Behavioral and Morphological Traits Interact to Promote the Evolution of Alternative Reproductive Tactics in a Lizard

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ABSTRACT: Alternative reproductive tactics (ARTs) are predicted to be the result of disruptive correlational selection on suites of morphological, physiological, and behavioral traits. ARTs are most obvious when they occur in discrete morphs with concomitant behavioral tactics. However, ARTs driven by behavior in species lacking obvious phenotypic differences are rarely documented and poorly understood. We quantified selection acting on phenotypic traits predicted to characterize ARTs by observing marked lizards in six semi-natural populations. We quantified reproductive fitness for each male using six microsatellite DNA loci from 226 offspring born to 56 females. Candidate models containing directional and correlational selection gradients were equally supported. As predicted, large males with large home ranges and large males that were observed frequently had the highest reproductive success. We also found evidence that large males that moved little but that were observed frequently and large males that moved frequently but that were observed little were predicted to have high fitness. Model predictions support our verbal hypothesis regarding the phenotypes characterizing ARTs and suggest that large males may be adopting subtly different tactics to acquire paternity. Our results suggest that disruptive correlational selection between behavioral traits may drive the evolution of ARTs in "cryptic" systems that lack overt polymorphisms.

Keywords: alternative reproductive tactics, disruptive selection, reproductive success, lizard, behavior, *Eulamprus quoyii*, sexual selection, correlational selection.

Introduction

Sexual selection is understood as a powerful evolutionary force that can drive phenotypic differences between the sexes, such as extreme sexual ornamentation and body size dimorphism (Andersson 1994). However, strong sexual selection can also generate phenotypic diversity within the sexes, particularly among males (Andersson 1994; Shuster 2010). Competition for mates generates variance in male mating success and can favor the evolution of alternative phenotypes, which allow males to successfully compete for female mating opportunities (Andersson 1994; Taborsky et al. 2008; Shuster 2010). These alternative reproductive tactics (ARTs) show a remarkable diversity of form across a wide range of taxa and can vary in their degree of genetic determination, with some alternative tactics being the result of allelic variation at a few loci of major effect with lower levels of plasticity (e.g., Sinervo and Lively 1996; Sinervo et al. 2000) and others being determined to a greater degree by environmental influences (i.e., condition dependent; Forslund 2003; Byrne and Roberts 2004; Reichard et al. 2004; Lidgard et al. 2005; Shine et al. 2005; Müller et al. 2007; Schradin and Lindholm 2011). For example, male side-blotched lizards exhibit one of three discrete morphs (orange, blue, and yellow), which are the result of alleles segregating at an autosomal OBY locus (Sinervo and Lively 1996). Orange males are hyperaggressive and defend large territories, while blue males defend smaller territories and are less aggressive. Yellow males do not defend territories but sneak matings from orange males (Sinervo and Lively 1996). In contrast, male dung beetles (*Onthophagus taurus*) exhibit two alternative phenotypes, horned and hornless males, which develop in response to varying rearing environments and body size thresholds (Emlen 1997). Once males have developed into these alternative morphs, the phenotypes are irreversible. Horned males are large and vigorously defend burrows by dung patches, while hornless males adopt "sneaker-like" tactics, digging intersecting tunnels of their own and sneaking copulations with females within the burrows guarded by large horned males (Emlen 1997; Moczek and Emlen 2000).

ARTs are predicted to arise through correlational selection for combinations of morphological, physiological, and behavioral traits (Sinervo and Svensson 2002; Sinervo and Calsbeek 2006; Miles et al. 2007). The form of selection on these suites of traits is thought to be disruptive, where

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extreme phenotypes with particular trait combinations experience a fitness advantage over intermediate forms (Gross 1985; Reuffler et al. 2006; Taborsky et al. 2008). Disruptive selection for ARTs may result from alternative tactics occupying divergent niches (Taborsky et al. 2008; Bergmüller and Taborsky 2010), which permit them to compete successfully for access to resources or mates or through frequency-dependent selection (Sinervo and Lively 1996). Despite the importance of disruptive selection in maintaining mating polymorphisms and potentially driving speciation, most ART examples involve discrete polymorphisms because of the ability to assign different strategies to each morph. However, few studies have demonstrated evidence for disruptive selection on traits that characterize alternative male mating phenotypes (references within Oliviera et al. 2008), likely due to the lack of intermediate phenotypes in most systems.

Much of our understanding of ARTs comes from systems where the alternative tactics can be clearly defined; however, there is often high variance in reproductive success in systems where males show no clear morphological discontinuities (e.g., Morrison et al. 2002). We would predict that in these systems selection would favor males that adopt alternative behavioral phenotypes, which are generally subtle and less conspicuous. In many systems with ARTs, morphological differences between individuals are discrete with few intermediate phenotypes; however, when ARTs are characterized by continuous behavioral differences they provide an excellent opportunity to test for disruptive selection because these traits often contain intermediate phenotypes. Furthermore, the relative contribution of the different behaviors defining ARTs to male reproductive success can be quantified (e.g., Baird et al. 2007) and verified using paternity analysis. Trait-based approaches for quantifying the reproductive success of alternative tactics are particularly suitable in these systems when we have an understanding of the traits that are important for fitness.

The lizard genus *Eulamprus* is a widely distributed and well-studied group of skinks in Australia. The genus is known for their high incidence of multiple paternity and high variance in male mating success (Morrison et al. 2002; Dubey et al. 2011; Noble et al. 2013*a*). In *Eulamprus heatwolei*, males exhibit alternative mating tactics, where some males act as residents while others are floaters (Morrison et al. 2002; Stapley and Keogh 2004; Keogh et al. 2012). In the wild, resident males have small home ranges and are observed frequently, while floater males have large home ranges and are observed much less often (Morrison et al. 2002; Stapley and Keogh 2004, 2005). Resident males also have a much lower tendency to move in a novel environment compared with floater males, and these behaviors form part of a behavioral syndrome (Stapley and Keogh 2004). These activity-related behaviors may play an important role in precopulatory sexual selection, and both resident and floater males have been shown to achieve high reproductive success (Morrison et al. 2002; Stapley and Keogh 2005; Keogh et al. 2012); however, selection on traits that characterize these tactics has not been demonstrated.

We studied a closely related species, *Eulamprus quoyii*, and tested for selection on key behaviors that have previously been used to define ARTs in *E. heatwolei* and that have an important bearing on fitness. Unlike *E. heatwolei*, *E. quoyii* is larger and shows higher levels of aggression, yet it exhibits behavior and ecology very similar to those of *E. heatwolei* (D. W. A. Noble and J. S. Keogh, personal observation). Given that male *E. quoyii* are aggressive and are known to form dominance hierarchies (Done and Heatwole 1977), we predicted that body size would be an important determinant of reproductive success (fig. 1). However, the existence of ARTs in the closely related *E. heatwolei* suggests that males adopting particular behavioral traits may elevate their reproductive success further (fig. 1). Floater males, which have high rates of movement and larger home ranges (Morrison et al. 2002; Stapley and Keogh 2005), are predicted to acquire paternity by virtue of higher rates of encounter with a potentially large number of females, while resident males are predicted to reside with groups of females or focus mating efforts on specific females (i.e., mate guarding). Indeed, this is supported by the fact that resident male *E. heatwolei* tend to sire more offspring from resident females. Remaining active for longer might allow these males to mate more regularly with resident females or mate guard (Stapley and Keogh 2005).

Detailed behavioral studies of lizards are difficult to execute in the wild, and paternity estimates can be troublesome depending on the proportion of the population sampled. We circumvented these constraints by establishing six breeding populations in large outdoor seminatural enclosures, where all the individuals were known and could be followed throughout the breeding season. We specifically addressed two questions: (1) Is there evidence for disruptive correlational selection acting on behavioral traits that might promote the evolution of alternative male mating tactics? (2) What behaviors are important contributors to male reproductive success? Since previous work had categorized "floater" and "territorial" males in *E. heatwolei* by the days they are observed active and also demonstrated that they vary in their home range and their movement propensity in the laboratory (Morrison et al. 2002; Stapley and Keogh 2005), we tested the hypothesis that behaviors (home range, movement rates, and total days active) form discrete axes that are under selection in the directions that define ARTs (fig. 1). To test predictions from our hypotheses, we evaluated the support for a series

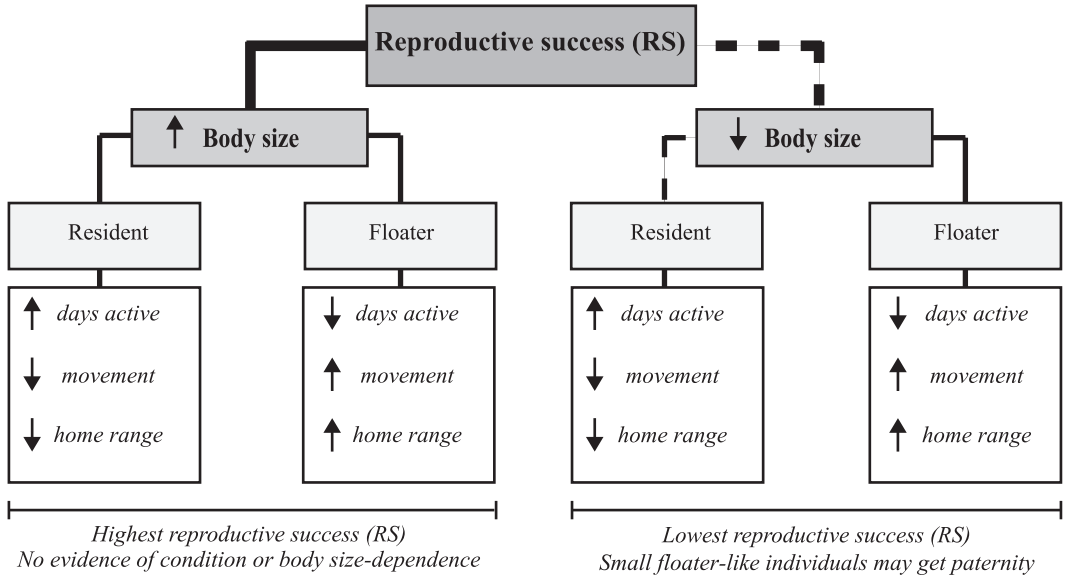

Figure 1: Predictions of how behavioral and morphological traits influence male reproductive success (RS) in eastern water skinks (*Eulamprus quoyii*). Body size is predicted to be the most important determinant of male RS, with large males gaining the highest RS because of their higher competitive abilities compared with smaller males. This is represented by the thick black line along the path from RS to body size. The thick dashed line leading to small males indicates that they have dramatically reduced RS by virtue of their small size. For simplicity, males can adopt two different alternative reproductive tactics along a continuum. Males at either extreme of this multivariate trait space are classified as "residents" (also known as "territorials"; Stapley and Keogh 2004, 2005) and "floaters." The suites of behavioral traits in the figure are predicted to further elevate the RS of a given male adopting these trait combinations. Solid lines represent higher RS, while dashed lines represent lower RS. The solid black line along the small male pathway indicates that small males adopting "floater-like" tactics may elevate their RS in some instances (e.g., Keogh et al. 2012). The thickness of the lines indicates the relative importance of morphology and behavior in determining male RS. For example, large males adopting the specified trait combinations are predicted to achieve the highest RS. Black arrows indicate larger or smaller body size and home range or higher and lower days active and movement. See the introduction for references to predictions.

of candidate models and tested whether predictions from these models (i.e., the directionality and effect sizes of parameter estimates) are congruent with the hypothesis that these traits may promote the evolution of ARTs in *E. quoyii*. We also explored how different behavioral traits contribute to a male's reproductive success by testing how they contribute to the total number of clutches sired by a male.

Material and Methods

Field Collection and Experimental Design

We collected eastern water skinks (*Eulamprus quoyii*) from five sites within 30 km of Macquarie University between August 12 and September 17, 2010. Only sexually mature skinks (snout-vent length [SVL] of >90 mm) were captured, either by hand or by noosing, and brought back to the laboratory for further processing.

For each individual, we measured SVL (to the nearest 1 mm) and mass (nearest 0.1 g) and took a small quantity of blood (~50–70 μL) or tail tissue for DNA. Lizards were sexed by the presence or absence of hemipenes and individually marked using passive integrated transponder (PIT) tags. Lizards were allocated to one of six outdoor enclosures (16 m × 10 m) located on the Macquarie University campus (see Noble et al. 2013*a* for more details on the enclosures). We released 18 males and 18 females ($n = 36$) into each enclosure, ensuring that each collection site was represented and that there was natural variation in body size ($n = 216$ lizards in total). These densities fall within the natural range observed in the wild (G. Swan, personal communication). Each enclosure (fig. S1; figs. S1, S2 are available online) contained two piles of large rocks connected by varying-sized logs while the remaining areas were more open with no rocks and logs, creating natural heterogeneity in their environment. Four large water containers were placed equidistant in the enclosures, and a stack of three ceramic roofing tiles (28 cm × 45 cm × 3.2 cm) were positioned on the ground every 2 m to form a grid. These tiles were numbered to facilitate scoring the location of lizards, and they also provided shelter for the lizards occupying these areas.

Quantifying Behavioral Axes of ARTs

All lizards were marked with a nontoxic paint marker and cloth tape (gray for females, brown for males) to facilitate individual identification. We released male skinks into the six enclosures 2 days prior to females. This replicated conditions in the wild, where males emerge earlier than females in spring. Lizards were given 4 days to acclimatize to the enclosures before behavioral observations commenced.

Water skinks were observed for the duration of the breeding season from September 22 to October 20, 2010 (by D. W. A. Noble and K. Wechmann), during the active periods of the day (0900–1700 hours). Both observers spent a full day sampling together to standardize behavioral recording prior to data collection. Each observer randomly sampled three enclosures per day, and we ensured that both observers sampled all six enclosures over a 2-day period. We used both scan and focal sampling (Martin and Bateson 1993) to quantify individual behavior. We first scanned each enclosure and recorded the position, sex, and identity of all lizards prior to choosing an individual for focal sampling. Scan sampling was done on each enclosure twice a day (once in the morning and afternoon). We recorded positions of lizards on an enclosure map, using the tile markers as reference points. To minimize observer interference, scan samples were conducted by slowly walking the perimeter of the enclosure and using binoculars to identify the identification tags on the backs of lizards. *Eulamprus quoyii* habituates readily to observers, and our presence did not have any noticeable effects on individual behavior. Individuals were haphazardly selected for focal sampling, and we ensured that a new individual was selected whenever possible to ensure representative sampling within each of the six enclosures. This was done to avoid biasing our behavioral sampling toward particular males that were more active or more easily sampled. Focal samples were 10 min in duration, and we recorded whether individuals were moving (locomotion) or remaining stationary. Locomotion was defined as any movement where the lizard moved greater than 10 cm from its initial position. Locomotion bouts were considered independent if lizards stopped for greater than 2 s. If a social interaction took place, the individuals involved, the location, and the outcome were recorded. We observed fighting (stereotypical biting of each others tail) and chasing (rapid approach of one individual followed by the retreat of a second) events between males and copulations between males and females. If individuals were out of view for more than 2 min, the focal sample was abandoned, and a new focal individual was located.

We calculated the proportion of time each individual spent moving as the time spent in locomotion divided by the total time in view. Individual locations were transferred from enclosure maps to electronic maps using GraphClick (ver. 3.0). Using these electronic coordinates, we calculated minimum convex polygons as estimates of individual home ranges (m^2) using the "adehabitat" package (Calenge 2006) in the statistical software package R (R Development Core Team 2010). To determine the minimum number of sightings needed to estimate home range area, we regressed home range area against the number of relocations using the same method as Morrison et al. (2002). We found that there was no longer a statistically significant relationship between home range area and the number of sightings when individuals with eight or more sightings were included.

Reproductive Success of Behavioral Tactics

At the end of the breeding season, females were collected from the enclosures and individually housed in plastic boxes (32 cm × 45 cm × 27 cm) in a temperature-controlled room until parturition. Heating cable was used to elevate one part of the cage to optimal body temperatures (~28°–32°C), thereby allowing females to behaviorally thermoregulate. Ultraviolet lighting was provided during daylight hours on a 12 : 12-h cycle. Lizards were fed crickets twice per week and dog food once per week, with added calcium and vitamin powder. Once females had given birth, we removed the offspring and weighed and measured each neonate. Lizards were toe-clipped for permanent identification, and a small amount of tail tissue was excised and stored in ethanol for DNA extraction.

Genomic DNA was extracted from blood and tissue samples using DNeasy blood and tissue extraction kits (Qiagen) according to the manufacturer's protocol. Six microsatellite DNA loci (Ek100, Ek107, Ek8, Ek37 [Scott et al. 2001], GQ16/17, and GQ20/21 [Sumner et al. 2001]) were amplified. Polymerase chain reactions (PCRs) were carried out in 20-μL reaction volumes containing 1.0 μL of genomic DNA, 10 μL of GoTaq (Promega), 0.5 μL (10 pmol μL^{-1}) of forward and reverse primers, and 8.0 μL of nuclease-free water. PCR conditions for each locus are described in Scott et al. (2001) and Sumner et al. (2001). Forward primers were labeled with different fluorescent dyes (TET, NAD, VIC, and FAM), and product from the final PCRs were pooled into a single plate, run on an ABI 3730 DNA analyzer (Applied Biosystems), and scored by the Australian Genomic Research Facility using AB Genemapper software (Applied Biosystems).

Parentage was assigned using the likelihood-based method in the program CERVUS (ver. 3.0; Kalinowski et al. 2007). We simulated 100,000 offspring with 95% loci typed and 1% mistyped loci, using a strict confidence level of 95% and a relaxed confidence level of 80%. The loci

used in our study were highly variable, ranging from 3 to 34 alleles at a single locus with mean polymorphic information content of 0.7014. The combined nonexclusion probability for a parent pair was 4.46×10^{-6}. Parentage was assigned conservatively, and we excluded offspring that contained one or more mismatches or that had five or fewer loci compared with putative sires. In some cases, males could be compared with offspring at only four loci because of differences in the loci missing between the male and offspring. In these situations, we assigned paternity to the male only if he had no mismatches and the trio (male, female, and offspring pair) LOD scores were significant. From these data we calculated (1) the number of offspring each male sired and (2) the total number of clutches containing offspring sired by each male.

Statistical Analyses

Statistical analyses were carried out using R (ver. 2.15.0; R Development Core Team 2010). In total, 28 males (26%) were not recaptured from the enclosures at the completion of the experiment, and we assumed that they had been preyed upon. Unfortunately, we could not include survival in our analyses because of the low number of males that died in any given enclosure and the lack of behavioral data on these males. To avoid biasing the results, we removed these males from the final analysis of reproductive success because they were part of the experiment for varying amounts of time during the breeding period; therefore, we were unable to standardize male mating opportunity. We also excluded males that had no focal samples ($n = 15$), that had fewer than 8 resightings ($n = 15$), and that were not genotyped at five microsatellite DNA loci ($n = 1$). We obtained complete data for 49 males distributed across the six enclosures with anywhere from 7 to 10 males per enclosure (mean = 8.17). Exclusion of these males may have important consequences for our results, so we ran two separate analyses. In the first analysis, as many individuals with complete data (e.g., males that died but that had complete data and sired offspring; too few points for home range estimates) were included. This increased our sample size slightly, to 56 males, and made our analysis slightly more conservative. Most missing information was because we lacked focal samples for many individuals. In the second analysis, we used a larger sample of males with home range area and days active data along with their morphology. We evaluated a limited number of candidate models (given missing movement data, which seemed to be important) with this larger sample size ($n = 66$), and the results are shown in tables S3–S5 (tables S1–S5 are available online). Sample sizes are provided for the different analyses because of the missing information in the data and because while most females could be identified, seven individuals expelled their PIT tags.

We modeled the number of offspring, relative reproductive success (w), and number of clutches sired as a function of our predictor variables using a generalized linear model (GLM) with a Tweedie (Poisson-gamma) error distribution and log link function. The Tweedie distribution was ideal for our purposes for a number of reasons. First, absolute reproductive success and clutch number were integer/count variables, while relative reproductive success was a positive noninteger variable. The Tweedie distribution allows one to model both types of variables under an overarching framework by introducing an index parameter, p. When $p = 1$, the distribution is equivalent to a Poisson probability distribution where the mean and variance are considered equal, and integer/count variables can be modeled accordingly. However, when $1 < p < 2$, the probability distribution is a compound Poisson-gamma, and a scale parameter is estimated allowing both zero and noninteger variables to be modeled. Second, because a scale parameter is estimated when $1 < p < 2$, Tweedie models can deal with overdispersed data (i.e., when the mean and variance do not increase linearly). Indeed, Poisson models for our data were slightly overdispersed, and this can lead to smaller SEs and elevated Type 1 error rates. To estimate what value of p was best for our data, we fitted our full models and varied p between 1.1 and 1.6 at intervals of 0.1 and compared sample size–corrected Akaike Information Criterion (AICc) between respective models. Models containing the value of p with the lowest AICc were deemed the best fit, and this value of p was used for all candidate models in the same analysis.

We estimated standardized selection gradients from our multivariate GLMs in a fashion similar to that of LeBas et al. (2004) and Chaine and Lyon (2008). Linear selection gradients (β_i) indicate sexual selection that changes the population mean, while nonlinear selection gradients (quadratic selection gradients [γ_{ii}] or correlational selection gradients [γ_{ij}]) describe how the phenotypic variance of a trait is changed (Lande and Arnold 1983; Brodie 1992; Brodie et al. 1995). We converted the number of offspring sired to relative reproductive success (i.e., the number of offspring sired divided by the population mean within each of the six enclosures) and standardized traits by their mean and SD (Lande and Arnold 1983; Brodie et al. 1995). Relative reproductive success was calculated using all males in each of the enclosures, as we had complete paternity data on these males even though we may not have had complete behavioral data. We present linear selection gradients (β_i) from our GLMs without the quadratic and cross product parameters, whereas quadratic and correlational selection gradients come from our full models (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Brodie et al.

Table 1: Candidate models evaluated on the basis of standardized predictor variables with relative reproductive success and number of offspring (absolute fitness) as response variables

		$n = 49$, Tweedie $p = 1.1$				$n = 56$, Tweedie $p = 1.1$			
Candidate model	k	Adj. R^2	AICc	ΔAICc	w_i	Adj. R^2	AICc	ΔAICc	w_i
Relative reproductive success:									
1	11	**.76**	**147.41**	**0**	**.3780**	.64	170.91	4.51	.0584
2	10	**.71**	**147.53**	**.12**	**.3560**	.62	170.49	4.09	.0720
3	12	.76	150.60	3.19	.0767	**.72**	**167.79**	**1.39**	**.2779**
4	11	.73	149.77	2.36	.1162	**.71**	**166.40**	**0**	**.5568**
5	12	.74	150.97	3.56	.0637	.63	172.35	5.95	.0284
6	13	.73	154.84	7.43	.0092	.62	175.41	9.01	.0062
7	15	.73	163.05	15.64	.0002	.61	182.87	16.47	.0001
8	16	.75	166.96	19.55	.0000	.61	186.62	20.22	.0000
9	17	.77	170.93	23.52	.0000	.73	184.41	18.01	.0001
10 (null)	1	NA	283.97	136.56	.0000	NA	325.13	158.73	.0000
No. offspring (absolute fitness):									
1	11	**.76**	**181.54**	**0**	**.3831**	.63	208.14	5.52	.0365
2	10	**.72**	**181.92**	**.38**	**.3168**	.62	207.61	4.99	.0476
3	12	.77	184.39	2.85	.0921	**.73**	**203.88**	**1.26**	**.3070**
4	11	.75	183.67	2.13	.1321	**.72**	**202.62**	**0**	**.5765**
5	12	.75	185.05	3.51	.0662	.64	208.83	6.21	.0258
6	13	.74	188.92	7.38	.0096	.63	211.68	9.06	.0062
7	15	.73	197.19	15.65	.0002	.62	218.90	16.28	.0002
8	16	.77	200.65	19.11	.0000	.64	221.99	19.37	.0000
9	17	.80	204.19	22.65	.0000	.77	219.04	16.42	.0002
10 (null)	1	NA	336.96	155.42	.0000	NA	377.48	174.86	.0000

Note: Results are presented from two separate analyses with different sample sizes. The number of model parameters, sample size–corrected Akaike Information Criterion (AICc), the difference in AICc between the top model and each candidate model (ΔAICc), Akaike weights (w_i), and adjusted R^2 (Adj. R^2) for each model are also presented. The set of predictors in each of the candidate models are listed in table 2 under "Relative and absolute reproductive success." The Tweedie index parameter is listed for each analysis and refers to the best-supported parameter for each of the analyses. Boldfaced models indicate those that are within 2 ΔAICc units of each other and have equal support. All predictor variables are standardized to mean = 0 and SD = 1. NA = not applicable.

1995). In addition, quadratic terms and their SEs were doubled (Stinchcombe et al. 2008).

We generated a set of candidate models on the basis of our verbal hypotheses about how our traits influence reproductive success (fig. 1) and compared the fit of our models using AICc, which is a more robust information criterion for model selection when the sample size–to–parameter ratio is small (Burnham and Anderson 2002). We estimated directional selection on SVL (body size), home range area, total days active, and proportion of time spent moving. In all models, the proportion of time spent moving was arcsine transformed because its distribution was highly right-skewed, and we attempted to reduce its influence on the selection analysis (see the supplementary material for additional analyses we performed to ascertain the effects of predictor distributions on model selection). Since previous studies suggest that males may be adopting ARTs, it is possible that traits may evolve as modules (Morrison et al. 2002; Stapley and Keogh 2004, 2005). Given our smaller sample size, we restricted our models to contain important two-way interactions between traits that we predicted would be under correlational selection (home range area, total days active, and proportion of time spent moving). We also included quadratic estimates for each of the behavioral traits (home range area, total days active, and proportion of time spent moving) that might be under disruptive selection. Since our behavioral traits (particularly total days active and movement rates) may be strongly influenced by a male's body condition, we included condition (residuals from a linear regression between mass and SVL) in some candidate models. This is a commonly used measure of body condition for lizards and removes the strong colinearity between SVL and mass in the models. We included enclosure as a covariate ("block") in all models to control for the differences in the number of females giving birth and the number of offspring produced in each enclosure. Although it is possible to model the enclosure variable as a random effect, we chose not to because of the small number of random-effects levels, which can lead to imprecise variance estimates. It is generally recommended that only variables with greater than five or six levels be modeled as random effects (Bolker et

Table 2: Predictors in each candidate model evaluated

Candidate model	Predictors
Relative and absolute reproductive success:	
1	ENCL + SVL + HRA + MOVE + TOTDAY + MOVE × TOTDAY
2	ENCL + SVL + HRA + MOVE + TOTDAY
3	ENCL + SVL + COND + HRA + MOVE + TOTDAY + MOVE × TOTDAY
4	ENCL + SVL + COND + HRA + MOVE + TOTDAY
5	ENCL + SVL + HRA + MOVE + TOTDAY + MOVE × TOTDAY + MOVE × HRA
6	ENCL + SVL + HRA + MOVE + TOTDAY + MOVE × TOTDAY + MOVE × HRA + HRA × TOTDAY
7	ENCL + SVL + HRA + MOVE + MOVE^2 + TOTDAY + TOTDAY^2 + MOVE × TOTDAY + MOVE × HRA + HRA × TOTDAY
8	ENCL + SVL + HRA + HRA^2 + MOVE + MOVE^2 + TOTDAY + TOTDAY^2 + MOVE × TOTDAY + MOVE × HRA + HRA × TOTDAY
9	ENCL + SVL + COND + HRA + HRA^2 + MOVE + MOVE^2 + TOTDAY + TOTDAY^2 + MOVE × TOTDAY + MOVE × HRA + HRA × TOTDAY
10	INT (NULL)
No. clutches sired:	
1	ENCL + SVL + TOTDAY + TOTDAY^2 + MOVE + HRA + HRA^2 + TOTDAY × HRA + MOVE × TOTDAY + MOVE × HRA
2	ENCL + SVL + TOTDAY + HRA
3	ENCL + SVL + TOTDAY
4	ENCL + SVL + HRA
5	ENCL + SVL + TOTDAY + HRA + TOTDAY × HRA
6	ENCL + SVL + HRA + MOVE
7	ENCL + SVL + TOTDAY + MOVE
8	ENCL + SVL + TOTDAY + TOTDAY^2 + HRA + HRA^2
9	ENCL + SVL + TOTDAY + HRA + HRA^2

Note: ENCL = enclosure, SVL = snout-vent length, HRA = home range area, MOVE = proportion of time spent moving, TOTDAY = total days active, COND = condition.

al. 2008). Although we are on the cusp of this recommendation, we erred of the side of caution and treated enclosure as a fixed effect. We repeated the above analyses using absolute fitness (i.e., number of offspring) and standardized traits. We retained our standardized traits for modeling absolute fitness because it improves the interpretation of regression coefficients, particularly in the presence of interactions (Schielzeth 2010).

In addition to testing hypotheses about how male traits influence absolute and relative reproductive success and whether there was evidence for correlational disruptive selection, we were also interested in testing hypotheses concerning the mechanisms by which these traits may influence the number of females mated. Since it was difficult to get accurate estimates of the number of females that overlapped a male's home range and because this may not necessarily be a good indicator of the number of females actually sired, we used the number of clutches in which a male sired offspring as our dependent variable and modeled it as a function of our predictor variables. We tested three alternative hypotheses. First, males that spend more time active will sire offspring from more females because remaining active would allow males to mate with females that become sexually receptive at different times or possibly exclude other males from accessing these females. If this were supported, then models with total days active would be best supported over models with home range area after controlling for body size. Second, males that move more over a larger area sire more offspring across more females because they are able to encounter more spatially dispersed females for which they may mate. If this were supported, then models with home range area and/or moving would be best supported over models with total days active. Third, both home range area and total days active may be important predictors of male mating success, particularly if males are adopting alternative tactics to acquire paternity. Support for this hypothesis would mean that models containing home range area and total days active would have the best support and possibly models with an interaction between home range area and total days active. Furthermore, we would predict a positive relationship between the number of clutches sired and the number of offspring produced.

In all analyses, we calculated ΔAICc between our best-

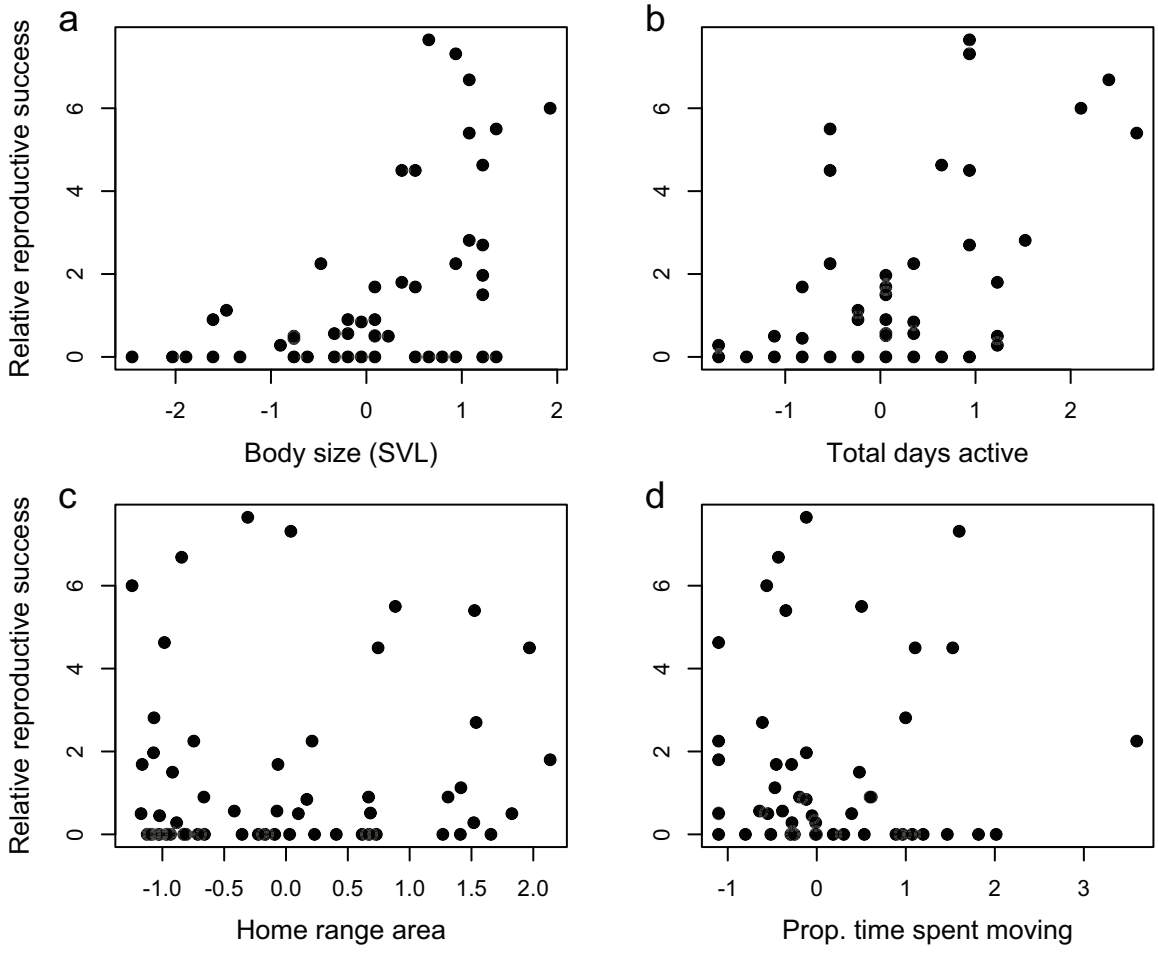

Figure 2: Relationships between relative reproductive success and each of our standardized traits. *a*, Male body size (snout-vent length [SVL]). *b*, Total days a male was observed active. *c*, Home range area (minimum convex polygon). *d*, Proportion of time a male spent moving in a 10-min focal sample.

approximating model and set of competing candidate models along with each model's Akaike weight (w_i), which provides an estimate of model support. Each model's Akaike weight can be interpreted as the probability of model *i* being the true model out of the models in the candidate set (Symonds and Moussalli 2011). We avoided discounting models with ΔAICc of less than 6 from the best-approximating model (Richards 2005; Symonds and Moussalli 2011). This was particularly true with our data because of our smaller sample sizes. Simpler models are often ranked as the best-approximating model when the quantity of data is low; however, it has been shown that the addition of more data can improve the rank of lower-ranked models (Richards 2005). In addition to evaluating model uncertainty, we were interested in testing specific predictions from our models. Therefore, models containing specific interactions that were within 6 ΔAICc units of each other were of particular interest to test whether their predictions were congruent with verbal models. To account for differences in parameter estimates between models, we took a model-averaging approach (Grueber et al. 2011; Symonds and Moussalli 2011). We used "conditional" or "natural" model averaging where parameters are averaged only over the models where that particular parameter is estimated (Grueber et al. 2011). We did this because interactions appeared to be weaker but potentially important. Model-averaged coefficients were estimated from our candidate model set for models that were within 6 ΔAICc units of the top model and weighted by the Akaike weight of each model. For all model averaging, we used our standardized traits (mean = 0 and SD = 1).

To visualize how our dependent variables change with respect to multiple predictor variables, we used the vis.gam function in the "mgcv" package in R (Wood 2006). This

Table 3: Selection gradients from generalized linear models from our two top-supported models of relative reproductive success as a function of the standardized traits

	Model 1				Model 2			
Variable (standardized trait)	β/γ_{ij}	SE	t	P	β	SE	t	P
Body size	1.35	.25	5.42	<.001	1.23	.24	5.19	<.001
Home range area (HRA)	.46	.16	2.92	<.001	.41	.15	2.68	.01
Total days active (TOTDAY)	.45	.13	3.50	<.001	.49	.13	3.74	<.001
Proportion of time spent moving (MOVE)	.11	.16	.71	.48	.13	.17	.77	.44
TOTDAY × MOVE	−.26	.15	−1.69	.09	NA	NA	NA	NA

Note: Relative reproductive success was modeled with a Tweedie probability distribution (log link). Models can be found in table 1; $n = 49$ analysis. NA = not applicable.

allows one to use a fitted parametric GLM to predict data while controlling for the influential effects of all other variables in the model. We visualized the predicted surfaces of our top models to determine whether behavioral and morphological traits influence reproductive success in the predicted direction on the basis of our hypotheses (fig. 1). We also explored how these traits affect the number of clutches a male sired to understand the mechanisms by which males obtain copulations. Only bivariate plots can be visualized, and we compared these plots to determine whether they support our specific predictions about what phenotype combinations would be expected to have high fitness. We avoided extrapolating predicted surfaces too far beyond the bounds of our data and computed predicted estimates only in areas that were within 0.15–0.18 units of a nearest data point. Since our models explained a large amount of variation in fitness traits, we also predicted the theoretical fitness landscape if we were to have particular combinations of phenotypes. In these instances, we were particularly interested in model predictions from equally supported models with interactions. Although nonparametric cubic splines can be used to visualize fitness surfaces (Schluter 1988; Brodie et al. 1995), we avoided these because of our limited data set and enclosure effects. Data sets for all analyses are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.jn0b9 (Noble et al. 2013*b*).

Results

Paternity and Reproductive Success

A total of 303 offspring were born from 63 females, and the number of offspring a female produced was positively related to both her body condition and SVL (multiple linear regression, $n = 56$; condition, $\beta = 0.26 \pm 0.06$, $t = 4.0$, $P < .0001$; SVL, $\beta = 0.16 \pm 0.03$, $t = 4.8$, $P < .0001$). Two hundred twenty-six offspring from 56 females could be assigned to a single sire (zero mismatches at all loci compared and significant trio LOD scores). A total of 21 males (42%) had no reproductive success, while 28 males (57%) sired at least one offspring. Twenty-nine clutches (52%) had more then one male sire offspring on the basis of paternity assignment and allelic diversity within the clutch. The number of offspring sired ranged from 1 to 17, and these males sired offspring across one to six unique clutches. Mean reproductive success varied across enclosures, ranging from an average of 1.11 offspring (enclosure 5) to 3.56 offspring (enclosure 6) with an overall average of 2.10 (SE = 0.33) across enclosures.

Behavioral Observations

A total of 17.3 h of focal observations were conducted on 56 individual males across the six enclosures. Aggressive interactions between males were uncommon, and only three fights and nine chases were recorded. Male home range size ranged from 3.07 to 72.7 m^2 (mean = 30.70 ± 2.50 m^2, $n = 66$), while they remained active anywhere from 5 to 20 days (mean = 11 ± 0.40 days, $n = 66$). SVL and home range size were not significantly correlated (Spearman rank correlation $r_s = -0.05$, $P = .67$, $n = 66$). Home range area was also not significantly correlated with the number of days a male was active ($r_s = 0.12$, $P = .33$, $n = 66$).

Correlational Disruptive Selection for ARTs and Predictors of Reproductive Success

Our models explained anywhere from 61% to 80% of the variation in relative and absolute reproductive success (tables 1, 2). There was a strong positive relationship between relative reproductive success and both male body size and total days active (fig. 2*a*, 2*b*). However, there was substantial variation and no relationship between relative reproductive success and either male home range area or proportion of time spent moving (fig. 2*c*, 2*d*). The lack of relationship in figure 2*c* and 2*d* was partly due to the fact that individuals with high fitness but small home ranges were observed to be active a lot and had lower than average movement rates.

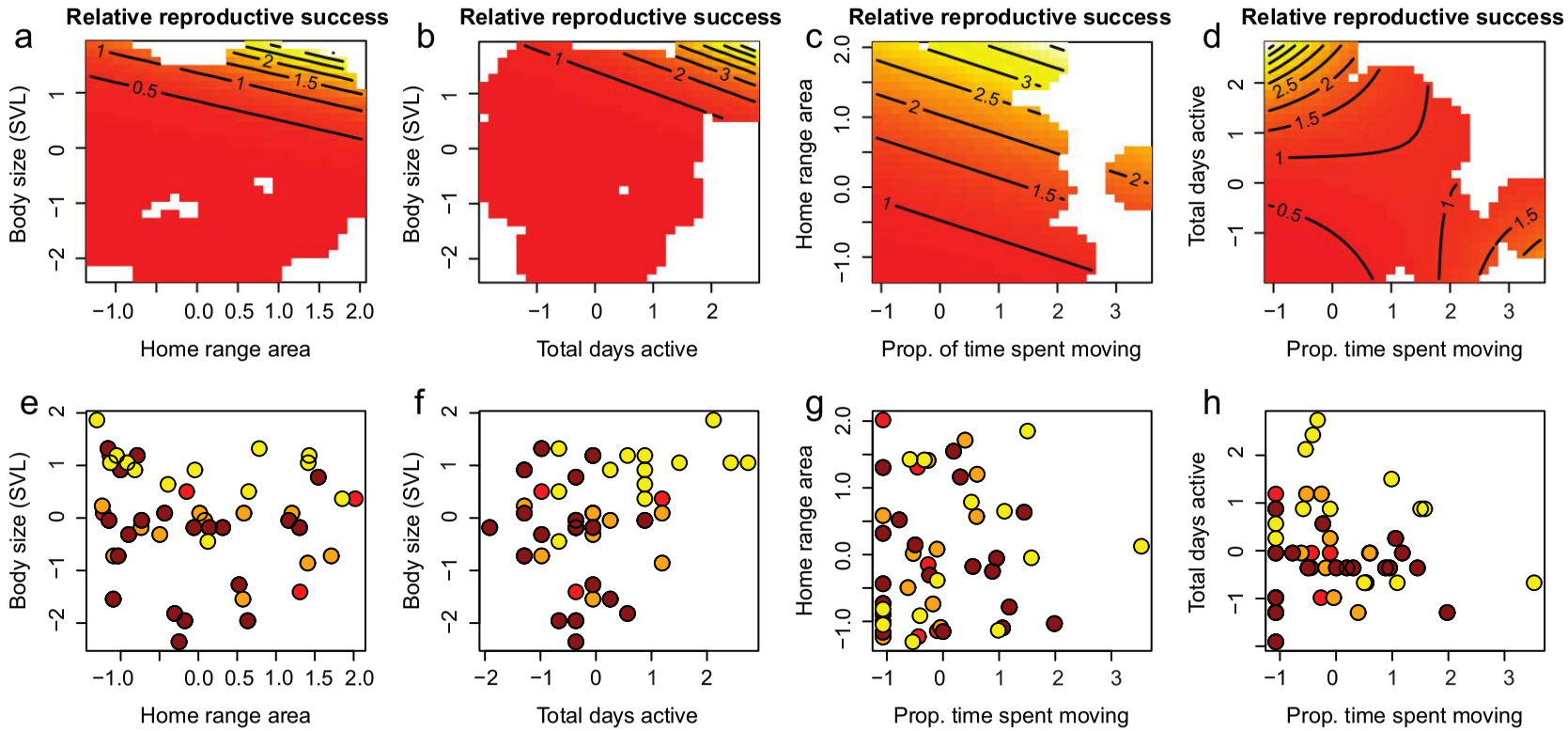

Figure 3: *a–d*, Predicted parametric contour plots of relative reproductive success as a function of our standardized traits from generalized linear models with a Tweedie error distribution and log link function. Contours are predicted where data are available and control for other influential parameters in the model. *e–h*, Raw data for multiple predictor variables plotted together. Colors indicate the relative reproductive success of individual lizards: dark red = no offspring, red = relative reproductive success of 1 and below, orange = relative reproductive success of greater than 1 and less than 2, yellow = relative reproductive success greater than 2. SVL = snout-vent length.

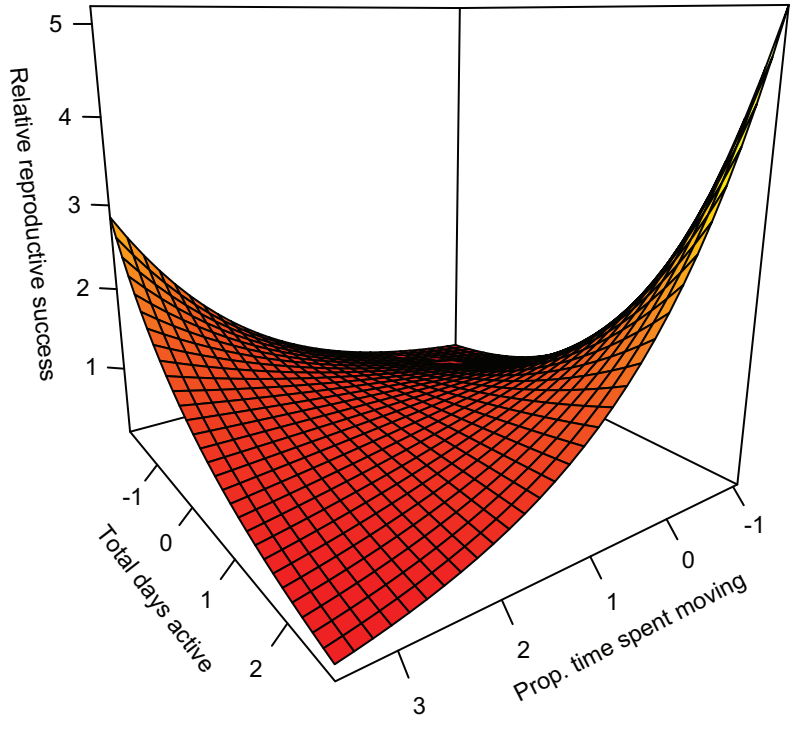

Figure 4: Predicted surface plot from a parametric generalized linear model of relative reproductive success and standardized traits (total days active and proportion of time spent moving), controlling for other variables in the model. Surface plots are extrapolated over the entire trait space and offer a theoretical expectation of the fitness landscape if all possible trait combinations were observed.

The best-supported models were those containing directional selection gradients for male body size (SVL), total days active, home range area, and proportion of time spent moving (tables 1, 3). Two models were equally supported in our analyses, one containing only main effects and a second containing an interaction between proportion of time spent moving and total days active, with the ΔAICc between the two models ranging from 0.12 to 0.38 ΔAICc units from each other (table 1; $n = 49$; full model coefficients are shown in table S6). This difference increased in the analyses with a larger sample size to 1.26–1.39 (table 1; $n = 56$), and condition was included in these models. We found similar support for these two models when using predictor variables that were converted to normalized quantiles prior to analyses (table S2), suggesting that this pattern could not simply be explained by the skewed distribution of the proportion of time spent moving. Model-averaged estimates for parameters in the tied models indicated that body size ($\beta_{mean} \pm$ adj. SE $= 1.30 \pm 0.26$), home range area ($\beta_{mean} \pm$ adj. SE $= 0.44 \pm 0.16$), total days active ($\beta_{mean} \pm$ adj. SE $= 0.46 \pm 0.14$), and proportion of time spent moving ($\beta_{mean} \pm$ adj. SE $= 0.13 \pm 0.46$) had positive effects on relative reproductive success, while there was support for an interaction between total days active and proportion of time spent moving ($\beta_{mean} \pm$ adj. SE $= -0.26 \pm 0.16$). We used our top models to predict reproductive success and test whether these were in line with predictions from our verbal hypothesis (fig. 1), while controlling for other variables in the model. Both the main effects and the interaction model (models 1 and 2; tables 1, 3) predict that large males that are observed frequently and large males that have large home ranges obtain high reproductive success when other variables in the model are held constant (fig. 3*a*, 3*b*, 3*e*, 3*f*). Models 1 and 2 also predict that large males with large home ranges that move more are expected to have high reproductive success (fig. 3*c*, 3*g*). The interaction between total days active and proportion of time spent moving predicted disruptive selection in that large males that moved little but that were observed frequently and males that moved a lot but that were observed less were predicted to have high reproductive success (fig. 3*d*, 3*h*). This was also evident when we predicted the entire fitness landscape (fig. 4). Correlational selection was still evident when male 151 was removed; however, it was no longer disruptive (see the supplementary material for details on analysis).

There was a strong positive relationship between the number of offspring sired and the number of clutches in

Table 4: Candidate models evaluated on the basis of standardized predictor variables with the number of clutches sired as the dependent variable

		$n = 49$, Tweedie $p = 1.1$				$n = 56$, Tweedie $p = 1.1$			
Candidate model	k	Adj. R^2	AICc	ΔAICc	w_i	Adj. R^2	AICc	ΔAICc	w_i
No. clutches sired:									
1	15	.64	164.08	22.30	.0000	.52	177.97	25.2	.0000
2	9	.61	144.47	2.69	.1091	.51	157.43	4.66	.0446
3	**8**	**.39**	**141.78**	**0**	**.4186**	.36	**152.77**	**0**	**.4580**
4	**8**	**.59**	**142.52**	**.74**	**.2892**	.50	**153.46**	**.69**	**.3244**
5	10	.59	147.77	5.99	.0209	.50	160.58	7.81	.0092
6	9	.60	145.70	3.92	.0590	.52	156.59	3.82	.0678
7	9	.43	145.43	3.65	.0675	.39	156.14	3.37	.0849
8	11	.63	150.53	8.75	.0053	.49	163.86	11.09	.0018
9	10	.63	147.02	5.24	.0305	.50	160.58	7.81	.0092

Note: Results are presented from two separate analyses with different sample sizes. The number of model parameters, sample size–corrected Akaike Information Criterion (AICc), the difference in AICc between the top model and each candidate model (ΔAICc), Akaike weights (w_i), and adjusted R^2 (Adj. R^2) for each model are also presented. The set of predictors in each of the candidate models are listed in table 2 under "No. clutches sired." The Tweedie index parameter is listed for each analysis and refers to the best-supported parameter for each of the analyses. Boldfaced models indicate those that are within 2 ΔAICc units of each other and have equal support. All predictor variables are standardized to mean = 0 and SD = 1.

which a male sired offspring ($r_s = 0.98$, $n = 49$, $P < .001$; fig. S2). There was much model uncertainty in our candidate set, and we found equal support for two candidate models (table 4; models 3 and 4); however, a number of other models were within 6 AICc units of these models (models 2, 5, 6, 7, and 9; table 4). Model-averaged coefficients from models within 6 ΔAICc units of our top model showed that body size ($\beta_{mean} \pm$ adj. SE = 0.90 ± 0.26), total days active ($\beta_{mean} \pm$ adj. SE = 0.28 ± 0.15), and home range area ($\beta_{mean} \pm$ adj. SE = 0.40 ± 0.15) all had a positive effect on the number of clutches sired. We predicted the expected number of clutches a male of a particular phenotype would be expected to sire from models 3 and 4, but we also present model 2 because both home range area and total days active are present in the same model, and estimates may change slightly (table 5). Our models made qualitatively similar predictions; individuals with large body size and with large home range areas were predicted to sire offspring across more clutches (fig. 5*a*, 5*c*), while larger individuals that were active longer were also predicted to sire offspring across more clutches (fig. 5*b*, 5*d*). In the best-supported models, the coefficient for home range area was larger than the total days a male was active (table 5). Thus, the influence of home range on number of clutches sired exceeded that of total days active.

Discussion

By quantifying male behavior in seminatural enclosures in combination with paternity testing of a known population, we provide evidence for directional selection on both behavioral and morphological traits related to reproductive success. Our analysis also suggests that disruptive correlational selection may also play an important role in shaping the suites of behavioral traits males adopt in this system. Models with correlational selection gradients were almost equally supported in our candidate set, and predictions from these models supported combinations of traits that are predicted to define ARTs. We showed that males with higher reproductive success also sired offspring across more females, and there was equal support for models containing a positive effect for total days active and home range area on the number of clutches sired. Model predictions regarding how these traits influence the number of clutches sired were also in accordance with ART predictions. Interestingly, home range area had a larger estimate in models with clutch number, while total days active had a larger estimate in models predicting offspring number controlling for body size effects.

The contributions of different behavioral and morphological attributes to male reproductive success are seldom addressed in a single statistical framework. This is particularly important with respect to understanding the independent contributions of a male's phenotype to his reproductive success and elucidates the precopulatory mechanisms contributing to paternity outcome. We found that male body size, total days active, and home range area were strong independent predictors of male reproductive success. In *Eulamprus quoyii*, large body size positively affected male reproductive success, and these results are congruent with a wide range of organisms that show body size effects on reproductive success (Andersson 1994 and references therein). Body size is an important determinant

Table 5: Parameters important in predicting the number of clutches a male sired

	Model 3			Model 4			Model 2		
Parameter	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Body size	.75	.20	<.001	1.10	.21	<.001	.94	.21	<.001
Total days active	.28	.15	.07	NA	NA	NA	.28	.14	.04
Home range area	NA	NA	NA	.40	.14	<.01	.40	.14	<.01

Note: Parameters are presented for the top-supported models (3 and 4) and for model 2, with all parameters in the same model. NA = not applicable.

of contest outcome and dominance status (Rowland 1989; Andersson 1994), with larger males often gaining access to higher-quality territories or larger groups of females (Wells 1977; Andersson 1994; Baird et al. 2007). Larger *E. quoyii* are known to be more dominant than smaller ones (Done and Heatwole 1977). This may explain why larger males achieve higher reproductive success; however, we do not yet understand the reasons for dominance or territoriality in *E. quoyii*, and future work will be necessary to understand how large males, using potentially different reproductive tactics, monopolize female mating opportunities.

Interestingly, labile behavioral traits may be more important to male reproductive success in systems where overt aggression is low (Baird et al. 2007). In their study of the mating success of male collard lizards (*Crotophytus collaris*), Baird et al. (2007) found that patrol rate (total distance traveled divided by observation time), territory area, and distant displays (total number of displays divided by observation time) were all more important predictors of male mating success than morphological variables. They suggest that this may be due to the lower occurrence of aggression between males in their population (Baird et al. 2007). Even though *E. quoyii* are aggressive, we found evidence for important roles for movement rates, home range size, and total days active in male reproductive success. Home range size and presumably movement rates are likely key determinants of male reproductive success when females are spatially and temporally dispersed (Emlen and Oring 1977) because males capable of covering larger areas are expected to interact with a larger number of sexually receptive females, increasing their chances of mating. Indeed, our data support home range area as a behavioral trait that is important for mate acquisition, since male *E. quoyii* with larger home range areas sired offspring across more clutches, suggesting that these lizards interact and copulate with more females. However, males that spend more time active during the breeding season are also expected to mate with more females, particularly if females are temporally variable in their receptivity or spatially clumped (Emlen and Oring 1977). Staying active longer, particularly with aggregations of females, may also allow males to copulate more frequently with females, giving them an advantage in postcopulatory sexual selection. We found evidence that total days active also positively influenced the number of clutches a male sired because models with total days active were as supported as those with home range area. Interestingly, comparing the strength of estimated coefficients between total days active and home range area between models of offspring number and clutch number suggests that total days active has a larger effect on the number of offspring sired, while home range area has a larger effect on the number of clutches sired. Although these differences are small, this finding suggests that males that are observed frequently and those with large home range areas may elevate their reproductive success in two subtly different ways. Males remaining active longer may mate more frequently and/or prevent females from mating with other males. Indeed, resident *Eulamprus heatwolei* are more likely to sire offspring with resident females (Stapley and Keogh 2005), and the proportion of females choosing to remain sedentary may have important consequences for their reproductive success. In contrast, males with larger home ranges probably copulate with spatially dispersed females, and it does appear that they are mating with more females than are "resident-like" males; however, they are not siring as many offspring within these clutches. Although a plausible hypothesis, this will require further testing.

Is There Evidence for Correlational Disruptive Selection on Behavioral Traits?

Disruptive selection has been championed as a major force generating and maintaining phenotypic diversity in populations, and it may play a major role in speciation (Reuffler et al. 2006). Recent advances in multivariate statistics have allowed for greater insight into the modes of selection in natural populations, and studies identifying both correlational and disruptive selection have increased over the years (Brodie 1992; Kingsolver et al. 2001; Sinervo and Svensson 2002; McGlothlin et al. 2005; Calsbeek and Smith 2007; Bolnick and Lau 2008; Hendry et al. 2009). However, measurements of selection on phenotypic traits have been biased, with greater than 90% of selection estimates based on morphological and life-history traits (Kingsolver et al.

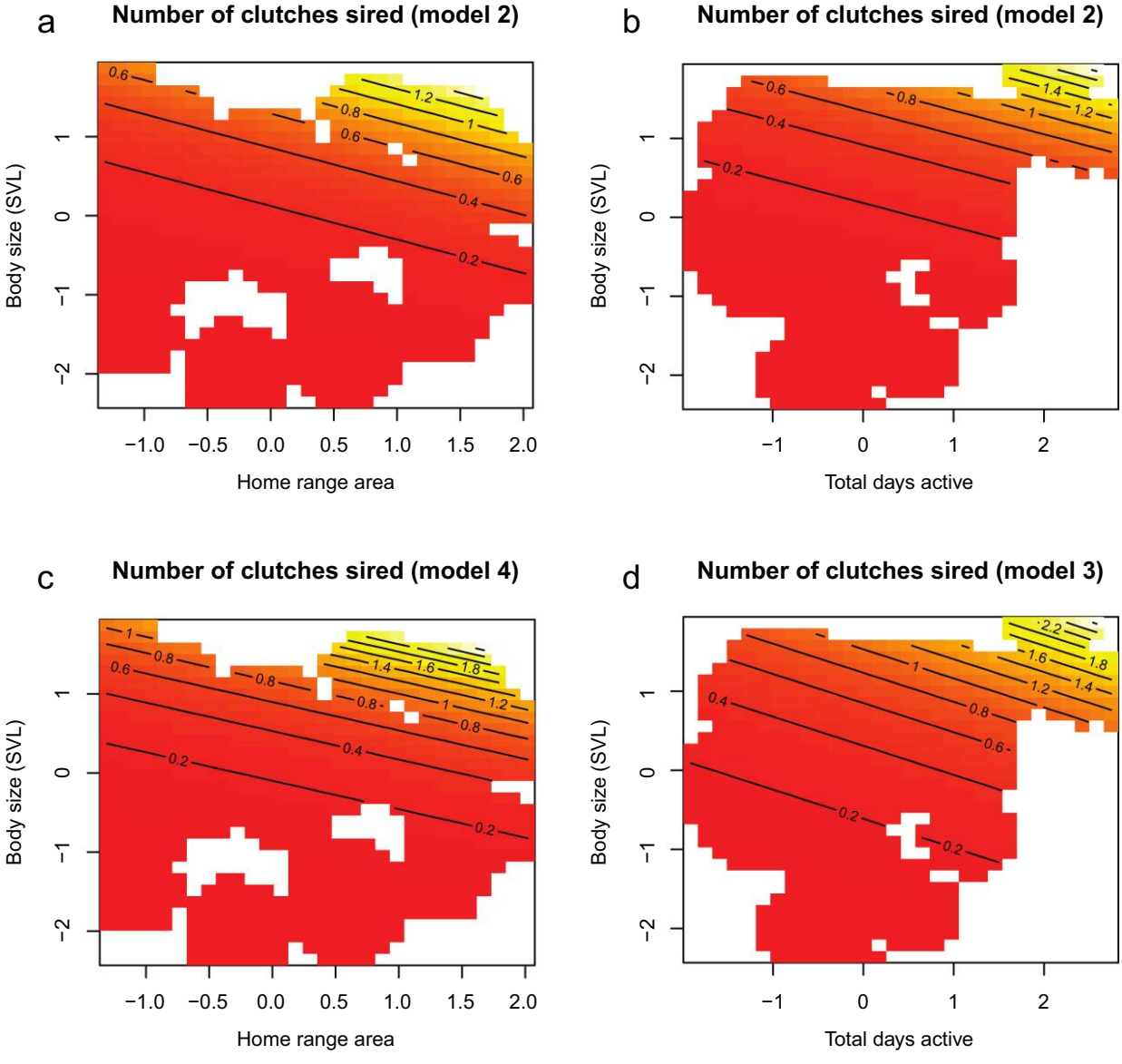

Figure 5: Predicted parametric contour plots of the number of clutches sired as a function of our standardized traits from our two top-supported generalized linear models (Tweedie error distribution, log link; models 4 and 3; *c*, *d*) and a model with both home range and days active (model 2; *a*, *b*). Plots explore the predicted number of clutches sired as a function of body size (snout-vent length [SVL]) and either total days active or home range area. We predicted only areas of the fitness surface that were close to existing data.

2001). We provide evidence for correlational disruptive selection acting on behavioral traits that are in accordance with phenotypic axes of ARTs in water skinks. To our knowledge, we provide the first evidence for such patterns. Large male lizards with high and low movement rates that are observed rarely or often, respectively, are predicted to achieve higher reproductive success when controlling for all other variables. This supports previous work in the related *E. heatwolei*, which defined and categorized ARTs using residency and total days active (Morrison et al. 2002; Stapley and Keogh 2005) and which has shown that resident and floater males differ in their propensity to move in the laboratory (Stapley and Keogh 2004). We did not find strong evidence for interactions between other behavioral traits we hypothesized to be part of the male phenotypes achieving high reproductive success; however, their coefficients were in the predicted direction, and it is possible that our sample size was insufficient to detect these effects, as they may be much weaker (Brodie 1992; Brodie et al. 1995).

In general, our selection estimates were large compared with many reported estimates in the literature (Kingsolver et al. 2001, 2012). This likely reflects the smaller sample sizes used in our study, which can bias selection estimates upward. However, such large selection estimates are also the result of strong sexual selection in this system, as there was high variance in male reproductive success (Kingsolver et al. 2012). Although larger sample sizes will be necessary to be completely confident about the strength of correlational selection gradients and to clarify model uncertainty, our data do suggest that interactions between behavioral traits are important in this system, particularly given that we detected evidence for them with relatively small sample sizes. Importantly, we also found that predictions from our statistical models that included biologically plausible interactions were in agreement with what we predicted from our verbal models on the basis of previous studies (Morrison et al. 2002; Stapley and Keogh 2004, 2005; Keogh et al. 2012). Nonetheless, this needs to be interpreted with caution because strong directional selection can also drive significant correlational selection gradients (Lande and Arnold 1983; Phillips and Arnold 1989; Brodie et al. 1995) and may be responsible for variation among males in the tactics they adopt to acquire paternity. This may be the case given that directional selection gradients predict phenotypes that are also in line with the traits predicted to characterize alternative tactics (i.e., strong directional selection for large home range [floater] but many days active [resident]). This may be an alternative explanation for the patterns we observed, and it is possible that it might lead to somewhat "discrete" variation in populations, particularly if constraints on what phenotypes males can adopt exist. For example, energetic constraints may limit the behavioral repertoire of individual males, and a trade-off may exist between remaining active for long periods and moving a lot over a large area. Selection may favor males adopting these different behavioral phenotypes, as they appear to be alternative mechanisms for acquiring paternity.

Implications for Our Understanding of ARTs

Understanding the evolutionary dynamics between ARTs requires data on each tactic's relative fitness (Austad 1984; Gross 1996; Taborsky et al. 2008; Shuster 2010). Our results provide interesting possibilities with respect to understanding the relative fitness of ARTs in *E. quoyii* because behavioral traits in ectotherms are strongly influenced by environmental conditions during mating (Olsson et al. 2011). Long-term studies in *Lacerta agilis* have shown the incidence of multiple paternity to be higher in warmer years, and the investigators attribute these changes to an increase in mate encounter rates and increased male activity (Olsson et al. 2011). Since ARTs in *E. quoyii* are linked to activity-related behavioral traits, it is reasonable to predict that environmental variation may affect the relative fitness of ARTs, and it highlights the importance of environmental variation to the relative fitness of alternative tactics, which has been emphasized by previous authors (Taborsky 1998; Shuster 2010).

In summary, we provide evidence for strong directional selection on behavioral traits predicted to be important for male reproductive success in *E. quoyii*, and our models suggest that correlational disruptive selection may also be acting on large males to potentially promote the evolution of alternative male mating tactics. Our study highlights how morphological and labile behavioral traits may interact in complex ways to create a fitness landscape, which might promote the evolution of alternative male mating tactics in systems where there are no obvious morphological differences between tactics. Testing the generality of this finding and understanding the behavioral mechanisms generating ARTs will be a fruitful avenue for future research.

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An eastern water skink (*Eulamprus quoyii*) from Sydney, Australia. Photograph by M. J. Whiting.