgments

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