



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA
BIOLOGÍA EVOLUTIVA

**EVOLUCIÓN DEL DIMORFISMO SEXUAL EN EL GÉNERO *SCOLOPORUS*
(SQUAMATA: PHRYNOSOMATIDAE): INTERACCIÓN ENTRE LA SELECCIÓN
NATURAL Y SEXUAL**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

M. EN C. VÍCTOR HUGO JIMÉNEZ ARCOS

TUTOR PRINCIPAL DE TESIS: DR. RAÚL CUEVA DEL CASTILLO MENDOZA
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA, UNAM

COMITÉ TUTOR: DR. FAUSTO ROBERTO MÉNDEZ DE LA CRUZ
INSTITUTO DE BIOLOGÍA, UNAM

DR. JUAN SERVANDO NÚÑEZ FARFÁN
INSTITUTO DE ECOLOGÍA, UNAM

MÉXICO, CD. MX. JULIO, 2018



Universidad Nacional
Autónoma de México

Dirección General de Bibliotecas de la UNAM

Biblioteca Central



UNAM – Dirección General de Bibliotecas
Tesis Digitales
Restricciones de uso

DERECHOS RESERVADOS ©
PROHIBIDA SU REPRODUCCIÓN TOTAL O PARCIAL

Todo el material contenido en esta tesis esta protegido por la Ley Federal del Derecho de Autor (LFDA) de los Estados Unidos Mexicanos (México).

El uso de imágenes, fragmentos de videos, y demás material que sea objeto de protección de los derechos de autor, será exclusivamente para fines educativos e informativos y deberá citar la fuente donde la obtuvo mencionando el autor o autores. Cualquier uso distinto como el lucro, reproducción, edición o modificación, será perseguido y sancionado por el respectivo titular de los Derechos de Autor.

OFICIO CPCB/432/2018

Asunto: Oficio de Jurado para Examen de Grado.


LIC. IVONNE RAMÍREZ WENCE
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 26 de febrero de 2018, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **JIMENEZ ARCOS VICTOR HUGO**, con número de cuenta **98140233**, con la tesis titulada **"Evolución del dimorfismo sexual en lagartijas del género *Sceloporus* (Squamata: Phrynosomatidae): interacción entre la selección natural y sexual"**, realizada bajo la dirección del **DR. RAÚL CUEVA DEL CASTILLO MENDOZA**:

Presidente: DR. ROBERTO EDMUNDO MUNGUÍA STEYER
Vocal: DR. ALEJANDRO GONZÁLEZ VOYER
Secretario: DR. FAUSTO ROBERTO MÉNDEZ DE LA CRUZ
Suplente: DRA. LETICIA MARGARITA OCHOA OCHOA
Suplente: DR. JUAN SERVANDO NUÑEZ FARFAN

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a 16 de mayo de 2018.


DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA



c.c.p. Expediente del (la) interesado (a)

Agradecimientos

Al Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México por la formación y conocimientos adquiridos durante mi formación académica.

Al Consejo Nacional de Ciencia y Tecnología por el apoyo económico por medio de la beca CONACYT 377215.

Al Programa “Ciencia Básica 2014” del Consejo Nacional de Ciencia y Tecnología proyecto No. 235987 otorgado al Dr. Raúl Cueva del Castillo Mendoza que permitió el desarrollo de esta tesis.

Al posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México por el apoyo PAEP 2016.

Al Dr. Raúl Cueva del Castillo Mendoza por su invaluable guía y consejos durante mi formación académica.

A los miembros de mi Comité Tutor: Dr. Fausto R. Méndez de la Cruz y Dr. Juan S. Núñez Farfán por su apoyo académico sin el cual este trabajo no hubiera podido terminarse.

Agradecimientos a título personal

Realizar estudios de posgrado, especialmente un doctorado, no es una tarea sencilla. Parte de lograr esa meta radica además de adquirir los conocimientos especializados, en resolver problemas potenciales durante el desarrollo de la investigación considerando el tiempo limitado para su ejecución. Es así que el posgrado comprende no solo la formación académica, también la adquisición de diversas herramientas y habilidades para lograr una formación integral. Considerando esto, quiero agradecer a mi tutor principal, Dr. Raúl Cueva del Castillo Mendoza por todos sus consejos y orientación a través de los años, más allá de la realización de este trabajo. Raúl es uno de los mejores profesores que he conocido en el área de biología evolutiva, y un gran investigador con una visión clara que incentiva la investigación. Agradezco todo el tiempo invertido en mi formación y su honestidad en cada una de estas etapas. Sus enseñanzas han permeado más allá del ámbito académico. Muchas gracias Raúl.

A mi Comité Tutor, Dr. Fausto R. Méndez de la Cruz y Dr. Juan S. Núñez Farfán por su apoyo durante la realización de este trabajo, especialmente durante la difícil parte del examen de candidatura. Ambos son grandes investigadores que han formado una gran cantidad y calidad de alumnos, y cuya experiencia se ve reflejada en cada uno de los consejos y comentarios que he recibido de su parte. A los miembros del jurado: Dr. Roberto E. Munguia Steyer, Dr. Alejandro Gonzalez Voyer y Dra. Leticia M. Ochoa Ochoa por sus valiosos aportes durante la revisión de la tesis.

Quiero agradecer a mis amigos que me brindaron su ayuda durante el trabajo de campo: Rafael Alejandro Calzada Arciniega, Aníbal H. Díaz de la Vega Pérez, Salomón Sanabria Urbán, Cesar Toscano Flores, Leopoldo D. Vázquez Reyes, Ricardo Palacios Aguilar, Misael J. Pérez Quintero, Samuel A. Santa Cruz Padilla, Luis E. Hernández Montes de Oca, Víctor Aguirre Hidalgo, Sandra F. Arias Balderas, J. Roberto García Aguilera, Abraham Aguirre Romero y todos aquellos a quien pude haber omitido que me brindaron ayuda y buenos momentos que hicieron más ameno el trabajo de campo, muchas gracias. Especialmente al Dr. Christopher Blair quien me ha brindado ayuda y comentarios invaluable para la generación de diversas publicaciones incluidas las asociadas a esta tesis, thanks a lot Chris. Al Dr. Roberto E. Munguia Steyer por el tiempo brindado durante ensayos de examen de candidatura y por sus valiosos consejos tanto académicos como personales.

Especialmente a mi familia. A mi esposa Marisol Gómez Hurtado por su infinita paciencia y comprensión durante mis ausencias en campo y trabajo de gabinete, quien a mi lado me brindo el apoyo necesario para la realización de este trabajo. Estoy infinitamente agradecido por todo tu amor y comprensión. A mi madre Beatriz S. Arcos Pino por su incansable apoyo y aliento, gracias por todos tus consejos y comentarios que me hacen ser mejor persona. A mis hermanos Hiram y Eunice Jiménez Arcos y sus respectivas familias, por su cariño, amor y preocupaciones en mis largas ausencias. A mi padre, cuyas enseñanzas están presentes todos los días a través de los recuerdos. La familia es un pilar central que nos da fortaleza, amor y descanso durante momentos difíciles, el rumbo en nuestro camino.

A todos los Profesores, Sinodales y Tutores que he tenido durante mi desarrollo académico. Al Posgrado en Ciencias Biológicas de la UNAM así como al CONACyT por el apoyo académico y económico sin el cual este trabajo no hubiera podido realizarse.

Índice

Abstract	1
Introducción general	2
Capítulo I	8
The interplay between natural and sexual selection in the evolution of sexual size dimorphism in <i>Sceloporus</i> lizards (Squamata: Phrynosomatidae)	
Artículo de requisito para la obtención de grado	
<i>Ecology and Evolution</i> , 7: 905-917	
Capítulo II	32
Habitat use and sexual dimorphism in <i>Sceloporus grammicus</i> (Squamata: Phrynosomatidae)	
Artículo enviado	
<i>Biological Journal of Linnean Society</i>	
Discusión y conclusiones generales	69

Resumen

El dimorfismo sexual es una característica ampliamente distribuida en animales bilaterales con reproducción sexual. La selección sexual explica la evolución de caracteres sexuales secundarios y/o mayor talla corporal en el sexo seleccionado. Por selección en fecundidad se esperan tallas corporales mayores en hembras o mayor volumen o tamaño abdominal favoreciendo la maduración de un mayor número o tamaño de huevos o crías. También la divergencia del nicho ecológico entre sexos puede generar dimorfismo sexual en cualquier rasgo asociado al uso o explotación de recursos, aunque no es posible predecir tendencias generales en talla y forma. La divergencia entre sexos puede resultar de la interacción entre la selección natural y sexual, debido a que los rasgos fenotípicos pueden estar sujetos a diferentes presiones selectivas. El estudio del impacto relativo de la selección natural y sexual proporciona un análisis completo de los mecanismos responsables de generar la divergencia adaptativa entre los sexos. Las lagartijas del género *Sceloporus* son un modelo ideal para evaluar la importancia relativa de la selección natural y sexual en la evolución del dimorfismo sexual. La gran variación morfológica, ecológica y conductual sugieren que ambas fuerzas evolutivas han moldeado la evolución del género. Además presentan modo reproductor ovíparo y vivíparo, y se ha sugerido que las hembras de especies vivíparas debido a la extensión en el periodo de gestación presentan mayor talla que hembras de especies ovíparas. El objetivo de esta tesis fue analizar el impacto relativo de la selección natural y sexual en la evolución del dimorfismo sexual en las lagartijas del género *Sceloporus* utilizando métodos comparativos filogenéticos. El dimorfismo sexual puede resultar del balance entre la selección natural y la selección sexual. Una vez que los efectos filogenéticos son controlados, nuestros resultados muestran un mayor impacto relativo de la selección sexual en la divergencia en talla en el género *Sceloporus*. La regla de Rensch es un patrón explicado por las ventajas selectivas de machos con mayor talla corporal y el incremento en la magnitud a medida que aumenta la talla promedio de las especies. En lagartijas la selección intrasexual es la principal causa de dimorfismo sexual en talla sesgado a machos. La historia evolutiva dentro del género sugiere un mayor rol diversificador de la selección sexual sobre la selección en fecundidad. A nivel interpoblacional (Capítulo 2), algunos rasgos están bajo diferentes fuerzas selectivas. Talla, tamaño de cabeza y extremidades pueden estar bajo selección sexual en machos. En las hembras, la longitud del tronco presentó un pendiente mayor a 1 (hiperalometría) en la población generalista. Es posible que la interacción entre selección natural y sexual tenga un efecto antagónico, como en lagartijas arborícolas (sobre tamaño de extremidades y cabeza en machos) o sinérgico (mayor longitud de tronco) en función del contexto ecológico. El género *Sceloporus* exhibe la mayor diversidad en México y las especies son encontradas en todos los tipos de vegetación. Su gran diversidad morfológica, ecológica y conductual sugieren que la selección natural y sexual han tenido un papel central en su evolución. Es probable que *Sceloporus* represente un ejemplo de una radiación adaptativa. Sin embargo, elementos básicos de historia natural, ecología y reproducción son desconocidos, especialmente en especies con distribución limitada a México. Estudios futuros deben encaminarse en obtener información de historia natural como una primera aproximación. Estudios experimentales evaluando la significancia adaptativa de los rasgos fenotípicos, tanto por selección natural, sexual y variables ecológicas (i.e. bióticas y abióticas) son necesarios para determinar los mecanismos que han conducido favorecido la divergencia y diversificación del género.

Abstract

Sexual dimorphism is a widely distributed characteristic in bilateral animals with sexual reproduction. Sexual selection explains the evolution of secondary sexual characters and / or greater body size in the selected sex. By selection in fecundity, larger body sizes are expected in females or larger volume or abdominal size favoring the maturation of a greater number or size of eggs or offspring. Also the divergence of the ecological niche between the sexes can generate sexual dimorphism in any feature associated with the use or exploitation of resources, although it is not possible to predict general trends in size or shape. Divergence between sexes can result from the interaction between natural and sexual selection, because phenotypic traits can be subject to different selective pressures. The study of the relative impact of natural and sexual selection provides a complete analysis of the mechanisms responsible for generating the adaptive divergence between the sexes. The lizards of the genus *Sceloporus* are an ideal model to evaluate the relative importance of natural and sexual selection in the evolution of sexual dimorphism. The great morphological, ecological and behavioral variation suggests that both evolutionary forces have shaped the evolution of the genus. They also have an oviparous and viviparous reproductive mode, and it has been suggested that females of viviparous species due to the extension in the gestation period are larger than females of oviparous species. The objective of this thesis was to analyze the relative impact of natural and sexual selection on the evolution of sexual dimorphism in lizards of the genus *Sceloporus* using comparative methods. Sexual dimorphism can result from the balance between natural selection and sexual selection. Once the phylogenetic effects are controlled, our results show a greater relative impact of sexual selection on the divergence in body size in the genus *Sceloporus*. Rensch's rule is a pattern explained by the selective advantages of males with larger body size and the increase in magnitude as the average size of the species increases. In lizards, intrasexual selection is the main cause of sexual dimorphism in males biased size. The evolutionary history within the genus suggests a greater diversifying role of sexual selection over fecundity selection. At the interpopulation level (Chapter 2), some features are under different selective forces. Body Size, head and limbs size may be under sexual selection in males. In the females, the length of the trunk presented a slope greater than 1 (hyperalometry) in the generalist population. It is possible that the interaction between natural and sexual selection has an antagonistic effect, as in arboreal lizards (on limb size and head in males) or synergistic (greater trunk length) depending on the ecological context. The genus *Sceloporus* exhibits the greatest diversity in Mexico and the species are found in all types of vegetation. Its great morphological, ecological and behavioral diversity suggest that natural and sexual selection have played a central role in its evolution. It is likely that *Sceloporus* represents an example of adaptive radiation. However, basic elements of natural history, ecology and reproduction are unknown, especially in species with limited distribution to Mexico. Future studies should aim to obtain natural history information as a first approximation. Experimental studies evaluating the adaptive significance of phenotypic traits, both natural selection, sexual and ecological variables (biotic and abiotic i.e.) are necessary to determine the mechanisms that have led to the divergence and diversification of gender.

Introducción general

El dimorfismo sexual es una característica ampliamente distribuida en animales bilaterales con reproducción sexual (Fairbairn 2013). Se han planteado tres hipótesis para explicar la evolución y mantenimiento del dimorfismo sexual. Las diferencias fenotípicas entre hembras y machos pueden evolucionar como resultado de distintos óptimos reproductivos entre ambos sexos (West-Eberhard 1983; Andersson 1994; Fairbairn et al. 2007). Así, la selección sexual explica la evolución de caracteres sexuales secundarios y/o mayor talla corporal en el sexo seleccionado (usualmente machos; Darwin 1871; West-Eberhard 1983; Andersson 1994). Este tipo de dimorfismo sexual evoluciona porque los caracteres sexuales o talla corporal incrementan las oportunidades de apareamiento o probabilidades de fertilización, ya sea por elección de pareja y/o incrementando las habilidades competitivas (Andersson 1994; Andersson & Simmons 2006). La selección en fecundidad explica tallas corporales mayores en hembras o mayor volumen o tamaño abdominal. Bajo esta hipótesis es de esperarse un incremento positivo entre la talla y el número o tamaño de la progenie (Fairbairn 1997; Fairbairn et al. 2007; Cueva del Castillo & Fairbairn 2011; Pincheira-Donoso & Hunt 2015). El dimorfismo sexual también puede originarse por la divergencia del nicho ecológico entre sexos, asociado a estrategias de dispersión distintas o adaptaciones para reducir la competencia trófica (revisado en Slatkin 1984; Shine 1989). Bajo esta hipótesis es de esperarse divergencia en rasgos asociados al uso o explotación de recursos (Losos et al. 2003). Sin embargo, está sujeto a debate si la divergencia del nicho ecológico es realmente independiente de otros factores selectivos (ver Fairbairn et al. 2007).

Debido a que los rasgos fenotípicos pueden estar sujetos a diferentes presiones selectivas, la divergencia entre sexos puede resultar de la interacción entre la selección natural y sexual. El estudio del impacto relativo de la selección natural y sexual proporciona un análisis completo de los mecanismos responsables de generar la divergencia adaptativa entre los sexos (Panhuis et al. 2001; Jones & Ratterman 2009; Cornwallis & Uller 2010; Bonduriansky 2011; Kraaijeveld et al. 2011; Maan & Seehausen 2011; Scordato et al. 2014). Si la selección en fecundidad es intensa, el volumen abdominal puede ser desproporcionalmente mayor en hembras aún con tallas corporales menores a machos (Braña 1996; Cox et al. 2003; Cox et al. 2007). No obstante, aun cuando la selección en fecundidad favorezca mayor talla en hembras, la importancia relativa de la selección sexual puede ser mayor generando patrones de dimorfismo sexual sesgados a machos (Fairbairn et al. 2007; Pincheira-Donoso et al. 2008; Pincheira-Donoso & Tregenza 2011). En diversos grupos de vertebrados e invertebrados, la magnitud del dimorfismo sexual cambia, aumentando o decreciendo en función de una mayor talla corporal promedio entre especies (Fairbairn et al. 2007; Webb & Freckleton 2007). El incremento en la magnitud del dimorfismo sexual se correlaciona con especies donde los machos son más grandes que las hembras, y es atribuido a una intensa selección sexual favoreciendo a los machos de mayor tamaño (Fairbairn et al. 2007; Cox et al. 2007; Stillwell et al. 2010). Aunque cabe señalar que en diversos grupos se ha favorecido la evolución de menor tamaño corporal en machos, favoreciendo mayor movilidad o agilidad lo que incrementa las oportunidades de fertilización (ver Serrano-Meneses & Székely 2006; Husak & Fox 2008). Aunque es menos común, el patrón donde la magnitud del dimorfismo sexual incrementa en función de una mayor talla corporal de las hembras es asociado a presiones intensas de selección en fecundidad (Foellmer & Moya-Laraño 2007; Webb & Freckleton 2007). Ambos patrones

son asociados a una mayor divergencia en el tamaño corporal de los machos comparado con la talla femenina. Este patrón es conocido como la regla de Rensch (Rensch 1950; Fairbairn 1997; Blanckenhorn et al. 2007).

Las lagartijas son organismos modelo en el estudio de la divergencia fenotípica entre sexos, debido a que usualmente los sexos difieren en talla y forma (Olsson et al. 2002; Cox et al. 2007). Además hay familias, géneros y especies con modo reproductor ovíparo y vivíparo (ver Lambert & Wiens 2013; Watson et al. 2014). En algunas especies vivíparas el desarrollo embrionario sucede en una placenta (e.g. familia Mabuyidae), mientras que en otras, las hembras retienen los huevos dentro del útero hasta que el desarrollo es completado (Méndez-de la Cruz et al. 1998). Debido a la extensión en el periodo de gestación, se ha sugerido que las especies vivíparas exhiben mayor talla corporal o abdómenes más grandes que las especies ovíparas (Qualls & Shine 1995; Braña 1996; Pincheira-Donoso & Tregenza 2011; Scharf & Meiri 2013; Sun et al. 2012). En ambos modos reproductores, especies no relacionadas cercanamente exhiben dimorfismo sexual con hembras de mayor tamaño y una relación positiva entre el número o tamaño de huevos o crías (Braña 1996; Cox et al. 2003; Cox et al. 2007; Pincheira-Donoso & Hunt 2015). Inclusive en especies con machos de mayor tamaño corporal, un incremento desproporcionado en la longitud del tronco de las hembras es asociado a la maduración de más o mayor tamaño de progenie (Braña 1996; Olsson et al. 2002; Cox et al. 2003).

No obstante en la mayoría de las especies de lagartijas los machos muestran talla corporal mayor a las hembras. También confrontaciones entre machos con movimientos acrobáticos y mordidas son comunes por defensa de territorio y acceso a apareamientos. Se ha planteado que rasgos fenotípicos como extremidades y cabezas son de mayor tamaño en

machos, puesto que incrementan las habilidades competitivas y las probabilidades de ganar confrontaciones con otros machos por territorios o parejas (Lappin et al. 2006; Husak & Fox 2008). Además las conductas de despliegue de coloración sexual son frecuentes en diversas familias (Carpenter et al. 1970; Carpenter 1978; Butler & Losos 2002; Alfaro-Juantorena & Jiménez-Arcos 2017). Durante los despliegues se muestran zonas con coloración sexual y se realizan elongaciones de extremidades y movimientos de cabeza. Estas conductas sugieren que la selección sexual puede favorecer mayor tamaño corporal de cabezas, extremidades y el desarrollo de coloración sexual conspicua en machos (Anderson & Vitt 1990; Wiens et al. 1999; Stuart-Fox & Ord 2004; Cox et al. 2007).

Las lagartijas del género *Sceloporus* son un modelo ideal para evaluar la importancia relativa de la selección natural y sexual en la evolución del dimorfismo sexual. Este género comprende más de 90 especies distribuidas desde el sur de Canadá hasta el norte de Panamá, con su mayor diversidad en México (Köhler & Heimes 2002; Bell et al. 2003). Se distribuyen en prácticamente todos los ecosistemas terrestres del país desde los 0 hasta más de 4000 msnm (Smith 1939; Sites et al. 1992). Las poblaciones son abundantes, siendo el elemento más conspicuo de la herpetofauna mexicana (Sites et al. 1992). Los organismos adultos presentan una gran diversidad en tallas, que van desde los 40 mm (*S. bicanthalis*; Rodríguez-Romero et al. 2010) hasta más de 100 mm (*S. magister*; Fitch 1985) de longitud hocico-cloaca (aproximación de talla corporal en lagartijas; Losos 1990, Cox et al. 2003; Cox et al. 2007). El dicromatismo sexual es común, los machos presentan parches ventrales de color azul (o rosa; e.g. *S. variabilis* y *S. smithi*), así como diversos patrones de coloración sexual en cabeza y cuerpo (Wiens et al. 1999; Köhler & Heimes 2002). El dicromatismo sexual y conductas de despliegue sugieren que la selección sexual

ha jugado un papel central en la divergencia fenotípica entre sexos dentro del género (Carpenter 1978; Martins 1994; Wiens et al. 1999). Asimismo, hay especies ovíparas y vivíparas, y en estas últimas los periodos de gestación son mayores (Méndez-de la Cruz et al. 1998). A nivel comparativo, sin incorporar métodos comparativos filogenéticos, se han registrado dimorfismo sexual en talla sesgado a ambos sexos dentro de la familia Phrynosomatidae (Cox et al. 2007) y dentro del género *Sceloporus* (Fitch 1978). Actualmente las relaciones filogenéticas del género son relativamente bien comprendidas, y diversas filogenias congruentes entre si están disponibles (Leaché 2010; Wiens et al. 2010; Leaché et al. 2016), lo que permite su incorporación al analizar la evolución adaptativa del grupo.

Debido a la gran diversidad morfológica, conductual y ecológica es probable que la selección natural y selección sexual hayan moldeado la divergencia fenotípica del género. El objetivo de esta tesis fue analizar el impacto relativo de la selección natural y sexual en la evolución del dimorfismo sexual en las lagartijas del género *Sceloporus*. Estudios previos han registrado dimorfismo sexual en talla sesgado a ambos sexos, con una tendencia a presentar machos de mayor tamaño corporal (ver Phrynosomatidae: Cox et al. 2007; *Sceloporus*: Fitch 1978). Sin embargo, estos estudios no consideran las relaciones filogenéticas entre las especies, por lo que no es posible separar los componentes asociados a una ancestría común, de aquellos que han sido resultado de la adaptación a las condiciones particulares en las que ha evolucionado cada especie (Felsenstein 1985; Harvey & Pagel 1991; Martins & Hansen 1997). En el Capítulo 1 de este trabajo, empleando métodos comparativos filogenéticos se analizó la relación entre la talla corporal de hembras y el tamaño de camada o nidada. Además se comparó la talla entre especies con

modo reproductor vivíparo y ovíparo. También se analizaron las tendencias alométricas en la magnitud del dimorfismo sexual en talla (i.e. regla de Rensch), y la reconstrucción de estados de carácter ancestral en el género y grupos externos. Este capítulo fue publicado en la revista *Ecology and Evolution*. En el Capítulo 2 se compararon las tendencias alométricas entre poblaciones en el dimorfismo sexual en la lagartija vivípara *S. grammicus* entre poblaciones con diferente uso de hábitat. También se exploraron las diferencias en el uso del hábitat entre sexos como aproximación de la divergencia del nicho ecológico y su impacto en el dimorfismo sexual. En la última parte presento la discusión y conclusiones generales sobre los hallazgos encontrados en esta tesis.

CAPÍTULO I

**The interplay between natural and sexual selection in the evolution of
sexual size dimorphism in *Sceloporus* lizards (Squamata:
Phrynosomatidae)**

ORIGINAL RESEARCH

The interplay between natural and sexual selection in the evolution of sexual size dimorphism in *Sceloporus* lizards (Squamata: Phrynosomatidae)

Víctor H. Jiménez-Arcos | Salomón Sanabria-Urbán | Raúl Cueva del Castillo

UBIPRO, Laboratorio de Ecología, Universidad Nacional Autónoma de México, FES Iztacala, Mexico City, Mexico

Correspondence

Raúl Cueva del Castillo, UBIPRO, Laboratorio de Ecología, Universidad Nacional Autónoma de México, FES Iztacala, A.P. 314, Tlalnepantla, 54090. Mexico, Mexico.
Email: rcueva@ecologia.unam.mx

Funding information

CONACyT: Ciencia Básica, Grant/Award Number: 235987; Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México (UNAM); CONACyT, Grant/Award Number: 377215

Abstract

Sexual size dimorphism (SSD) evolves because body size is usually related to reproductive success through different pathways in females and males. Female body size is strongly correlated with fecundity, while in males, body size is correlated with mating success. In many lizard species, males are larger than females, whereas in others, females are the larger sex, suggesting that selection on fecundity has been stronger than sexual selection on males. As placental development or egg retention requires more space within the abdominal cavity, it has been suggested that females of viviparous lizards have larger abdomens or body size than their oviparous relatives. Thus, it would be expected that females of viviparous species attain larger sizes than their oviparous relatives, generating more biased patterns of SSD. We test these predictions using lizards of the genus *Sceloporus*. After controlling for phylogenetic effects, our results confirm a strong relationship between female body size and fecundity, suggesting that selection for higher fecundity has had a main role in the evolution of female body size. However, oviparous and viviparous females exhibit similar sizes and allometric relationships. Even though there is a strong effect of body size on female fecundity, once phylogenetic effects are considered, we find that the slope of male on female body size is significantly larger than one, providing evidence of greater evolutionary divergence of male body size. These results suggest that the relative impact of sexual selection acting on males has been stronger than fecundity selection acting on females within *Sceloporus* lizards.

KEYWORDS

dimorphism, fecundity, Lizards, natural selection, Rensch's rule, *Sceloporus*, sexual selection

1 | INTRODUCTION

In animal species that reproduce sexually, adult males and females often differ in body size. This difference is termed sexual size dimorphism (SSD) and generally evolves because body size is commonly related to reproductive success through different pathways in females and males (Blanckenhorn, 2005; Fairbairn, Blanckenhorn, & Székely,

2007). In females, body size is strongly correlated with fecundity, whereas in males, body size is correlated with mating success. As result of these differences, the body size that conveys maximal fitness often differs between the sexes (Fairbairn et al., 2007). The impact of sexual selection on SSD has been well established in many studies of individual species as well as in many phylogenetically controlled comparisons among species (Andersson, 1994; Fairbairn, 1997; Fairbairn

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

et al., 2007). In addition, fecundity selection favors large female body size in species where females mature large numbers of eggs or live young within their abdomens, as in most fish, insects, and spiders (Blanckenhorn, 2005; Fairbairn, 1997; Fairbairn et al., 2007; Ruckstuhl & Neuhaus, 2005). SSD also can arise through ecological niche divergence, such as sex-specific foraging/dispersal strategies or adaptations to reduce intersexual trophic competition (reviews in Blanckenhorn, 2005; Fairbairn, 1997; Fairbairn et al., 2007; Hedrick & Temeles, 1989; Reiss, 1989; Ruckstuhl & Neuhaus, 2005; Shine, 1989). However, it is unlikely that niche divergence between males and females is truly independent of sexual divergence in reproductive roles (Butler & Losos, 2002; Butler, Schoener, & Losos, 2000; Fairbairn et al., 2007).

In many vertebrate and invertebrate taxa, the magnitude of SSD changes systematically with mean body size, either increasing or decreasing as body size increases (Fairbairn et al., 2007; Webb & Freckleton, 2007). The former pattern is common in species where males are larger than females, while the latter occurs commonly in species in which females are the larger sex. Both patterns are explained by greater evolutionary divergence in male size, compared with female size; a pattern known as Rensch's rule (Fairbairn, 1997; Rensch, 1950). This allometric trend is usually attributed to sexual selection acting on male body size (Fairbairn et al., 2007; Stillwell et al., 2010). The converse trend, where female size varies more than male size, is less common, but seems to be the result of strong fecundity selection acting on females (Fairbairn et al., 2007; Foellmer & Moya-Laraño, 2007; Webb & Freckleton, 2007). Lizards exhibit a broad range of SSD. However, in the majority of species, males are larger than females (Cox, Butler, & John-Alder, 2007; Cox, Skelly, & John-Alder, 2003), mainly because body size often determines success in agonistic encounters, and it is correlated with dominance and territoriality (Carpenter, 1995; McMann, 1993; Molina-Borja, Padron-Fumero, & Alfonso-Martin, 1998; Perry et al., 2004). Nonetheless, in some species, females are larger than males, suggesting that fecundity selection may have favored the evolution of large female body size because it may allow females to (1) accommodate more offspring (Cox et al., 2003; Stuart-Fox, 2009; Zamudio, 1998) and (2) increase the capacity for storing energy to be invested in reproduction (Calder, 1984; Pincheira-Donoso & Tregenza, 2011).

Lizards species can be oviparous or viviparous (Blanckenhorn, 2000; Méndez-de la Cruz, Villagrán-Santa Cruz, & Andrews, 1998). In some viviparous species, the embryos develop in a placenta with little or no shell forming, whereas in other species, the female retains the eggs within the uterus until development is complete. In any case, because placental gestation or extended egg retention requires more space within the abdominal cavity associated with an increased gestation period (Pincheira-Donoso & Tregenza, 2011; Qualls & Shine, 1995), it has been suggested that the females of viviparous lizards possess larger body size or greater abdomens than their oviparous relatives (Braña, 1996; Scharf & Meiri, 2013; Yan-Yan et al., 2012).

The lizard genus *Sceloporus* serves as an excellent example of SSD in lizards. This is a widely distributed genus (from southwestern Canada to northern Panama), which can be found in several environments and along broad altitudinal ranges (0 to >4,000 m; Sites et al.,

1992; Smith, 1939). There are both oviparous and viviparous species in the genus (Méndez-de la Cruz, Villagrán-Santa Cruz & Andrews, 1998). In the majority of species, males are the larger sex and exhibit a conspicuous coloration formed by belly and gular patches. However, these characteristics are also present in the females of some species within the group (Calisi & Hews, 2007; Carpenter, 1978; Fitch, 1978; Jiménez-Cruz et al., 2005; Köhler & Heimes, 2002; Ramírez-Bautista & Pavón, 2009; Ramírez-Bautista et al., 2008; Ramírez-Bautista, Stephenson, Lozano, et al., 2012; Weiss, 2006). In addition, conspicuous coloration is also present on the dorsum, including the head, tail, and limbs (e.g., *Sceloporus minor*, *S. aureolus*, *S. horridus*: Köhler & Heimes, 2002; Stephenson & Ramírez-Bautista, 2012). The sexual coloration in males, principally the belly and gular patches, is related to species recognition, territory defense, agonistic interactions, and courtship (Carpenter, 1978; Martins, 1994; Sites et al., 1992; Wiens, Reeder, & Nieto Montes de Oca, 1999), which suggests that sexual selection has generated much of the divergence among males and females in *Sceloporus* lizards. However, in other species, females are larger than males (Fitch, 1978), suggesting that in these species, selection on female fecundity has been stronger than sexual selection on males.

In this study, we explore the relationship between female body size, fecundity and reproductive modes, and the potential impact of these relationships on body size divergence between females and males of *Sceloporus* lizards. In addition, we tested Rensch's rule in order to evaluate the relative impact of sexual selection on the evolution of SSD, and we performed an ancestral character reconstruction to infer the evolutionary trends of SSD in these lizards. We expected differences in body size between oviparous and viviparous females and that these differences affect the body size relationships between the sexes. Nonetheless, if sexual selection has been the main force driving the evolution of SSD in *Sceloporus*, we predict that the regression of male size on female size will have a slope steeper than 1, following the Rensch's rule.

2 | METHODS

2.1 | Data collection

Our study comprised data collected for 56 *Sceloporus* species, four *Urosaurus* species and *Petrosaurus thalassinus* for a total of 61 evolutionary units (*Urosaurus* and *P. thalassinus* were used as outgroup taxa). The *Sceloporus* species sampled included all major species groups of the genus (Leaché, 2010; Wiens et al., 2010); 41 species were oviparous and 20 were viviparous (Table 1). We performed a literature search for data on snout-vent length (SVL; a standard measure used as a proxy for lizard size; Cox et al., 2003; Losos, 1990) for both females and males and clutch/litter sizes (number of eggs or embryos) for the species studied. We collected information from the literature by executing searches on Google Scholar using the terms "snout-vent length," "clutch size," "litter size," "number of eggs/embryos," "sexual size dimorphism," or "reproductive cycle" for a list of species of the genus *Sceloporus*, reported by Wiens, Kozak, and Silva (2013). Google

TABLE 1 Mean snout-vent length (SVL), clutch/litter size, and reproductive mode (O = oviparous and V = viviparous) for 56 *Sceloporus* species and five outgroup taxa

Species	SVL females (mm)		SVL males (mm)		Clutch size		Reproductive mode	References
<i>Petrosaurus thalassinus</i>	99.15 (71–110)	(44)	107.23 (80–152)	(44)	8.6 (4–18)	(10)	O	Goldberg and Beaman (2004)
<i>Sceloporus adleri</i>	63.11 (54–78.8)	(23)	65.28 (59–72)	(14)	6.57 (2–11)	(14)	V	Fitch (1978), Santos-Bibiano (unpublished data)
<i>S. aeneus</i>	51.88 (43.4–59.1)	(194)	52.98 (43.4–62.8)	(138)	7.3 (7–12)	(32)	O	Jiménez-Arcos (2013)
<i>S. angustus</i>	62.8 (61–66)	(5)	78.2 (65–86)	(6)	5.5 (4–7)	(5)	O	Goldberg (2014)
<i>S. arenicolus</i>	53.8 (49–62.2)	(339)	54.5 (49–64.9)	(507)	5 (4–6)	(?)	O	Fitzgerald et al. (2011)
<i>S. bicanthalis</i>	51.84 (42.4–58)	(85)	43.6 (42–53.2)	(42)	7.18 (3–9)	(68)	V	Rodríguez-Romero et al. (2010), This study ^a
<i>S. chrysostictus</i>	51.3	(82)	53.95	(82)	2.4 (1–4)	(16)	O	Fitch (1985), Köhler and Heimes (2002)
<i>S. clarkii</i>	88.08 (72–120)	(57)	103 (91–138)	(56)	10.85 (1–24)	(39)	O	Fitch (1978, 1985), Parker and Pianka (1973)
<i>S. consobrinus</i>	68.4 (54–77)	(58)	60.5 (50–68)	(44)	9.9	(39)	O	Vinegar (1975a)
<i>S. couchii</i>	50	(36)	58	(32)	4	(?)	O	García de la Peña et al. (2004), Lemos-Espinal and Smith (2007)
<i>S. cozumelae</i>	45.48 (41–57)	(33)	50.72 (43–60)	(57)	1.8	(12)	O	Fitch (1978)
<i>S. cryptus</i>	67.06 (58.5–76.6)	(8)	61.6 (58.9–68.5)	(6)	9 (6–12)	(4)	V	This study ^b
<i>S. cyanogenys</i>	63	(15)	66	(15)	16.45 (6–18)	(36)	V	Fitch (1985), García-de la Peña, Castañeda, and Lazcano (2005)
<i>S. dugesii</i>	61.5 (50–78)	(91)	65.9 (50–98)	(73)	4.4 (1–10)	(27)	V	Ramírez-Bautista and Dávila-Ulloa (2009)
<i>S. edwardtaylori</i>	107	(?)	107	(?)	8.5 (8–9)	(2)	O	Köhler and Heimes (2002)
<i>S. for. formosus</i>	67.46 (50–83.3)	(113)	67.98 (50–87.4)	(99)	8.63 (6–18)	(16)	V	Ramírez-Bautista and Pavón (2009), This study ^b
<i>S. for. scitulus</i>	66.49 (62.5–84.9)	(82)	70.88 (63.3–87.3)	(73)	6.04 (2–12)	(27)	V	Ramírez-Pinilla et al. (2009), This study ^a
<i>S. gadoviae</i>	54.95 (45.7–57.2)	(6)	64.9 (69.6–73.5)	(6)	3.6 (1–5)	(20)	O	Lemos-Espinal, Smith, and Ballinger (1999), This study ^a
<i>S. graciosus</i>	57.59 (48–69)	(197)	55.18 (48–63)	(182)	4.55 (1–10)	(381)	O	Burkholder and Tanner (1974), Fitch (1978, 1985), Tinkle (1973)
<i>S. grammicus</i>	56.05 (42.1–72.5)	(278)	60.06 (45–79.9)	(412)	5.35 (2–12)	(167)	V	Ramírez-Bautista, Stephenson, Hernández-Íbarra, et al. (2012), Ramírez-Bautista, Stephenson, Lozano, et al. (2012), This study ^a
<i>S. grandaevus</i>	58.5 (58–59)	(2)	72.1 (67–78)	(5)	6.5 (6–7)	(2)	O	Goldberg (2014)
<i>S. horridus</i>	82.17 (60–100)	(46)	85.49 (52–118)	(82)	14 (7–18)	(16)	O	Valdéz-González and Ramírez-Bautista (2002), This study ^a
<i>S. hunsakeri</i>	64.13	(19)	73.96	(20)	7.5 (5–10)	(2)	O	Galina Tessaro et al. (2015)
<i>S. jalapae</i>	46 (42–50)	(24)	49.3 (45–62)	(17)	5.6 (4–8)	(10)	O	Ramírez-Bautista et al. (2005)
<i>S. jarrovi</i>	66.21 (60–86)	(787)	69.67 (46–98)	(668)	7.35 (2–16)	(405)	V	Ballinger (1973), Gadsden and Estrada-Rodríguez (2007)

(continues)

TABLE 1 (Continued)

Species	SVL females (mm)		SVL males (mm)		Clutch size			Reproductive mode	References
<i>S. licki</i>	63.83	(13)	71.46	(24)	6	(?)	O	Galina Tessaro et al. (2015)	
<i>S. macdougalli</i>	83.84 (72.5–95.4)	(29)	88.82 (81.8–92.5)	(7)	3.88 (2–5)	(9)	V	Martínez Bernal (2004)	
<i>S. magister</i>	93.64 (80–120)	(54)	111.45 (80–140)	(53)	6.98 (2–12)	(43)	O	Fitch (1978, 1985)	
<i>S. malachiticus</i>	75.49 (64–86)	(208)	79.12 (67–90)	(146)	6 (3–10)	(44)	V	Fitch (1978, 1985)	
<i>S. megalepidurus</i>	44.99 (37–48)	(36)	47.28 (39–55)	(76)	2.04 (1–4)	(25)	V	Fitch (1978), Godínez-Cano (1985)	
<i>S. melanorhinus</i>	87.9 (62–98)	(30)	84.6 (62–95)	(32)	7.7 (5–9)	(12)	O	Ramírez-Bautista et al. (2006)	
<i>S. merriami</i>	48.13 (39–55)	(164)	52.24 (42–61)	(355)	4.33 (2–7)	(127)	O	Fitch (1978), Grant and Dunham (1990)	
<i>S. minor</i>	65.65 (41.6–92.9)	(182)	70.32 (53.6–99.4)	(169)	6.09 (2–13)	(46)	V	Ramírez-Bautista et al. (2008, 2014)	
<i>S. mucronatus</i>	78.89 (56.5–102)	(170)	87.02 (55.2–111.2)	(146)	5.8 (2–13)	(49)	V	Ortega-León et al. (2007), Villagrán-Santa Cruz et al. (2009), This study ^a	
<i>S. nelsoni</i>	52.14 (48–58)	(21)	60.15 (53–65)	(26)	6.25 (4–8)	(4)	O	Fitch (1978)	
<i>S. occidentalis</i>	74.63 (68–87)	(43)	68.35 (61–81)	(46)	8.12 (3–14)	(243)	O	Fitch (1978), Herrel, Meyers, and Vanhooydonck (2002)	
<i>S. ochoterenae</i>	44.39 (31–67)	(110)	48.23 (44–56)	(143)	6.77 (3–7)	(35)	O	Bustos-Zagal et al. (2011), Smith and Lemos-Espinal (2003)	
<i>S. olivaceus</i>	93 (63–107)	(107)	82.9 (60–93)	(34)	14.3 (8–30)	(14)	O	Blair (1960)	
<i>S. omiltemanus</i>	83.08	(39)	98.11	(25)	6.23 (6–8)	(13)	V	Ramírez-Pinilla et al. (2009)	
<i>S. orcutti</i>	92 (85–106)	(77)	102 (90–115)	(17)	11 (8–15)	(4)	O	Mayhew (1963)	
<i>S. parvus</i>	46.85 (44.7–49)	(?)	50	(?)	3.8	(>2)	O	García-Vázquez, Trujano-Ortega, and Contreras-Arquieta (2014), Lemos-Espinal and Dixon (2013)	
<i>S. pictus</i>	47.86 (44–52)	(7)	48.88 (47–51)	(8)	3.6 (2–6)	(5)	V	Fitch (1978)	
<i>S. poinsettii</i>	89.45 (79–116)	(55)	96.79 (77–130)	(79)	10.5 (4–23)	(90)	V	Fitch (1978, 1985), Gadsden et al. (2005)	
<i>S. pyrocephalus</i>	53.41 (47–62)	(88)	62.01 (50–75)	(84)	5.65 (4–9)	(24)	O	Fitch (1978), Ramírez-Bautista and Olvera Becerril (2004)	
<i>S. spi. caeruleopunctatus</i>	87.22 (77–96)	(18)	88.29 (82–99)	(17)	12.82 (8–19)	(23)	O	Calderón-Espinosa, Andrews, and Méndez de la Cruz (2006), Fitch (1978)	
<i>Sceloporus spi. spinosus</i>	91.11 (65.7–110.5)	(164)	92.66 (60–112)	(164)	14.09 (6–22)	(38)	O	Méndez de la Cruz et al. (2013), Ramírez-Bautista, Stephenson, Hernández-Íbarra, et al. (2012), Ramírez-Bautista, Stephenson, Lozano, et al. (2012), Ramírez-Bautista et al. (2014), Valdéz-González and Ramírez-Bautista (2002)	
<i>S. scalaris</i>	51.25 (40–60)	(203)	45.53 (40–55)	(45)	8.28 (4–15)	(109)	O	Carbajal-Márquez and Quintero-Díaz (2013), Fitch (1978, 1985), Vitt (1977)	

(Continues)

TABLE 1 (Continued)

Species	SVL females (mm)		SVL males (mm)		Clutch size		Reproductive mode	References
<i>S. siniferus</i>	49.88 (40–61)	(139)	52.49 (53–61)	(235)	4.94 (2–8)	(15)	O	Fitch (1978), Ramírez-Bautista et al. (2015)
<i>S. smaragdinus</i>	62.24 (55–77)	(17)	67.22 (60–80)	(14)	4.2 (3–6)	(10)	V	Fitch (1978)
<i>S. subpictus</i>	66.47 (63.1–69)	(41)	63.54	(1)	13 (12–14)	(2)	V	This study ^b
<i>S. torquatus</i>	94.03 (65–110)	(4)	101.51 (43.2–115.9)	(37)	7.78 (3–17)	(84)	V	Feria Ortiz, Salgado Ugarte, and Nieto-Montes de Oca (2001), Guillette and Méndez-de la Cruz (1993), This study ^a
<i>S. tristichus</i>	63.3 (48–67)	(57)	55.9 (53–73)	(54)	7.2	(29)	O	Vinegar (1975b)
<i>S. undulatus</i>	61.11 (53–72)	(118)	55.78 (45–65)	(177)	8.02 (3–15)	(376)	O	Fitch (1978, 1985), Herrel et al. (2002)
<i>S. utiformis</i>	63.41 (51–73)	(104)	61.25 (45–84)	(122)	6.94 (3–10)	(31)	O	Fitch (1978), Ramírez-Bautista and Gutiérrez-Mayén (2003)
<i>S. variabilis</i>	52.65 (44–68)	(424)	61.99 (42–74)	(457)	3.92 (1–7)	(216)	O	Benabid (1994), Cruz-Elizalde & Ramírez-Bautista (2016 and references in table 6), Fitch (1978, 1985)
<i>S. virgatus</i>	63.81 (51–74.2)	(54)	50.42 (48–58)	(22)	9.44 (4–16)	(228)	O	Abell (1999), Herrel et al. (2002), Vinegar (1975a)
<i>S. woodi</i>	57.24	(64)	51.89	(78)	4.62 (2–8)	(231)	O	Jackson and Telford (1974), Williams (2010)
<i>Urosaurus bicarinatus</i>	45.84 (40–53)	(249)	49.66 (38–61)	(322)	6.26 (2–11)	(50)	O	Ramírez-Bautista, Uribe-Peña, and Guillette (1995), Ramírez-Bautista and Vitt (1998)
<i>U. graciosus</i>	38.69 (44–66)	(60)	62.35 (42–66)	(42)	4.05 (2–10)	(25)	O	Fitch (1985), Vitt, Van Loben Sels, and Ohmart (1978)
<i>U. nigricaudus</i>	51.82 (44–60)	(121)	62.47 (57.2–65.4)	(42)	4.05 (2–6)	(25)	O	Romero-Schmidt, Ortega-Rubio, and Acevedo-Beltran (1999)
<i>U. ornatus</i>	49.98 (45–58)	(14)	50.87 (47–60)	(34)	7.25 (2–12)	(1454)	O	Fitch (1985), Martin (1973), Van Loben Sels and Vitt (1984)

Size and clutch/litter size ranges are shown in parentheses below mean values. Numbers between parentheses refer to sample sizes. The symbol (?) represents a lack of sample size data in the literature.

^aOnly SVL data obtained in this study.

^bBoth SVL and litter size data obtained in this study.

Scholar was used as the search engine instead of other engines because it cataloged full-text versions of published papers. Moreover, terms that were included in our search like “clutch size,” “litter size,” and “snout-vent length” were not the principal focus of the papers, and the phrases were usually referred to only briefly. Thus, we were less likely to locate the pertinent information using literature databases that contain only keywords, titles, and abstracts (see Dornhaus, Powell, & Bengston, 2012). We excluded data in which the number of vitellogenesis follicles were reported as part of clutch size, because the follicular atresia may occur in any stage of the ovogenesis, including previtellogenic and vitellogenic follicles, and thus does not

represent an accurate estimation of clutch/litter size (Méndez-de la Cruz et al., 2013). For species with data on more than one clutch per reproductive season, we used the average of all clutches reported in the literature.

In addition to this data set, we incorporated unpublished measurements collected by us from the individuals of ten species. Both SVL and litter size data were incorporated for *S. cryptus*, *S. formosus formosus*, and *S. subpictus* (all viviparous species). SVL data from both sexes were collected for *S. bicanthalis*, *S. formosus scitulus*, *S. gadoviae*, *S. grammicus*, *S. horridus*, *S. mucronatus*, and *S. torquatus*. Litter size was obtained from direct observations of females giving birth in captivity

(see Bastiaans et al., 2014 for care details). Digital calipers were used to take SVL measurements to the nearest 0.1 mm (Mitutoyo CD-15DC; Mitutoyo Corp., Tokyo, Japan). All lizards captured for this study were unharmed and released at their original capture locations following data collection.

The number of eggs or embryos was used as an estimation of fecundity. Prior to further analyses, all measurements were \log_{10} -transformed to improve linear fits. In addition, we estimated a sexual size dimorphism index (SDI) on SVL following the Lovich and Gibbons (1992) criteria. This index expresses SSD as $[(\text{length of larger sex}/\text{length of smaller sex}) - 1]$. For convention, the SDI is arbitrarily changed to negative when males are the larger sex and positive when females are the larger sex (Cox et al., 2007).

2.2 | Phylogenetic reconstruction

We inferred the phylogenetic relationships between the 56 studied species of *Sceloporus* using the nucleotide sequences of eight nuclear (BDNF, ECEL, PNN, PRLR, PTPN, R35, RAG1, TRAF6) and five mitochondrial genes (12S, 16S, ND1, ND2, ND4) available on GenBank. We also retrieved the same genetic information from five outgroup taxa which included four *Urosaurus* species, representing the sister group of *Sceloporus* (Leaché, 2010; Wiens et al., 2010) and *Petrosaurus thalassinus*. The number of species sampled for each gene was BDNF = 48, ECEL = 25, PNN = 47, PRLR = 27, PTPN = 26, R35 = 48, TRAF6 = 46, 12S = 57, 16S = 56, ND1 = 54, ND2 = 35, and ND4 = 57. All matrices were similar to previous studies (Leaché, 2010; Wiens et al., 2010). However, we treated the two subspecies of *S. formosus* (i.e., *S. formosus formosus* and *S. formosus scitulus*) as putative species based on previous evidence for distinct lineages (Pérez-Ramos & Saldaña de La Riva, 2008; Wiens & Reeder, 1997). A similar situation is present in *S. spinosus* (with *S. spinosus spinosus* and *S. spinosus caeruleopunctatus*). Wiens et al. (2010) recognized these taxa as putative species, which was also supported by more recent evidence (Grummer et al., 2015). Our inclusion of these taxa as distinct evolutionary lineages was not an endorsement of their recognition as different species, but we did not want to ignore important previous taxonomic work on these groups (see Pérez-Ramos & Saldaña de La Riva, 2008; Wiens & Reeder, 1997; Wiens et al., 2013).

We used MUSCLE algorithm (Edgar, 2004) to align each gene data set using the default parameters in the software MEGA (version 7; Kumar, Stecher, & Tamura, 2016). We then used the software MESQUITE (Maddison & Maddison, 2015) to combine the sequences of each gene, and to make the final concatenated matrix for all genes (see below). We provide the GenBank accession numbers of the sequences used in Appendix S1. Our concatenated alignment consisted of genetic information from 61 terminals (56 *Sceloporus* species, five outgroups taxa) and 11,113 characters. We estimated the best partition scheme and nucleotide substitution models for the data using the greedy algorithm of PARTITIONFINDER (version 1.1.1; Lanfear et al., 2014). We conducted a concatenated Bayesian inference (BI) analysis in MRBAYES (version 3.2.6; Ronquist et al., 2012) by applying the specific substitution model estimated for each partition. The BI

analysis consisted of four independent runs, each with 10,000,000 generations and four chains, sampling every 1,000 generations. We used default priors for other parameters in the analysis. We assessed parameter convergence and proper mixing of independent runs using TRACER (version 1.6; Rambaut & Drummond, 2013). All parameter values sampled during the MCMC of the analysis resulted in ESS values greater than 200. We discarded 25% of the samples obtained prior to stability as burn-in to obtain a final consensus tree (See Appendix S1 for details).

Our analysis only considered the phylogeny that resulted from a concatenated matrix of both mitochondrial and nuclear loci, utilizing a total evidence approach for *Sceloporus* species and outgroup taxa. Although this approach may be controversial because nuclear and mitochondrial genes may have incongruent histories due to incomplete lineage sorting and exhibit different substitutions rates (see Maddison, 1997), concatenated matrices have improved the resolution of the phylogenetic relationships of phrynosomatid lizards (Wiens et al., 2010). Moreover, our phylogenetic results were largely congruent with a recent phylogenetic study on *Sceloporus* that involved a wider taxonomic and genetic sampling, as well as different methodological approaches (concatenation and coalescent-based methods) to infer phylogenetic relationships (Leaché et al., 2016).

2.3 | Comparative analyses

We converted the molecular branch lengths from the Bayesian analysis to units of time using a penalized likelihood method (Sanderson, 2002). For branch length conversion, we used the R (version 3.1.3; R Core Team 2015) package "ape" (Paradis, Claude, & Strimmer, 2004) and performed all the comparative analysis on the resulting ultrametric phylogeny. For more details, see Appendix S1.

2.4 | Reproductive modes, female body size, fecundity, and SDI

We used the phylogenetic generalized least squares (PGLS) model to test for an association between fecundity, body size, and reproductive mode. The PGLS approach incorporates phylogenetic information into linear models to account for the statistical nonindependence of residuals using a variance-covariance matrix (see Martins & Hansen, 1997) specified by the phylogeny. For all models, the maximum likelihood value of the weighting parameter λ was estimated simultaneously with the models (Gonzalez-Voyer & Kolm, 2010; Revell, 2010). The λ parameter indicates whether trait evolution is independent of the phylogeny ($\lambda = 0$) or evolving according to Brownian motion ($\lambda = 1$). Intermediate values of λ suggest a process in which the effect of the given phylogeny is weaker than expected by Brownian motion evolution (Pagel, 1999). The models were fitted as implemented in the R package "caper" (Orme et al., 2012). The first model included fecundity (dependent variable), \log_{10} SVL female (independent variable), and reproductive mode (categorical independent variable) as well as the interaction between SVL and reproductive mode. In order to evaluate the impact of fecundity on SDI, we first saved the residuals

of the previous model and then constructed a model with SDI as the dependent variable, reproductive mode as a categorical independent variable, and the fecundity residuals as a covariate. We used the residuals to eliminate potential confounding effects associated with female body size.

2.5 | Rensch's rule and ancestral reconstruction of SDI

Rensch's rule predicts that the slope of a regression of male body size on female body size will be steeper than 1. To test this prediction in the studied species, we used the phylogenetic independent contrasts method (PIC method; Felsenstein, 1985), as implemented by the R package "caper" (Orme et al., 2012) to control for the phylogenetic nonindependence of species (Harvey & Pagel, 1991). We examined the studentized residuals for outliers $> |\pm 3|$, but found none in our data set. Also, in order to verify whether the standardized contrasts are independent from their estimated nodal values (see Felsenstein, 1985), we plotted the standardized contrasts against their estimated nodal values using the "plot" function provided by "caper". Ultimately, we tested the allometric relationship between independent contrasts of \log_{10} SVL male (dependent variable) and \log_{10} SVL female (independent variable) by fitting major axis regression using the R package "smatr" (Warton et al., 2012). Major axis regression offers an accurate approach to test the null hypothesis of isometry ($h_0: \beta = 1$), because both variables were measured on the same scale and residual variance is minimized in both x and y dimensions, rather than the y dimension only (Cox et al., 2007; Pincheira-Donoso & Tregenza, 2011; Warton et al., 2006). Given that the mean value of contrasts is expected to be zero (Sanabria-Urbán et al., 2015), we forced the major axis regression through the origin. We used the Wald statistic (r_w) and confidence intervals (95%) of the slope to test the null hypothesis (see Warton et al., 2006). In addition, in order to explore the evolutionary trends in body size and SDI, we performed an ancestral character reconstruction following Revell (2013). This method estimates the maximum likelihood value for internal nodes and then interpolates the states along the branches of the tree (see Revell, 2013, 2014 for details). For the reconstruction and visualization of ancestral state reconstruction of SDI (see Figure 3), we used the R package "phytools" (Revell, 2012).

3 | RESULTS

3.1 | Reproductive modes, body size, and fecundity

After controlling for phylogenetic nonindependence among of the species studied, the results of the PGLS analysis were highly significant ($r^2 = 0.3$, $F_{3,57} = 8.025$, $p = .0001$). We found a strong and significantly positive relationship between body size and fecundity ($\beta = 0.98 \pm 0.26$, $t = 3.801$, $p = .0003$; Figure 1). Nonetheless, there were no differences in fecundity between reproductive modes ($\beta = -0.15 \pm 0.85$, $t = -0.174$, $p = .86$). The interaction between

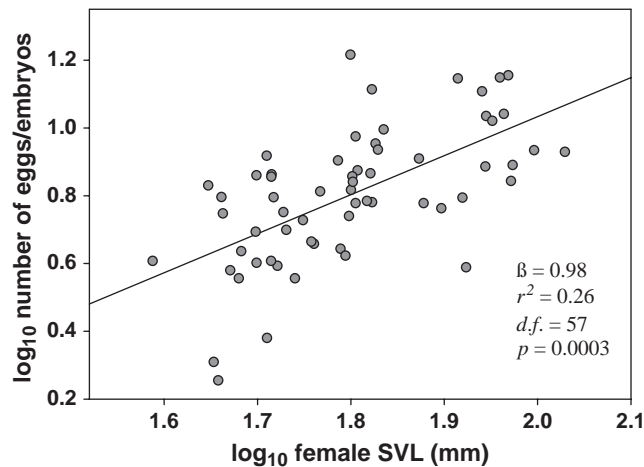


FIGURE 1 The relationship between the SVL of females and fecundity. Note this graph is shown only for illustrative purposes and was created with ordinary least squares linear model

reproductive modes and body size was not significant ($\beta = 0.04 \pm 0.47$, $t = 0.086$, $p = .93$), indicating a similar fecundity response to an increase in the body size of both oviparous and viviparous species. The model showed intermediate λ values ($\lambda = 0.54$), indicating a relatively weak phylogenetic effect on the relationships between body size and fecundity.

3.2 | Reproductive modes, fecundity, and SDI

The results of PGLS analysis were not significant ($r^2 = .003$, $F_{3,57} = 0.071$, $p = .98$). There were no significant differences in the SDI of oviparous and viviparous lizards ($\beta = 0.01 \pm 0.05$, $t = 0.433$, $p = .67$). Similarly, there were no significant effects of fecundity residuals on SDI ($\beta = -0.005 \pm 0.08$, $t = -0.063$, $p = .95$). The model showed a high λ value ($\lambda = 0.95$), indicating a strong phylogenetic effect on the relationships between fecundity residuals and SSD.

3.3 | Rensch's rule and ancestral reconstruction of SDI

The results of the major axis regression of independent contrasts indicated strong coevolution between females and males ($r = .80$; $df = 58$, $p = .0001$, Figure 2). The regression showed a slope significantly steeper than 1.0 ($\beta = 1.17$, $r_w = .29$, $p = .02$; Figure 2). Most of the taxa (46 species, 75%) showed male-biased SSD, and 14 species (23%) showed some degree of female-biased SSD. The males and females of only one species showed similar body sizes (*S. edwardtaylori*). The SDI reconstruction showed six independent origins of the female-biased SSD. In a clade with male-biased SSD (*formosus* group), the branch of *S. cryptus* and *S. subpictus* showed a female-biased SSD. Other independent origin of female-biased SSD was found in the *scalaris* (*S. bicanthalis* and *S. scalaris*) group. Another origin for *undulatus* group (*S. olivaceus*, *S. occidentalis*, *S. virgatus*, *S. woodi*, *S. undulatus*, *S. consobrinus*, and *S. tristichus*). Finally, three additional species independently evolved female-biased SSD: *S. utiformis* (*utiformis*

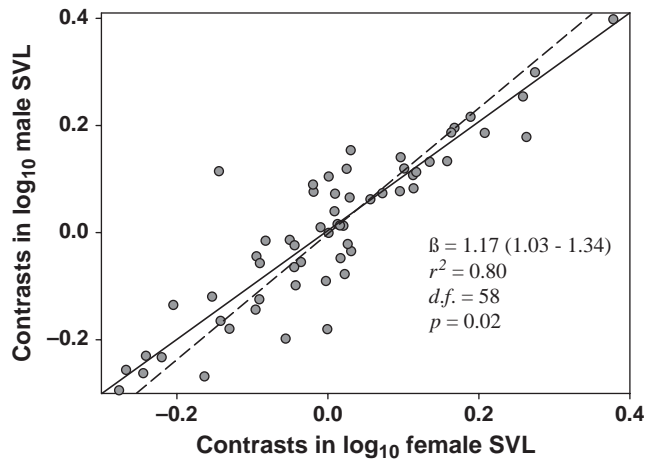


FIGURE 2 Independent contrasts of SVL of males as a function of SVL of females. The solid line indicates isometry ($\beta = 1$), while the dashed line denotes the allometric relationship between both variables as fitted by major axis regression. Values in parentheses indicate the upper and lower confidence interval (95%) for the slope and p value the probability for a $\beta > 1$

group), *S. graciosus* (*gracioso* group), and *S. melanorhinus* (*clarkii* group; Figure 3).

4 | DISCUSSION

Once we control for phylogenetic effects, our results confirm a strong relationship between female body size and fecundity, suggesting that in *Sceloporus* lizards selection on fecundity has had a main role on the evolution of female body size. However, regardless of the reproductive mode (oviparous or viviparous), the size of females of *Sceloporus* is similar and has evolved in a similar fashion. We must point out that the similar response in the relationship of body size with increase in the clutch/litter size between both reproductive modes does not imply that the overall reproductive output (i.e., reproductive fitness of the female's life) is similar. The potential impact of fecundity selection on the different reproductive modes may be underestimated (Niewiarowski et al., 2004; Pincheira-Donoso & Hunt, 2015; Shine, 2005). Oviparous species like *S. gadoviae*, *S. siniferus*, *S. undulatus*, and *S. variabilis* may have multiple clutches in a reproductive season (i.e., per year; Cruz-Elizalde & Ramírez-Bautista, 2016; Ramírez-Bautista et al., 2005; Ramírez-Bautista et al., 2015; Vinegar, 1975b), whereas other species like *S. magister*, *S. melanorhinus*, and *S. spinosus* have just one clutch per year, but they may have more than one reproductive event in their life (Méndez-de la Cruz et al., 2013; Parker & Pianka, 1973; Ramírez-Bautista et al., 2006; Valdéz-González & Ramírez-Bautista, 2002). On the other hand, all viviparous species have one litter per year, but in the majority of species, females can have several reproductive events (Méndez-de la Cruz et al., 1998; Ramírez-Bautista et al., 2014; Villagrán-Santa Cruz, Hernández-Gallegos, & Méndez-de La Cruz, 2009).

The differences in the gestation period between reproductive modes do not have any impact on the evolution of SSD, but according to the Rensch's rule, the slope of the regression of males on females is significantly steeper, providing evidence of greater evolutionary divergence in male size than in female size. Fitch (1978) noted that the high variation of SSD in *Sceloporus* lizards, and the implications of sexual and natural selection in order to explain the differences in body size between females and males. For lizard species in which body size often determines male mating success, males are typically larger than females (Cox et al., 2007). Body size often determines success in agonistic encounters, and it is correlated with dominance and territoriality (Carpenter, 1995; Martins, 1994; McMann, 1993; Molina-Borja et al., 1998; Perry et al., 2004). However, in other species, females are larger than males, suggesting that fecundity selection may have favored the evolution of larger-than-average female body size (Cox et al., 2003; Zamudio, 1998). Furthermore, as *Sceloporus* lizards follow Rensch's rule, it can be argued that this allometric trend is the result of sexual selection favoring large male body size and that the relative impact of sexual selection on males has been stronger than fecundity selection on female body size (Fairbairn, 1997; Fairbairn et al., 2007; Pincheira-Donoso & Tregenza, 2011).

The reconstruction of the evolution of SSD in *Sceloporus* lizards suggests that the ancestor and most of the extant species show a pattern of male-biased SSD. This could indicate that directional sexual selection acting on males has been greater than the selection acting on female fecundity. Territoriality and aggressive behaviors are common in *Sceloporus*: These are mainly associated with defense of mates in males (Martins, 1994), and resources (e.g., food, water, perches) in both sexes (Cooper & Wilson, 2007; Martins, 1994; Vinegar, 1975c; Woodley & Moore, 1999). In general, larger individuals have an advantage when defending territories in agonistic encounters (Martins, 1994; Swierk, 2014). However, female-biased SSD has evolved independently at least six times (Figure 3). Perhaps in these taxa, selection on fecundity has been stronger than sexual selection. Nonetheless, it is possible that in these species, sexual selection has also favored small male body size (see Cox et al., 2007; Olsson et al., 2002), albeit there is no clear pattern as to the ecological factors associated with the evolution of female-biased SSD. These species, like other *Sceloporus* species that show male-biased SSD, live in different environments, including tropical deciduous forest, grasslands, scrubland, woodlands, and open coniferous forests, and can be found from sea level up to elevations >4,000 m. Moreover, species showing female-biased SSD are oviparous and viviparous (e.g., *undulatus* group versus *S. bicanthalis*, respectively), and with single or multiples clutches per reproductive season (e.g., *S. melanorhinus* versus *S. consobrinus*, respectively). The diversity of ecological and social factors provides opportunities for changes in the direction and magnitude of natural and sexual selection between and within species. However, the information available for female preference and agonistic interactions between males are, in the majority of species, severely scarce or absent (see Martins, 1994; Swierk, 2014).

Previous studies in Phrynosomatidae do not support Rensch's rule (Cox et al., 2007). However, these results could be obscured by

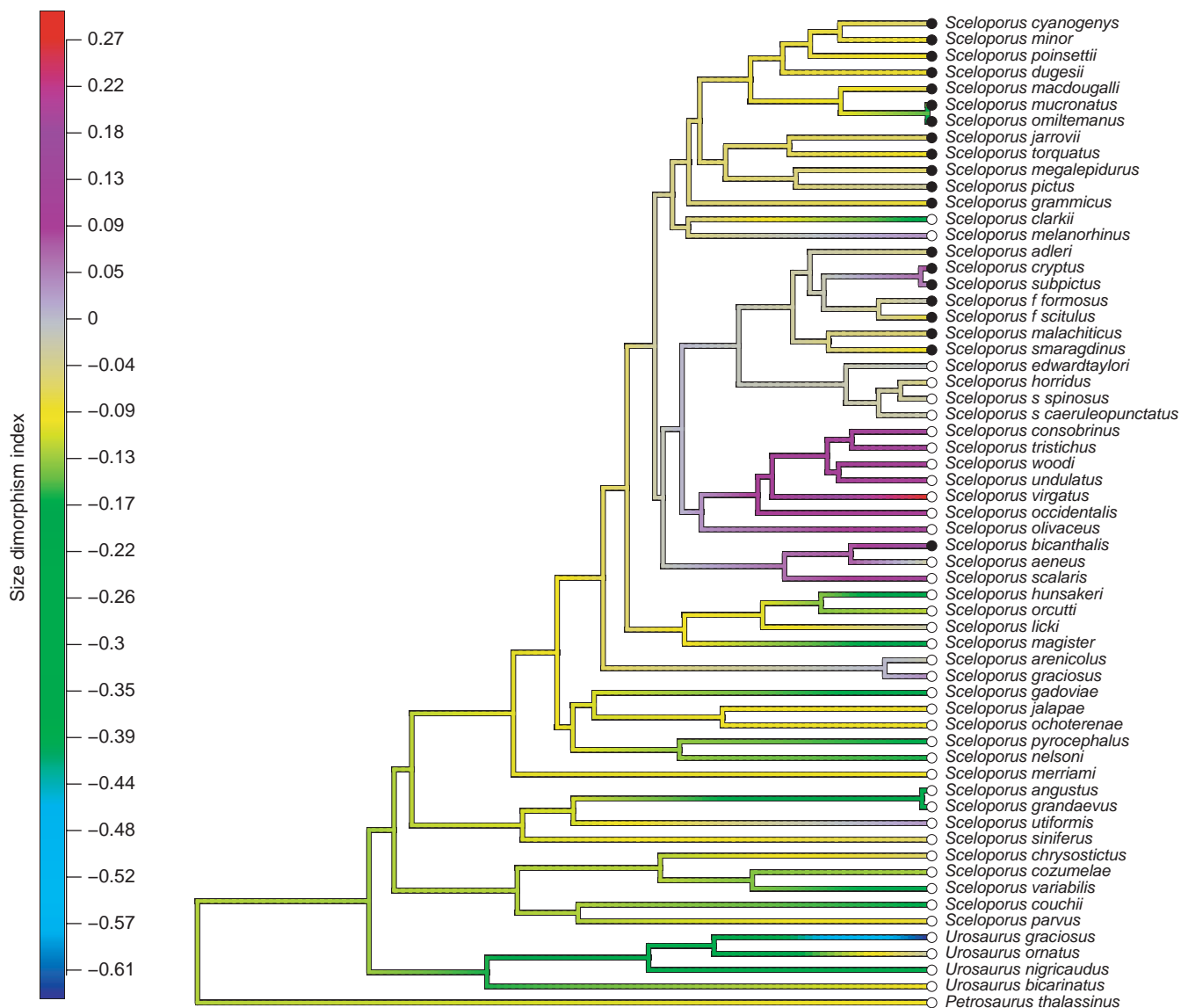


FIGURE 3 Maximum likelihood ancestral reconstruction of SDI for 56 species of *Sceloporus* and five outgroup taxa performed in R package “phytools” (Revell, 2012). For the analysis, we used the ultrametric phylogeny and the values of SDI estimated for each species. The values in the color ramp represent the range of SDI registered for the study species. Negative values indicate male-biased SSD (blue to paleyellow) and positive values female-biased SSD (palepurple to red). Open and filled circles indicate, respectively, oviparous and viviparous lizard species

the large diversity in morphology, behavior, ecology, and life-history traits between different lizards genera (Cox et al., 2003). In addition, these studies do not consider the phylogenetic relationship between the species (see Cox et al., 2007). Conversely, our results are similar to previous studies in the genus *Liolaemus* (Liolaemidae). The clutch/litter size increases as a function of female body size. Nonetheless, fecundity is not correlated with SSD, but *Liolaemus* species appear to follow Rensch's rule (Pincheira-Donoso & Tregenza, 2011). Both *Sceloporus* and *Liolaemus* species occupy a great diversity of environments, along wide latitudinal and altitudinal ranges and showing great variation in morphological, ecological, behavior, and life-history traits (Pincheira-Donoso, Scolaro, & Sura, 2008; Sites et al., 1992). The similarity between our results and those reported in *Liolaemus* suggests that fecundity selection may have driven the divergence in female body size

but that the diversifying effects of sexual selection may often exceed fecundity selection on females in both genera.

The genus *Sceloporus* includes more than 90 species and has been proposed as a group with an accelerated diversification rate (Bell, Smith, & Chiszar, 2003; Leaché, 2010; Wiens et al., 2010). *Sceloporus* lizards have colonized diverse niches throughout its distribution range, from northern Panama to southwestern Canada, and show one of the widest altitudinal ranges for reptiles. Due to the broad spread of niches, it is likely that the relative impact of natural and sexual selection has changed along novel environmental conditions, generating divergence from the optimum body size of females and males. In any case, the causal mechanisms associated with changes in the direction of SSD bias toward females in this group remain an open question that demand further investigation.

ACKNOWLEDGMENTS

This work was supported by CONACyT: Ciencia Básica grant No. 235987 to RCC. Víctor Hugo Jiménez Arcos acknowledges to Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México (UNAM), and CONACyT for doctoral scholarship (No. 377215). This article is a requirement for obtaining the degree of Doctor en Ciencias del Posgrado en Ciencias Biológicas, UNAM. The authors wish to thank Alejandro Serrano Meneses for his invaluable suggestions to improve an earlier version of the manuscript and to Christopher Blair for his invaluable suggestions to improve the English and overall manuscript quality. We thank R. Santos-Bibiano for providing data from *Sceloporus adleri*, as well as C. M. Gómez-Hurtado, A. H. Díaz de la Vega-Pérez, A. Calzada-Arciniega, M. Pérez-Quintero, C. Toscano-Flores, and M. Illescas-Aparicio for their help in the field. We thank four anonymous reviewers who also made invaluable suggestions to the manuscript.

CONFLICT OF INTEREST

None declared.

REFERENCES

- Abell, A. J. (1999). Variation in clutch size and offspring size relative to environmental conditions in the lizard *Sceloporus virgatus*. *Journal of Herpetology*, 33(2), 173–180.
- Andersson, M. (1994). *Sexual selection*. Princeton: Princeton University Press.
- Ballinger, R. E. (1973). Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). *Ecology*, 54(2), 269–283.
- Bastiaans, E., Bastiaans, M. J., Morinaga, G., Gaytán, J. G. C., Marshazrl, J. C., Bane, B., ... Sinervo, B. (2014). Female preference for sympatric vs. allopatric male throat color morphs in the mesquite lizard (*Sceloporus grammicus*) species complex. *PLoS One*, 9(4), 44–48.
- Bell, E. L., Smith, H. M., & Chiszar, D. C. (2003). An annotated list of the species-group names applied to the lizard genus *Sceloporus*. *Acta Zoologica Mexicana*, 174, 103–174.
- Benabid, M. (1994). Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. *Herpetologica Monographs*, 8(1994), 160–180.
- Blair, F. W. (1960). *The rusty lizard, a population study*. Austin: University of Texas Press.
- Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small?. *75(4)*, 385–407.
- Blanckenhorn, W. U. W. (2005). Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111(11), 977–1016.
- Braña, F. (1996). Sexual dimorphism in lacertid lizards: Male head increase vs female abdomen increase? *Oikos*, 75(3), 511–523.
- Burkholder, G. L., & Tanner, W. W. (1974). Life history ecology of the Great Basin sagebrush swift, *Sceloporus graciosus graciosus* Baird and Girard, 1853. *Brigham Young University Science Bulletin. Biological Series*, 14(5), 1–42.
- Bustos-Zagal, M. G., Méndez-de la Cruz, F. R., Castro-Franco, R., & Villagrán-Santa Cruz, M. (2011). Ciclo reproductor de *Sceloporus ochoterenae* en el estado de Morelos, México. *Revista Mexicana de Biodiversidad*, 82, 589–597.
- Butler, M. A., & Losos, J. B. (2002). Multivariate sexual dimorphism, sexual selection, and adaptation in greater antillean *Anolis* lizards. *Ecological Monographs*, 72(4), 541–559.
- Butler, M., Schoener, T. W., & Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution*, 54(1), 259–272.
- Calder, W. A. (1984). *Size, function and life history*, Cambridge, MA: Harvard University Press.
- Calderón-Espinosa, M. L., Andrews, R. M., & Méndez de la Cruz, F. R. (2006). Evolution of Egg retention in the *Sceloporus spinosus* group: Exploring the role of physiological, environmental, and phylogenetic factors. *Herpetological Monographs*, 20, 147.
- Calisi, R. M., & Hews, D. K. (2007). Steroid correlates of multiple color traits in the spiny lizard, *Sceloporus pyrocephalus*. *Journal of Comparative Physiology B*, 177, 641–654.
- Carbajal-Márquez, R. A., & Quintero-Díaz, G. E. (2013). Natural history: *Sceloporus scalaris* clutch size. *Herpetological Review*, 44(4), 660–661.
- Carpenter, C. C. (1978). Comparative display behavior in the genus *Sceloporus* (Iguanidae). *Contributions in Biology and Geology to the Milwaukee Public Museum*, 18, 1–71.
- Carpenter, G. C. (1995). Modeling dominance: The influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetologica Monographs*, 9(1995), 88–101.
- Cooper, W. E., & Wilson, D. S. (2007). Sex and social costs of escaping in the striped plateau lizard *Sceloporus virgatus*. *Behavioral Ecology*, 18(4), 764–768.
- Cox, R. M., Butler, M. A., & John-Alder, H. B. (2007). The evolution of sexual size dimorphism in reptiles. In D. J. Fairbairn, W. U. Blanckenhorn, & T. Székely (Eds.), *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford, UK: Oxford University Press.
- Cox, R. M., Skelly, S. L., & John-Alder, H. B. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, 57(7), 1653–1669.
- Cruz-Elizalde, R., & Ramírez-Bautista, A. (2016). Reproductive cycles and reproductive strategies among populations of the Rose-bellied Lizard *Sceloporus variabilis* (Squamata: Phrynosomatidae) from central Mexico. *Ecology and Evolution*, 6(6), 1753–1768.
- Dornhaus, A., Powell, S., & Bengston, S. (2012). Group size and its effects on collective organization. *Annual Review of Entomology*, 57(1), 123–141.
- Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32(5), 1792–1797.
- Fairbairn, D. J. (1997). Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics*, 28(1997), 659–687.
- Fairbairn, D. J., Blanckenhorn, W. U., & Székely, T. (2007). *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism*. Oxford, UK: Oxford University Press.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125(1), 1–15.
- Feria Ortiz, M., Salgado Ugarte, I. H., & Nieto-Montes de Oca, A. (2001). Diet and reproductive biology of the viviparous lizard *Sceloporus torquatus torquatus* (Squamata: Phrynosomatidae). *Journal of Herpetology*, 35(1), 104–112.
- Fitch, H. S. (1978). Sexual size differences in the genus *Sceloporus*. *University of Kansas Science Bulletin the University of Kansas Science Bulletin*, 51(13), 441–461.
- Fitch, H. S. (1985). Variation in clutch and litter size in new world reptiles. *Miscellaneous Publications of the Museum of Natural History of the University of Kansas*, 76, 1–76.
- Fitzgerald, L. A., Painter, C. W., Hibbits, T. J., Ryberg, W. A., & Smolensky, N. (2011). *The Range and Distribution of Sceloporus arenicolus in Texas: Results of surveys conducted 8–15 June 2011, Texas*. Retrieved from http://irnr.tamu.edu/media/285120/tx_dsl_final.pdf
- Foellmer, M. W., & Moya-Laraño, J. (2007). Sexual size dimorphism in spiders: Patterns and processes. In D. J. Fairbairn, W. U. Blanckenhorn & T. Székely (Eds.), *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism* (pp. 38–49). Oxford, UK: Oxford University Press.

- Gadsden, H., & Estrada-Rodríguez, J. L. (2007). Ecology of the spiny lizard *Sceloporus jarrovi* in the Central Chihuahuan Desert. *The Southwestern Naturalist*, 52(4), 600–608.
- Gadsden, H., Rodríguez-Romero, F. D. J., de Méndez- la Cruz, F. R., & Gil-Martínez, R. (2005). Ciclo reproductor de *Sceloporus poinsettii* Baird Y Girard 1852 (Squamata: Phrynosomatidae) en el centro del Desierto Chihuahuense, México. *Acta Zoologica Mexicana*, 21(3), 93–107.
- Galina Tessaro, P., Aguilera-Miller, E. F., & Álvarez-Castañeda, S. T. (2015). *Contribución a la distribución, ecología y estado de conservación de dos especies del género Sceloporus, endémicas de la región del Cabo, Baja California Sur, México, DF*. Retrieved from <http://www.conabio.gob.mx/institucion/proyectos/resultados/InfHK012.pdf>
- García de la Peña, C., Contreras-Balderas, A., Castañeda, G., & Lazcano, D. (2004). Infestación y distribución corporal de la nigua *Eutrombicula alfreddugesi* (Acari: Trombiculidae) en el lacertilio de las rocas *Sceloporus couchii* (Sauria: Phrynosomatidae). *Acta Zoológica Mexicana*, 20(2), 159–165.
- García-de la Peña, C., Castañeda, G., & Lazcano, D. (2005). Observations on Ectoparasitism by *Eutrombicula alfreddugesi* (Acari: Trombiculidae) in a population of *Sceloporus cyanogenys*. *Bulletin of the Chicago Herpetological Society*, 40(3), 52–53.
- García-Vázquez, U. O., Trujano-Ortega, M., & Contreras-Arquieta, A. (2014). Natural history: Reproduction of *Sceloporus parvus*. *Herpetological Review*, 45(3), 507.
- Gibbons, J. W. (1992). A review of techniques for quantifying sexual size dimorphism. *Growth, Development & Aging*, 56(4), 269–281.
- Godínez-Cano, E. (1985). Ciclo reproductivo de *Sceloporus megalapidurus megalapidurus* Smith (Reptilia: Sauria: Iguanidae), en la parte oriental de Tlaxcala, México, Bachelor thesis. Universidad Nacional Autónoma de México, México, DF.
- Goldberg, S. R. (2014). Natural history: Reproduction in *Sceloporus angustus*. *Herpetological Review*, 45(4), 699.
- Goldberg, S. R., & Beaman, K. R. (2004). Reproduction in the san lucas banded rock lizard, *Petrosaurus thalassinus* (Phrynosomatidae) from Baja California Sur, Mexico. *Bulletin of the Southern California Academy of Sciences*, 103(3), 147–149.
- Gonzalez-Voyer, A., & Kolm, N. (2010). Sex, ecology and the brain: Evolutionary correlates of brain structure volumes in tanganyikan cichlids. *PLoS One*, 5(12), 1–9.
- Grant, B. W., & Dunham, A. E. (1990). Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. *Ecology*, 71(5), 1765–1776.
- Grummer, J. A., Calderón-Espinosa, M. L., Nieto-Montes de Oca, A., Smith, E. N., Méndez-de la Cruz, F. R., & Leaché, A. D. (2015). Estimating the temporal and spatial extent of gene flow among sympatric lizard populations (genus *Sceloporus*) in the southern Mexican highlands. *Molecular Ecology*, 24(7), 1523–1542.
- Guillette, L. J., & Méndez-de la Cruz, F. R. (1993). The reproductive cycle of the viviparous Mexican lizard *Sceloporus torquatus*. *Journal of Herpetology*, 27(2), 168–174.
- Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford, UK: Oxford Series in Ecology and Evolution.
- Hedrick, A. V., & Temeles, E. J. (1989). The evolution of sexual dimorphism in animals: Hypotheses and tests. *Trends in Ecology and Evolution*, 4(5), 136–138.
- Herrel, A., Meyers, J. J., & Vanhooydonck, B. (2002). Relations between microhabitat use and limb shape in phrynosomatid lizards. *Biological Journal of the Linnean Society*, 77(1), 149–163.
- Jackson, J. F., & Telford, S. R. J. (1974). Reproductive ecology of the Florida scrub lizard *Sceloporus woodi*. *Copeia*, 1974(3), 689–694.
- Jiménez-Arcos, V. H. (2013). Variación fenotípica asociada a la coloración sexual en una población de *Sceloporus aeneus* (Squamata: Phrynosomatidae), Master thesis. Universidad Nacional Autónoma de México, México, DF. 69 p.
- Jiménez-Cruz, E., Ramírez-Bautista, A., Marshall, J. C., Lizana-Avia, M., & Nieto-Montes de Oca, A. (2005). Reproductive cycle of *Sceloporus grammicus* (Squamata: Phrynosomatidae) From Teotihuacán, México. *The Southwestern Naturalist*, 50(2), 178–187.
- Köhler, G., & Heimes, P. (2002). *Stachelleguane*. Germany: Herpeton, Verlag.
- Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, p.msw054. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/27004904>
- Lanfear, R., Calcott, B., Kainer, D., Mayer, C., & Stamatakis, A. (2014). Selecting optimal partitioning schemes for phylogenomic datasets. *BMC evolutionary biology*, 14(1), 1–14.
- Leaché, A. D. (2010). Species trees for spiny lizards (Genus *Sceloporus*): Identifying points of concordance and conflict between nuclear and mitochondrial data. *Molecular Phylogenetics and Evolution*, 54(1), 162–171.
- Leaché, A. D., Banbury, B. L., Linkem, C. W., & de Oca, A. N. M. (2016). Phylogenomics of a rapid radiation: Is chromosomal evolution linked to increased diversification in North American spiny lizards (Genus *Sceloporus*)? *BMC evolutionary biology*, 16(1), 63.
- Lemos-Espinal, J. A., & Dixon, J. R. (2013). *Amphibians and reptiles of San Luis Potosí*. Eagle Mountain: Eagle Mountain Publishing.
- Lemos-Espinal, J. A., & Smith, H. M. (2007). *Anfibios y Reptiles del Estado de Chihuahua, México/Amphibians and reptiles of the State of Chihuahua, México*. México, DF: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.
- Lemos-Espinal, J. A., Smith, G. R., & Ballinger, R. E. (1999). Reproduction in Gadow's spiny lizard, *Sceloporus gadoviae* (Phrynosomatidae), from arid tropical México. *The Southwestern Naturalist*, 44(1), 57–63.
- Losos, J. B. (1990). The evolution of form and function: Morphology and Locomotor performance in West Indian *Anolis* lizards. *Evolution*, 44(5), 1189–1203.
- Maddison, W. P. (1997). Gene trees in species trees. *Systematic Biology*, 46(3), 523–536.
- Maddison, W. P., & Maddison, D. R. (2015). Mesquite: A modular system for evolutionary analysis Version 3.04. Retrieved from <http://mesquite-project.org>
- Martin, R. F. (1973). Reproduction in the tree lizard (*Urosaurus ornatus*) in central Texas; drought conditions. *Herpetologica*, 29(1), 27–32.
- Martínez Bernal, R. L. (2004). Contribución al conocimiento de la biología de la especie endémica *Sceloporus macdougalli* en el Istma de Tehuantepec, Oaxaca, México, Bachelor thesis. Universidad Nacional Autónoma de México, México, DF.
- Martins, E. P. (1994). Phylogenetic perspectives on the Evolution of lizard territoriality. In L. J. Vitt & E. R. Pianka (Eds.), *Lizard ecology: Historical and experimental perspectives* (pp. 117–144). Princeton: Princeton University Press.
- Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, 149(4), 646–667.
- Mayhew, W. W. (1963). Reproduction in the granite spiny lizard, *Sceloporus orcutti*. *Copeia*, 1963(1), 144–152.
- McMann, S. (1993). Contextual signalling and the structure of dyadic encounters in *Anolis carolinensis*. *Animal Behaviour*, 46, 657–668.
- Méndez-de la Cruz, F. R., Villagrán-Santa Cruz, M., & Andrews, R. M. (1998). Evolution of viviparity in the lizard genus *Sceloporus*. *Herpetologica*, 54(4), 521–532.
- Méndez-De La Cruz, F. R., Villagrán-Santa Cruz, M., López-Ortiz, M. L., & Hernández-Gallegos, O. (2013). Reproductive cycle of a high-elevation, oviparous lizard (*Sceloporus spinosus*: Reptilia: Phrynosomatidae). *The Southwestern Naturalist*, 58(1), 54–63.
- Molina-Borja, M., Padron-Fumero, M., & Alfonso-Martin, T. (1998). Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (Family Lacertidae). *Ethology*, 104(4), 314–322.
- Niewiarowski, P. H., Angilletta Jr, M. J., & Leaché, A. D. (2004). Phylogenetic comparative analysis of life-history variation among populations of the

- lizard *Sceloporus undulatus*: An example and prognosis. *Evolution*, 58(3), 619–633.
- Olsson, M., Shine, R., Wapstra, E., Ujvari, B., & Madsen, T. (2002). Sexual dimorphism in lizard body shape: The roles of sexual selection and fecundity selection. *Evolution*, 56(7), 1538–1542.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2012). Caper: Comparative Analyses of Phylogenetics and Evolution in R. Version 0.5. Retrieved from <http://cran.r-project.org/web/packages/caper/caper.pdf>
- Ortega-León, A. M., Smith, E. R., Zúñiga-Vega, J. J., & Méndez-de la Cruz, F. R. (2007). Growth and demography of one population of the Lizard *Sceloporus mucronatus mucronatus*. *Western North American Naturalist*, 67(4), 492–502.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289–290.
- Parker, W. S., & Pianka, E. R. (1973). Notes on the ecology of the iguanid lizard. *Sceloporus Magister*, 29(2), 143–152.
- Pérez-Ramos, E., & Saldaña de La Riva, L. (2008). Morphological revision of lizards of the *formosus* group, genus *Sceloporus* (Squamata: Sauria) of southern México, with description of a new species. *Bulletin of the Maryland Herpetological Society*, 44(3), 77–97.
- Perry, G., LeVering, K., Girard, I., & Garland, T. (2004). Locomotor performance and social dominance in male *Anolis cristatellus*. *Animal Behaviour*, 67(1), 37–47.
- Pincheira-Donoso, D., & Hunt, J. (2015). Fecundity selection theory: Concepts and evidence. *Biological Reviews*, 2015, 1–16.
- Pincheira-Donoso, D., Scolaro, A. J., & Sura, P. (2008). A monographic catalogue on the systematics and phylogeny of the South American iguanian family Liolaemidae (Squamata, Iguania). *Zootaxa*, 1800(2008), 1–85.
- Pincheira-Donoso, D., & Tregenza, T. (2011). Fecundity selection and the evolution of reproductive output and sex-specific body size in the *Liolaemus* lizard adaptive radiation. *Evolutionary Biology*, 38(2), 197–207.
- Qualls, C. P., & Shine, R. (1995). Maternal body-volume as a constraint on reproductive output in lizards: Evidence from the evolution of viviparity. *Oecologia*, 103(1995), 73–78.
- Rambaut, A., & Drummond, A. (2013). Tracer V1.6 [Internet]. Retrieved from <http://beast.bio.ed.ac.uk/software/>
- Ramírez-Bautista, A., & Dávila-Ulloa, E. (2009). Reproductive characteristics of a population of *Sceloporus dugesii* (Squamata: Phrynosomatidae) from Michoacán, Mexico. *The Southwestern Naturalist*, 54(4), 400–408.
- Ramírez-Bautista, A., & Gutiérrez-Mayén, G. (2003). Reproductive ecology of *Sceloporus utiformis* (Sauria: Phrynosomatidae) from a Tropical Dry Forest of México. *Journal of Herpetology*, 37(1), 1–10.
- Ramírez-Bautista, A., & Olvera Becerril, V. (2004). Reproduction in the boulder spiny lizard, *Sceloporus pyrocephalus* (Sauria : Phrynosomatidae), from a Tropical Dry Forest of México. *Journal of Herpetology*, 38(2), 225–231.
- Ramírez-Bautista, A., & Pavón, N. P. (2009). Sexual dimorphism and reproductive cycle in the arboreal spiny lizard *Sceloporus formosus* Wiegmann (Squamata: Phrynosomatidae) from central Oaxaca, Mexico. *Revista Chilena de Historia Natural*, 82(4), 553–563.
- Ramírez-Bautista, A., Stephenson, B. P., Hernández-Íbarra, X., Hernández-Salinas, U., Cruz-Elizalde, R., Lozano, A., & Smith, G. R. (2012). Reproductive strategy of male and female eastern *Sceloporus spinosus* (Squamata, Phrynosomatidae), México. *Acta Herpetologica*, 7(2), 239–252.
- Ramírez-Bautista, A., Stephenson, B. P., Lozano, A., Uribe-Rodríguez, H., & Leyte Manrique, A. (2012). Atypical reproductive cycles in a population of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the Mexican Plateau. *Ecology and Evolution*, 2(8), 1903–1913.
- Ramírez-Bautista, A., Uribe-Peña, Z., & Guillette, L. J. J. (1995). Reproductive biology of the lizard *Urosaurus bicarinatus bicarinatus* (Reptilia: Phrynosomatidae) from Rio Balsas Basin, Mexico. *Herpetologica*, 51(1), 24–33.
- Ramírez-Bautista, A., & Vitt, L. J. (1998). Reproductive biology of *Urosaurus bicarinatus* (Sauria: Phrynosomatidae) from a tropical dry forest of Mexico. *The Southwestern Naturalist*, 43(3), 381–390.
- Ramírez-Bautista, A., Ortiz-Cruz, A. L., Del Coro Arizmendi, M., & Campos, J. (2005). Reproductive characteristics of two syntopic lizard species, *Sceloporus gadoviae* and *Sceloporus jalapae* (Squamata: Phrynosomatidae), from Tehuacan Valley, Puebla, Mexico. *Western North American Naturalist*, 65(2), 202–209.
- Ramírez-Bautista, A., Balderas-Valdivia, C., & Ortiz-Pulido, R. (2006). Reproductive cycle of male and female spiny lizards, *Sceloporus melanorhinus*, in a tropical dry forest. *The Southwestern Naturalist*, 51(2), 157–162.
- Ramírez-Bautista, A., Ramos-Flores, O., Stephenson, B. P., & Smith, G. R. (2008). Reproduction and sexual dimorphism in two populations of *Sceloporus minor* of the Guadalcázar Region, San Luis Potosí, Mexico. *Herpetological Journal*, 18, 121–127.
- Ramírez-Bautista, A., Stephenson, B. P., Serrano Muñoz, C., Cruz-Elizalde, R., & Hernández-Salinas, U. (2014). Reproduction and sexual dimorphism in two populations of the polymorphic spiny lizard *Sceloporus minor* from Hidalgo, México. *Acta Zoologica*, 95(4), 397–408.
- Ramírez-Bautista, A., Luría-Manzano, R., Cruz-Elizalde, R., Pavón, N. P., & David Wilson, L. (2015). Variation in reproduction and sexual dimorphism in the long-tailed spiny lizard, *Sceloporus siniferus*, from the southern Pacific coast of Mexico. *Salamandra*, 51(2), 73–82.
- Ramírez-Pinilla, M. P., Calderón-Espinosa, M. L., Flores-Villela, O., Muñoz-Alonso, A., & de la Cruz, F. R. M. (2009). Reproductive activity of three sympatric viviparous lizards at omiltemi, Guerrero, Sierra Madre del Sur, Mexico. *Journal of Herpetology*, 43(3), 409–420.
- Reiss, M. J. (1989). *The allometry of growth and reproduction*. Cambridge: Cambridge University Press.
- Rensch, B. (1950). Die Abhängigkeit der relativen Sexual differenz von der Körpergröße. *Bonner Zoologische Beiträge*, 1, 58–69.
- Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, 1(4), 319–329.
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3(2), 217–223.
- Revell, L. J. (2013). Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution*, 4(8), 754–759.
- Revell, L. J. (2014). Modern phylogenetic comparative methods and their application in evolutionary biology. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology*, 77–103. Retrieved from <http://link.springer.com/10.1007/978-3-662-43550-2>
- Rodríguez-Romero, F. J., Méndez de la, C. F. R., Hernández, G. O., & Velázquez, R. (2010). Fenología reproductora de alta montaña en dos especies de lacertilios emparentados (Squamata: Phrynosomatidae). In O. Hernández-Gallegos, F. R. de Méndez- la Cruz, & F. J. Méndez-Sánchez (Eds.), *Reproducción en reptiles: Morfología, ecología y evolución* (p. 169). Toluca: Universidad Autónoma del Estado de México.
- Romero-Schmidt, H. L., Ortega-Rubio, A., & Acevedo-Beltrán, M. (1999). Reproductive characteristics of the black-tailed brush lizard, *Urosaurus nigricaudus* (Phrynosomatidae). *Revista de Biología Tropical*, 47(4), 1111–1115.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., ... Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3), 539–542.
- Ruckstuhl, K. E., & Neuhaus, P. (2005). *Sexual Segregation in Vertebrates. Ecology of the Two Sexes*. Cambridge: Cambridge University Press.
- Sanabria-Urbán, S., Song, H., Oyama, K., González-Rodríguez, A., Serrano-Meneses, M. A., & Cueva del Castillo, R. (2015). Body size adaptations

- to altitudinal climatic variation in neotropical grasshoppers of the genus *Sphenarium* (Orthoptera: Pyrgomorphidae). *PLoS One*, 10(12), e0145248.
- Sanderson, M. J. (2002). Estimating absolute rates of molecular evolution and divergence times: A penalized likelihood approach. *Molecular Biology and Evolution*, 19(1), 101–109.
- Scharf, I., & Meiri, S. (2013). Sexual dimorphism of heads and abdomens: Different approaches to “being large” in female and male lizards. *Biological Journal of the Linnean Society*, 665–673.
- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The Quarterly Review of Biology*, 64(4), 419–461.
- Shine, R. (2005). Life-history evolution in reptiles. *Annual Review of Ecology, Evolution, and Systematics*, 36(1), 23–46.
- Sites, J. W., Archie, J. W., Cole, C. J., & Flores-Villela, O. (1992). A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): Implications for ecological and evolutionary studies. *Bulletin of the American Museum of Natural History*, 213, 1–110. A1992HZ58300001.
- Smith, H. M. (1939). The Mexican and Central American lizards of the genus *Sceloporus*. *Field Museum of Natural History. Zoological Series*, 26(1), 1–397.
- Smith, G., & Lemos-Espinal, J. (2003). Body size, sexual dimorphism, and clutch size in two populations of the lizard *Sceloporus ochoteranae*. *Southwestern Naturalist*, 48(1), 123–126.
- Stephenson, B. P., & Ramírez-Bautista, A. (2012). Did sexually dimorphic dorsal coloration evolve by a pre-existing bias in males in the lizard *Sceloporus minor*? *Evolutionary Ecology*, 26(5), 1277–1291.
- Stillwell, R., Blanckenhorn, W. U., Teder, T., Davidowitz, G., & Fox, C. W. (2010). Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: From physiology to evolution. *Annual Review of Entomology*, 55, 227–245.
- Stuart-Fox, D. (2009). A test of Rensch's rule in dwarf chameleons (*Bradypodion* spp.), a group with female-biased sexual size dimorphism. *Evolutionary Ecology*, 23(3), 425–433.
- Swierk, L. N. (2014). *Mate choice and competition in the eastern fence lizard, Sceloporus undulatus*. PhD dissertation: The Pennsylvania State University.
- Tinkle, D. W. (1973). A population analysis of the sagebrush lizard, *Sceloporus graciosus* in Southern Utah. *Copeia*, 1973(2), 284–296.
- Valdéz-González, M. A., & Ramírez-Bautista, A. (2002). Reproductive characteristics of the spiny lizards, *Sceloporus horridus* and *Sceloporus spinosus* (Squamata: Phrynosomatidae) from México. *Journal of Herpetology*, 36(1), 36–43.
- Van Loben Sels, R. C., & Vitt, L. J. (1984). Desert lizard reproduction: Seasonal and annual variation in *Urosaurus ornatus* (Iguanidae). *Canadian Journal of Zoology*, 62, 1779–1787.
- Villagrán-Santa Cruz, M., Hernández-Gallegos, O., & Méndez-de La Cruz, F. R. (2009). Reproductive cycle of the lizard *Sceloporus mucronatus* with comments on intraspecific geographic variation. *Western North American Naturalist*, 69(4), 437–446.
- Vinegar, M. A. (1975a). Comparative aggression in *Sceloporus virgatus*, *S. undulatus consobrinus*, and *S. u. tristichus* (Sauria: Iguanidae). *Animal Behaviour*, 23(PART 2), 279–286.
- Vinegar, M. B. (1975b). Demography of the striped plateau lizard, *Sceloporus virgatus*. *Ecological Society of America*, 56(1), 172–182.
- Vinegar, M. B. (1975c). Life history phenomena in two populations of the lizard *Sceloporus undulatus* in southwestern New Mexico. *American Midland Naturalist*, 93(2), 388–402.
- Vitt, L. J. (1977). Observations on clutch and egg size and evidence for multiple clutches in some lizards of southwestern United States. *Herpetologica*, 33(3), 333–338.
- Vitt, L. J., Van Loben Sels, R. C., & Ohmart, R. D. (1978). Lizard reproduction: Annual variation and environmental correlates in the iguanid lizard *Urosaurus graciosus*. *Herpetologica*, 34(3), 241–253.
- Warton, D. I., Wright, I. J., Falster, D. S., & Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biological Reviews*, 81(2), 259–291.
- Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). Smatr 3- an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, 3(2), 257–259.
- Webb, T. J., & Freckleton, R. P. (2007). Only half right: Species with female-biased Sexual Size Dimorphism consistently break Rensch's rule. *PLoS One*, 2(9).
- Weiss, S. L. (2006). Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). *Behavioral Ecology*, 17, 726–732.
- Wiens, J. J., Kozak, K. H., & Silva, N. (2013). Diversity and niche evolution along aridity gradients in north american lizards (Phrynosomatidae). *Evolution*, 67(6), 1715–1728.
- Wiens, J. J., & Reeder, T. W. (1997). Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. *Herpetological Monographs*, 11(1997), 1–101.
- Wiens, J. J., Reeder, T. W., & Nieto Montes de Oca, A. (1999). Molecular phylogenetics and evolution of sexual dichromatism among populations of the yarrow's spiny lizard (*Sceloporus jarrovi*). *Evolution*, 53(6), 1884–1897.
- Wiens, J. J., Kuczynski, C. A., Arif, S., & Reeder, T. W. (2010). Phylogenetic relationships of phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*. *Molecular Phylogenetics and Evolution*, 54(1), 150–161.
- Williams, S. C. (2010). *Sources and Consequences of Ecological Intraspecific Variation in the Florida Scrub Lizard (Sceloporus woodi)*. Georgia Southern University. Electronic Theses & Dissertations. Retrieved from <http://digitalcommons.georgiasouthern.edu/etd> Recommended.
- Woodley, S., & Moore, M. (1999). Female territorial aggression and steroid hormones in mountain spiny lizards. *Animal Behaviour*, 57(5), 1083–1089.
- Yan-Yan, S., Du, Y., Yang, J., Fu, T. B., Lin, C. X., & Ji, X. (2012). Is the evolution of viviparity accompanied by a relative increase in maternal abdomen size in lizards? *Evolutionary Biology*, 39(3), 388–399.
- Zamudio, K. R. (1998). The evolution of female-biased sexual size dimorphism: A population-level comparative study in horned lizards (*Phrynosoma*). *Evolution*, 52(6), 1821–1833.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Jiménez-Arcos, V. H., Sanabria-Urbán, S. and Cueva del Castillo, R. (2017), The interplay between natural and sexual selection in the evolution of sexual size dimorphism in *Sceloporus* lizards (Squamata: Phrynosomatidae). *Ecology and Evolution*, 7: 905–917. doi: 10.1002/ece3.2572

1 **Appendix 1.**

2 The Table S1 and S2 showed the GenBank accession numbers for the 61 species used in the phylogenetic analyses.

3 Nuclear and mitochondrial genes are listed alphabetically.

4 *Table S1. GenBank accession numbers of the eight nuclear genes used for the present study*

	BDNF	ECEL	PNN	PRLR	PTPN	R35	RAG1	TRAF6
<i>P_thalassinus</i>		GQ895767.1	KP820518.1	GQ896079.1	GQ896211.1	KP820536.1	GQ896006.1	GQ895940.1
<i>S_adleri</i>								
<i>S_aeneus</i>						KF437157.1		
<i>S_angustus</i>				GQ896082.1	GQ896214.1			GQ895944.1
<i>S_arenicolus</i>	GQ464421.1		KC853996.1			GQ464645.1	GQ464701.1	
<i>S_bicanthalis</i>	GQ464435.1	KR360374.1	GQ464603.1	KR359866.1	KR359920.1	GQ464659.1	GQ464715.1	KR360099.1
<i>S_chrysostictus</i>								
<i>S_clarkii</i>	GQ464412.1	GQ895769.1	GQ464580.1	GQ896083.1	GQ896215.1	GQ464636.1	GQ464692.1	GQ895945.1
<i>S_couchi</i>	GQ464461.1	GQ895770.1	GQ464629.1	GQ896084.1	GQ896216.1	GQ464685.1	GQ464741.1	GQ895946.1
<i>S_cozumelae</i>								
<i>S_cryptus</i>	GQ464415.1		GQ464583.1			GQ464639.1	GQ464695.1	
<i>S_cyanogenys</i>								
<i>S_dugesii</i>	GQ464439.1		GQ464607.1			GQ464663.1	GQ464719.1	
<i>S_edwardtaylori</i>	GQ464414.1		GQ464582.1			GQ464638.1	GQ464694.1	
<i>S_f_formosus</i>		GQ895771.1		GQ896085.1	GQ896217.1			GQ895947.1
<i>S_f_scitululus</i>	GQ464416.1		GQ464584.1			GQ464640.1	GQ464696.1	
<i>S_gadoviae</i>	GQ464453.1	GQ895772.1	GQ464621.1	GQ896086.1	GQ896218.1	GQ464677.1	GQ464733.1	GQ895948.1
<i>S_graciosus</i>	GQ464422.1	GQ895773.1	GQ464590.1	GQ896087.1	GQ896219.1	GQ464646.1	GQ464702.1	GQ895949.1
<i>S_grammicus</i>	GQ464424.1	GQ895774.1	GQ464592.1	GQ896088.1	GQ896220.1	GQ464648.1	GQ464704.1	GQ895950.1
<i>S_grandaevus</i>	GQ464452.1		GQ464620.1			GQ464676.1	GQ464732.1	

<i>S_horridus</i>	GQ464437.1		GQ464605.1			GQ464661.1	GQ464717.1	
<i>S_hunsakeri</i>	GQ464427.1		GQ464595.1			GQ464651.1	GQ464707.1	
<i>S_jarrovi</i>	GQ464440.1		GQ464608.1			GQ464664.1	GQ464720.1	
<i>S_jalapae</i>	GQ464456.1	GQ895775.1	GQ464624.1	GQ896089.1	GQ896221.1	GQ464680.1	GQ464736.1	GQ895951.1
<i>S_licki</i>	GQ464428.1		GQ464596.1			GQ464652.1	GQ464708.1	
<i>S_melanorhinus</i>	GQ464413.1		GQ464581.1			GQ464637.1	GQ464693.1	
<i>S_mucronatus</i>	GQ464443.1		GQ464611.1			GQ464667.1	GQ464723.1	
<i>S_omiltemanus</i>								
<i>S_macdougalli</i>	GQ464442.1		GQ464610.1			GQ464666.1	GQ464722.1	
<i>S_magister</i>	GQ464429.1	GQ895777.1	GQ464597.1	GQ896091.1		GQ464653.1	GQ464709.1	GQ895953.1
<i>S_malachiticus</i>	GQ464417.1		GQ464585.1			GQ464641.1	GQ464697.1	
<i>S_megalepidurus</i>	GQ464432.1	GQ895778.1	GQ464600.1	GQ896092.1	GQ896222.1	GQ464656.1	GQ464712.1	GQ895954.1
<i>S_merriami</i>	GQ464459.1	GQ895779.1	GQ464627.1	GQ896093.1	GQ896223.1	GQ464683.1	GQ464739.1	GQ895955.1
<i>S_minor</i>								
<i>S_nelsoni</i>								
<i>S_occidentalis</i>	GQ464448.1		GQ464616.1	KP820502.1		GQ464672.1	GQ464728.1	
<i>S_ochoterenae</i>	GQ464457.1		GQ464625.1			GQ464681.1	GQ464737.1	
<i>S_olivaceus</i>	GQ464434.1	GQ895780.1	GQ464602.1	GQ896094.1	GQ896224.1	GQ464658.1	GQ464714.1	GQ895956.1
<i>S_orcutti</i>	GQ464430.1		GQ464598.1			GQ464654.1	GQ464710.1	
<i>S_parvus</i>	GQ464462.1	GQ895781.1	GQ464630.1	GQ896095.1	GQ896225.1	GQ464686.1	GQ464742.1	GQ895957.1
<i>S_pictus</i>			GQ464601.1			GQ464657.1	GQ464713.1	
<i>S_poinsettii</i>	GQ464445.1	GQ895782.1	GQ464613.1	GQ896096.1	GQ896226.1	GQ464669.1	GQ464725.1	GQ895958.1
<i>S_pyrocephalus</i>	GQ464454.1	GQ895783.1	GQ464622.1	GQ896097.1	GQ896227.1	GQ464678.1	GQ464734.1	GQ895959.1
<i>S_s_caeruleo.</i>		GQ895785.1			GQ896230.1			GQ895962.1
<i>S_s_spinosus</i>	GQ464438.1		GQ464606.1			GQ464662.1	GQ464718.1	
<i>S_scalaris</i>	GQ464436.1	GQ895784.1	GQ464604.1	GQ896098.1	GQ896228.1	GQ464660.1	GQ464716.1	GQ895960.1
<i>S_siniferus</i>	GQ464460.1		GQ464628.1	GQ896099.1	GQ896229.1	GQ464684.1	GQ464740.1	GQ895961.1
<i>S_smaragdinus</i>	EU085927.1						EU085721.1	
<i>S_subpictus</i>	GQ464419.1		GQ464587.1			GQ464643.1	GQ464699.1	
<i>S_torquatus</i>	GQ464446.1	GQ895786.1	GQ464614.1	GQ896100.1	GQ896231.1	GQ464670.1	GQ464726.1	GQ895963.1

<i>S_consobrinus</i>	GQ494864.1		GQ494849.1			GQ494834.1	GQ494819.1	
<i>S_tristichus</i>	GQ494860.1		GQ494845.1			GQ494830.1	GQ494815.1	
<i>S_undulatus</i>	GQ464449.1	GQ895787.1	GQ464617.1	GQ896101.1	GQ896232.1	GQ464673.1	GQ464729.1	GQ895964.1
<i>S_utiformis</i>	GQ464455.1		GQ464623.1		GQ896233.1	GQ464679.1	GQ464735.1	GQ895965.1
<i>S_variabilis</i>	GQ464464.1	GQ895788.1	GQ464632.1	GQ896102.1	GQ896234.1	GQ464688.1	GQ464744.1	GQ895966.1
<i>S_virgatus</i>	GQ464450.1		GQ464618.1			GQ464674.1	GQ464730.1	
<i>S_woodi</i>	GQ464451.1		GQ464619.1			GQ464675.1	GQ464731.1	
<i>U_bicarinatus</i>	JN648384.1	GQ895790.1		GQ896104.1	GQ896236.1		GQ896030.1	GQ895968.1
<i>U_graciosus</i>	JN648393.1	GQ895791.1		GQ896105.1			JN648493.1	GQ895969.1
<i>U_nigricaudus</i>	GQ464465.1	GQ895792.1	GQ464633.1	GQ896106.1	GQ896237.1	GQ464689.1	GQ464745.1	GQ895970.1
<i>U_ornatus</i>	KP820848.1	GQ895793.1	KP820515.1	GQ896107.1	GQ896238.1	KP820533.1	GQ896033.1	GQ895971.1

5

6

Table S2. GenBank accession numbers of the five mitochondrial genes used for the present study

	12S	16S	ND1	ND2	ND4
<i>P_thalassinus</i>	L40445.1	L41451.1	KP899454.1	KP899454.1	KP899454.1
<i>S_adleri</i>	AF000799.1	AF000839.1	AY297519.1	AY297519.1	GQ895850.1
<i>S_aeneus</i>					JN985666.1
<i>S_angustus</i>	L40450.1	L41457.1	AF049859.1	AF049859.1	AF210360.1
<i>S_arenicolus</i>	GQ464524.1	AF000863.1	GQ464468.1		GQ464748.1
<i>S_bicanthalis</i>	GQ464525.1	AF000840.1	GQ464469.1		GQ464749.1
<i>S_chrysostictus</i>	L40451.1	L41458.1			AF210367.1
<i>S_clarkii</i>	GQ464527.1	L41459.1	GQ464471.1	AY297511.1	GQ464751.1
<i>S_couchi</i>	GQ464528.1	AF000829.1	GQ464472.1		GQ464752.1
<i>S_cozumelae</i>	AF000790.1	AF000830.1			
<i>S_cryptus</i>	GQ464529.1	AF000842.1	GQ464473.1		GQ464753.1
<i>S_cyanogenys</i>	DQ525893.1	L41460.1	AY297524.1	AY297524.1	DQ525868.1
<i>S_dugesii</i>	GQ464530.1	L41461.1	GQ464474.1		GQ464754.1

<i>S_edwardtaylori</i>	GQ464531.1		GQ464475.1		GQ464755.1
<i>S_f_formosus</i>	L40455.1	L41462.1	AY297498.1	AY297498.1	
<i>S_f_scitulus</i>	GQ464532.1		GQ464476.1		GQ464756.1
<i>S_gadoviae</i>	GQ464533.1	AF000836.1	GQ464477.1		GQ464757.1
<i>S_graciosus</i>	GQ464534.1	L41463.1	GQ464478.1	AF049860.1	GQ464758.1
<i>S_grammicus</i>	GQ464535.1	L41464.1	GQ464479.1	AY297509.1	GQ464759.1
<i>S_grandaevus</i>	GQ464536.1		GQ464480.1		GQ464760.1
<i>S_horridus</i>	GQ464538.1	AF000844.1	GQ464482.1		GQ464762.1
<i>S_hunsakeri</i>	GQ464539.1	AF000845.1	GQ464483.1	AY297506.1	GQ464763.1
<i>S_jarrovia</i>	GQ464541.1	L41465.1	GQ464485.1	AY297512.1	GQ464765.1
<i>S_jalapae</i>	GQ464540.1	AF000837.1	GQ464484.1	AY297504.1	GQ464764.1
<i>S_licki</i>	GQ464542.1	AF000848.1	GQ464486.1		GQ464766.1
<i>S_melanorhinus</i>	GQ464549.1	AF000852.1	GQ464493.1		GQ464773.1
<i>S_mucronatus</i>	GQ464551.1	DQ525902.1	GQ464495.1	AY297497.1	GQ464775.1
<i>S_omiltemanus</i>		AF000888.1			AF154233.1
<i>S_macdougalli</i>	GQ464544.1	AF000849.1	GQ464488.1		GQ464768.1
<i>S_magister</i>	GQ464546.1	L41466.1	GQ464490.1	AF528741.1	GQ464770.1
<i>S_malachiticus</i>	GQ464547.1	L41467.1	GQ464491.1	AY297518.1	GQ464771.1
<i>S_megalepidurus</i>	GQ464548.1	AF000862.1	GQ464492.1		GQ464772.1
<i>S_merriami</i>	GQ464550.1	L41468.1	GQ464494.1	AY297520.1	GQ464774.1
<i>S_minor</i>	DQ525891.1	AF000866.1			DQ525872.1
<i>S_nelsoni</i>					AF210351.1
<i>S_occidentalis</i>	GQ464552.1	AB079242.1	GQ464496.1	AY297515.1	GQ464776.1
<i>S_ochoterenae</i>	GQ464553.1	AF000853.1	GQ464497.1	AF528743.1	GQ464777.1
<i>S_olivaceus</i>	GQ464554.1	L41471.1	GQ464498.1	AY297521.1	GQ464778.1
<i>S_orcutti</i>	GQ464555.1	L41472.1	GQ464499.1	AY297508.1	GQ464779.1
<i>S_parvus</i>	GQ464558.1	AF000832.1	GQ464502.1		GQ464782.1
<i>S_pictus</i>	GQ464559.1	AF000831.1	GQ464503.1	AY297500.1	GQ464783.1
<i>S_poinsettii</i>	GQ464560.1	L41473.1	GQ464504.1	AY297510.1	GQ464784.1
<i>S_pyrocephalus</i>	GQ464561.1	AF000833.1	GQ464505.1	AY297502.1	GQ464785.1

<i>S_s_caeruleo.</i>	EF025755.1	AF000864.1			EF025748.1
<i>S_s_spinosus</i>	EF025756.1	L41475.1	GQ464509.1	AY297525.1	EF025749.1
<i>S_s_scalaris</i>	GQ464562.1	L41474.1	GQ464506.1	AF528742.1	GQ464786.1
<i>S_s_siniferus</i>	GQ464563.1	AF000834.1	GQ464507.1	AY297494.1	GQ464787.1
<i>S_s_smaragdinus</i>	EU086043.1	AF000855.1	AY297517.1	AY297517.1	EU085838.1
<i>S_s_subpictus</i>	GQ464565.1	AF000857.1	GQ464511.1		GQ464791.1
<i>S_s_torquatus</i>	DQ525888.1	DQ525905.1	GQ464513.1		GQ464793.1
<i>S_s_consobrinus</i>	AF000820.1	AF000860.1	AF440079.1		
<i>S_s_tristichus</i>	AF440068.1	AF440024.1	EF031910.1		
<i>S_s_undulatus</i>	GQ464570.1	AF000886.1	GQ464514.1	AY297514.1	GQ464794.1
<i>S_s_utiformis</i>	GQ464571.1	HM012692.1	GQ464515.1	AF528740.1	GQ464795.1
<i>S_s_variabilis</i>	GQ464573.1	L41479.1	GQ464517.1	AY297507.1	GQ464797.1
<i>S_s_virgatus</i>	GQ464574.1	L41480.1	GQ464518.1	AY297516.1	GQ464798.1
<i>S_s_woodi</i>	GQ464575.1	AF000858.1	GQ464519.1	AY297513.1	GQ464799.1
<i>U_bicarinatus</i>		HM012694.1	JN648463.1	JN648424.1	AF210338.1
<i>U_graciosus</i>	L41433.1	L41484.1	AF049862.1	JN648433.1	GQ895841.1
<i>U_nigricaudus</i>	GQ464577.1	KP091282.1	GQ464521.1	JN648426.1	GQ464801.1
<i>U_ornatus</i>	AF194247.1	L41487.1	JN648470.1	AY297493.1	AY141065.1

8 *Phylogeny Estimation and divergence times*

9 The phylogeny was estimated based on a concatenate data matrix of 11,113 characters.

10 The best nucleotide substitution models for the nuclear genes are showed in Table S1.

11 *Table S1. Nucleotide substitutions models selected for eight nuclear genes*

12

Nuclear gene data partitions	Nucleotide substitution model
BDNF	K80 + I
ECEL	K80 + Γ
PNN	GTR + Γ
PRLR	K80 + Γ
PTPN	HKY + Γ
R35	K80 + I + Γ
RAG1	HKY + Γ
TRAF6	K80 + Γ

13

14 For the mitochondrial genes, the best scheme and nucleotide substitution models are
15 showed in Table S2.

16 *Table S1. Nucleotide substitutions models selected for eight nuclear genes*

17

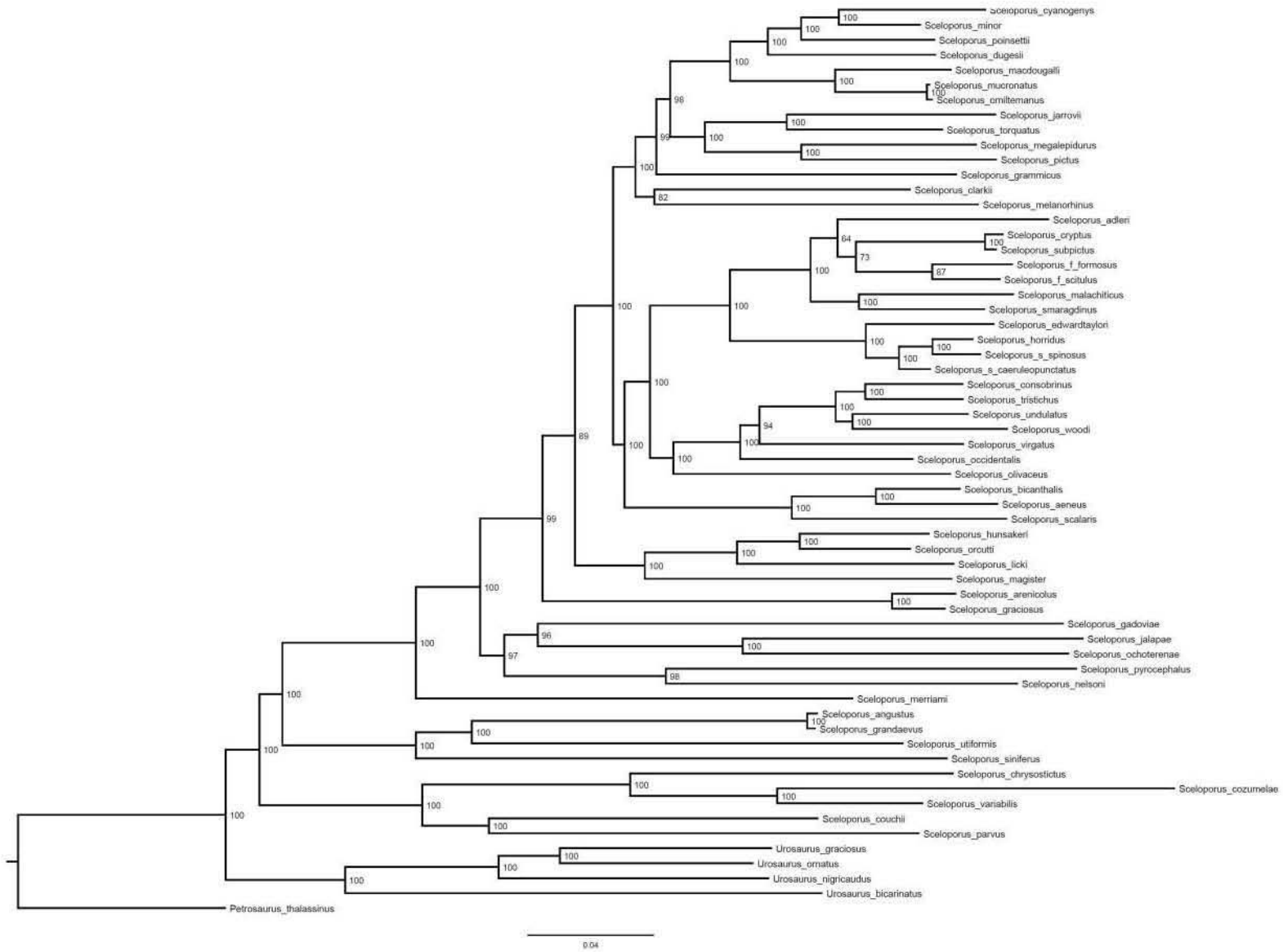
Nuclear gene data partitions	Nucleotide substitution model
12S	GTR + I + Γ
16S	GTR + Γ
ND1	
<i>1st position</i>	GTR + I + Γ
<i>2nd position</i>	HKY + I + Γ
ND2	
<i>1st position</i>	GTR + I + Γ
<i>2nd position</i>	HKY + I + Γ
ND4	
<i>1st position</i>	GTR + I + Γ
<i>2nd position</i>	GTR + Γ

18

19

20 For converted the molecular branch lengths from the Bayesian analysis to units of time we
21 used a penalized likelihood method with the `chronopl()` function in R package ‘ape’
22 (Sanderson 2002). The penalized likelihood is a semiparametric approach that allows
23 differential rates of evolution across the phylogenetic tree. The method used a trade-off
24 between a parametric formulation where each branch has its own rate, and a nonparametric
25 term where changes in rates are minimized between contiguous branches. A smoothing
26 parameter (λ) controls this trade-off. If $\lambda = 0$, then the parametric component
27 dominates and rates vary as much as possible among branches, whereas for increasing
28 values of λ , the variation are smoother to tend to a clock-like model (same rate for all
29 branches). We used a λ value of 0.5 for our analysis which maintained an
30 intermediated value in the substitution rates.

31 Figure 1S. Phylogeny of 56 *Sceloporus* species based on a combined, and partitioned analysis of eight nuclear genes and five
 32 mitochondrial genes. The maximum likelihood values are show in the nodes.



CAPÍTULO II

Habitat use and sexual dimorphism in *Sceloporus grammicus* (Squamata: Phrynosomatidae)



Habitat use and sexual dimorphism in *Sceloporus grammicus* (Squamata: Phrynosomatidae).

Journal:	<i>Biological Journal of the Linnean Society</i>
Manuscript ID	Draft
Manuscript Type:	Original article
Date Submitted by the Author:	n/a
Complete List of Authors:	Jiménez-Arcos, Víctor; Universidad Nacional Autónoma de México; FES Iztacala, UBIPRO; Lab de Ecología Díaz de la Vega-Pérez, Aníbal; Consejo Nacional de Ciencia y Tecnología-Centro Tlaxcala de Biología de la Conducta , Universidad Autónoma de Tlaxcala Toscano-Flores, Cesar; Universidad Nacional Autónoma de México; FES Iztacala, UBIPRO; Lab de Ecología Cueva del Castillo, Raul; Universidad Nacional Autónoma de México; FES Iztacala, UBIPRO; Lab de Ecología
Keywords:	sexual dimorphism, allometry, natural selection, sexual selection, lizards

SCHOLARONE™
Manuscripts

Review

1 Introduction

2 Allometry refers to the relationships observed between body size and other
3 organismal traits (Pélabon *et al.*, 2014). Scaling traits of individuals of the same
4 developmental stage are called static allometry (Bonduriansky & Day, 2003; Pélabon *et al.*,
5 2014; Stillwell *et al.*, 2016). Allometric slopes can evolve adaptively if natural selection
6 persistently favors the scaling relationships that are observed between traits and size
7 (Petrie, 1988, 1992; Eberhard *et al.*, 1998; Frankino, Emlen, & Shingleton, 2009). The
8 allometric equation of log–log transformed measurements allows linear comparison of
9 slopes; when trait size scales with body size. The relationship is called isometric when the
10 slope has a value of $|1|$, which can be positive or negative. When the traits scales
11 disproportionality with body size it is classified as hyperallometry (slope > 1 ; < -1) or
12 hypoallometry (slope between 0 and 1; -1 ; Bonduriansky & Day, 2003; Mirth, Frankino, &
13 Shingleton, 2016; Stillwell *et al.*, 2016).

14 Natural and sexual selection are recognized to cause allometric scaling of
15 morphological traits, showing positive scaling with body size (Bonduriansky & Day, 2003;
16 Voje, 2016). However, it is poorly known how different types of selection affect the
17 allometric slope (see Pélabon *et al.*, 2014). One mechanism to determine whether a certain
18 trait is under natural or sexual selection might be to compare scaling relationships between
19 the sexes. If the same selective pressures operate on the same trait in both males and
20 females, there is little reason to expect differences in the allometric slopes between the
21 sexes (Voje 2016), although other sources of divergence (e.g. ontogenetic constraints)
22 should be considered.

1
2
3 23 Differences between females and males in size and shape (sexual dimorphism; SD)
4
5 24 may result from natural selection on female fecundity. The fecundity selection hypothesis
6
7 25 explains the positive relationship between female body size and the quantity or quality of
8
9 26 progeny in species where females are larger than males (Fairbairn, 1997; Blanckenhorn,
10
11 27 2005; Ruckstuhl & Neuhaus, 2005; Cox, Butler, & John-Alder, 2007; Fairbairn,
12
13 28 Blanckenhorn, & Székely, 2007). Even if males are larger than females, fecundity selection
14
15 29 can favor the evolution of relatively larger trunks and abdominal volume in females (Braña,
16
17 30 1996; Cox, Skelly, John-Alder, 2003; Fairbairn *et al.*, 2007; Pincheira-Donoso & Hunt,
18
19 31 2015). In addition, it is well established that sexual selection explains the evolution of
20
21 32 secondary sexual characters and an increase in male body size (Darwin, 1871; West-
22
23 33 Eberhard, 1983; Andersson, 1994).

24
25
26
27
28
29
30 34 Because larger traits are favored by strong directional selection due to sexual
31
32 35 competition and female choice, selection favors the evolution of positive allometric traits
33
34 36 (but see Bonduriansky & Day, 2003; Bonduriansky, 2007). Classical examples of this
35
36 37 deviation include peacock's tails, enlarge chelae of fiddler crabs, and the lager body size of
37
38 38 pinipeds, in which males can be up to ten times the size of the females (Andersson 1994;
39
40 39 Fairbairn *et al.*, 2007). The SD also can be result of the divergence of ecological niche
41
42 40 between females and males, where differences are expected in size and shape of any
43
44 41 phenotypic trait directly related to the acquisition and exploitation of resources (Selander,
45
46 42 1966; Slatkin, 1984; Shine, 1989; Butler, Schoener, & Losos, 2000; Losos, Butler, &
47
48 43 Schoener, 2003). Nonetheless, the direction of SD under the niche divergence hypothesis is
49
50 44 not predictable, and it cannot be established if the ecological niche partition is the cause or
51
52
53
54
55
56
57
58
59
60

1
2
3 45 consequence of other selective pressures (e.g. sexual selection; Shine, 1989; Fairbairn *et*
4
5 46 *al.*, 2007).

6
7
8
9 47 Because individual traits can be under different selective pressures, the phenotypic
10
11 48 divergences between populations could be result for the interplay between natural and
12
13 49 sexual selection (Serrano-Meneses & Székely, 2006; Cornwallis & Uller, 2010; Maan &
14
15 50 Seehausen, 2011; Scales & Butler, 2016). The study of the relative impact of natural and
16
17 51 sexual selection provides a complete analysis of the mechanisms responsible for generating
18
19 52 adaptive divergence (Panhuis *et al.*, 2001; Jones & Ratterman, 2009; Cornwallis & Uller,
20
21 53 2010; Bonduriansky, 2011; Kraaijeveld, Kraaijeveld-Smit, & Maan, 2011; Maan &
22
23 54 Seehausen, 2011; Network, 2012; Safran *et al.*, 2013; Scordato *et al.*, 2014).

24
25
26
27
28
29 55 Lizards are ideal models to investigate the mechanisms of phenotypic divergence
30
31 56 associated with the interplay between natural and sexual selection. Under fecundity
32
33 57 selection, distantly related lizard species show female-biased size dimorphism and a
34
35 58 positive relationship between body size and number or size of the offspring (Cox *et al.*,
36
37 59 2003; Cox *et al.*, 2007; Jiménez-Arcos, Sanabria-Urbán, & Cueva del Castillo, 2017). Even
38
39 60 in species in which males are larger than females, the allometric relationship between size
40
41 61 and the trunk length are larger in females (Braña, 1996; Cox *et al.*, 2003, Cox *et al.*, 2007;
42
43 62 Pincheira-Donoso & Hunt, 2015). Nevertheless, in most species traits that are involved in
44
45 63 sexual displays (“push-up” behavior) and agonistic encounters are larger in males than in
46
47 64 females (Carpenter 1978; Martins 1994; Butler *et al.*, 2000; Butler & Losos 2002; Butler
48
49 65 2007; Kaliontzopoulou *et al.* 2015; Baeckens *et al.*, 2017). The “push-up” behavior is
50
51 66 associated with territorial defense and mate acquisition, and it can be found among diverse
52
53
54
55
56
57
58
59
60

1
2
3 67 lizard species with distinct degrees of territoriality and habitat use requirements (Carpenter,
4
5 68 1978; Anderson & Vitt, 1990; Butler *et al.*, 2000).
6
7

8
9 69 The habitat impacts the evolution of lizard size and shape (Losos 1990a, 2009;
10
11 70 Perry *et al.*, 2004; Melville & Swain 2000; Herrel *et al.*, 2002; Kaliontzopoulou *et al.*,
12
13 71 2015). In climbing species that inhabit rocks or canyons-walls it would be expected that
14
15 72 heads and bodies will be flat and the length of both pairs of limbs are expected to be short
16
17 73 and similar. These features allow maintenance of the center of gravity closer to substrate,
18
19 74 which reduces the risk of fall during climbing (Garland & Losos, 1994; Zaaf & Van
20
21 75 Damme, 2001; Olberding *et al.*, 2016). Conversely, tree-dwelling lizards are expected to
22
23 76 possess shorter limbs and longer and narrower bodies associated with enhanced
24
25 77 maneuverability for displacement on reduced perches (Losos, 1990b; Sinervo & Losos,
26
27 78 1991; Herrel, Meyers, & Vanhooydonck, 2001; Herrel *et al.*, 2002). Interestingly, limbs
28
29 79 and heads are involved in sexual behaviors and agonistic confrontations in males, which
30
31 80 can be associated with mate acquisition, suggesting that these attributes are also targets of
32
33 81 sexual selection in diverse lizards species (Carpenter, Badham, & Kimble, 1970; Carpenter,
34
35 82 1978; Hover, 1985; Butler & Losos, 2002).
36
37
38
39
40
41

42 83 The mesquite lizard (*Sceloporus grammicus*) represents an excellent model to study
43
44 84 the relative impact of natural and sexual selection on interpopulation phenotypic
45
46 85 divergence. *Sceloporus grammicus* inhabits a diverse array of microhabitats including wall-
47
48 86 rocks, stumps, trunks and arboreal-cacti of the genus *Opuntia* spp., within a wide range of
49
50 87 macrohabitats ranging from desert scrub to high elevation forest, from Texas to Oaxaca,
51
52 88 Mexico (Jiménez-Cruz *et al.*, 2005; Ramírez-Bautista *et al.*, 2012; Bastiaans *et al.*, 2014).
53
54
55 89 In addition, *S. grammicus* performs push-ups with elongation of the limbs and dorso-lateral
56
57
58
59
60

1
2
3 90 flattening to demonstrate belly and gular sexual color patches—behaviors generally
4
5 91 associated with antagonistic male interactions (Carpenter, 1978; Bastiaans, 2013).
6
7
8

9 92 In this study we compare the SD patterns among three populations of *S. grammicus*
10
11 93 that differ in habitat use. We selected three populations that comprise the principal habitat
12
13 94 of *S. grammicus* along its distribution. The arboreal population utilizes branches of the cacti
14
15 95 like-trees of the genus *Opuntia*, which represents narrower perches. The saxicolous
16
17 96 population occupies higher and wider perches in wall rocks in abandoned human buildings.
18
19 97 The third population can be classified as a “generalist-climbing” population. Lizards in
20
21 98 these populations are found on trunks, branches of conifers, stumps and wall rocks
22
23 99 simultaneously. Because lizards in these populations exhibit differential habitat use, the
24
25 100 direction and intensity of natural and sexual selection pressures are expected to be different.
26
27
28
29
30

31 101 In this study we test if the allometric relationship between females and males results
32
33 102 in changes in the magnitude of SD in body, head and appendicular characters. Tree-
34
35 103 dwelling lizard species have relatively short limbs, flat heads, and elongated bodies (Losos,
36
37 104 1990b; Sinervo & Losos, 1991; Herrel *et al.*, 2001, 2002). However, because of sexual
38
39 105 selection we predict that males of the arboreal population will exhibit larger limbs and
40
41 106 heads (Losos, 1990a; Herrel *et al.*, 2001, 2002), resulting in different allometric slopes
42
43 107 between sexes. Furthermore, in arboreal populations elongated bodies (i.e. distance
44
45 108 between limbs) are also favored by fecundity selection. Thus, we expect that the allometric
46
47 109 slope between females and males are similar, in contrast to the other two populations where
48
49 110 the allometric slope will be different between females and males. For saxicolous and
50
51 111 generalist-climbing populations, because of sexual selection we predict that the allometric
52
53
54
55
56
57
58
59
60

1
2
3 112 slope between limbs and heads regressed on body size will be steeper in males than
4
5 113 females.
6
7

8 114 **Material and Methods**

9 115 *Habitat use and morphometry*

10
11
12 116 We collected females and males lizards from three populations that show qualitative
13
14
15 117 differences in the structural habitat. We collected 38 females and 28 males from an arboreal
16
17
18 118 population in Los Manantiales, Mexicaltzingo, Mexico, Mexico (20° 02'. 46.12" N; 99° 32'
19
20
21 119 18.90" W; elevation 2500 m), which corresponded to an ecotone between xerophytic scrub
22
23
24 120 and oak forest. Most individuals were recorded on branches of cacti like-trees (85% in
25
26
27 121 branches and 15% on rocks). *Sceloporus mucronatus* and *S. torquatus* also inhabit the area.
28
29
30 122 These species occupy rocky outcrops and are larger than *S. grammicus*. For the saxicolous
31
32 123 population we collected 50 females and 41 males in San Cristobal, Ixtenco, Tlaxcala,
33
34 124 Mexico (19° 14' 43.27" N; 97° 55' 33.87" W; elevation 2700 m) within habitat consisting of
35
36 125 crops and some remnants of oak forest. Lizards in this population inhabit rock walls of
37
38
39 126 human abandoned buildings ranging from approximately one to five meters in height where
40
41 127 the majority of lizards were collected (93%). The remaining lizards were captured on trunks
42
43 128 (4%), branches (1%), and the ground (1%). *Sceloporus aeneus* and *S. spinosus* were also
44
45
46 129 present in this area, with the former restricted to the ground and the latter usually found
47
48
49 130 climbing branches of *Opuntia*, trees, and rocks. In the generalist-climbing population we
50
51 131 collected 50 females and 33 males on rock walls (43%), stumps (33%), stacks of fallen
52
53 132 branches (12%), and trunks (12%) within the vicinity of Estación Científica La Malinche,
54
55 133 Ixtenco, Tlaxcala, Mexico (19° 14' 27.85" N; 97° 58' 38.32" W; elevation 3000 m). In this
56
57
58
59
60

1
2
3 134 population only *S. aeneus* was sympatric, but was mainly associated with the ground (i.e.
4
5 135 non-climber). All the lizards were marked with ink to maintain identity and were released
6
7
8 136 at the collection site once the measurements had been completed.
9

10
11 137 Although the structural habitat of three populations showed qualitative differences,
12
13 138 we compared the perch height and perch diameter for the sites where females and males
14
15 139 were collected. With a commercial measuring tape (Milwaukee 1 mm precision), the height
16
17 140 of the perch was measured from the perch site to the ground. Because of habitat differences
18
19 141 in perch diameter between lizard populations (saxicolous lizards use rock walls over five
20
21 142 meters wide, whereas arboreal populations use narrower perches); measurements of the
22
23 143 perch diameter were reduced. For each individual we estimated a perch index by adding up
24
25 144 the measurements of SVL, fore limb, and hind limb lengths, and the sum was multiplied by
26
27 145 10. This index indicates that values close to 10 do not represent limitations for vertical and
28
29 146 horizontal displacement, which is associated with wider perches (Losos & Sinervo, 1989;
30
31 147 Sinervo & Losos, 1991).
32
33
34
35
36
37

38 148 For each lizard we measured the snout-vent length (SVL; a standard measure used
39
40 149 as a proxy for lizard size; Losos 1990a; Cox *et al.* 2003), head width (HW), head height
41
42 150 (HH), head length (HL), relative trunk-length (TL; distance between limbs), fore limb
43
44 151 length (FLL; sum of all fore limb segments) and hind limb length (HLL; sum of all hind
45
46 152 limb segments). The measures were taken to the nearest 0.01 mm using digital calipers
47
48 153 (Mitutoyo CD-15DC; Mitutoyo Corp., Tokyo, Japan).
49
50
51
52

53 154
54
55
56 155
57
58
59
60

1
2
3 156 **Statistical Analysis**
4

5
6 157 ***Comparison of height and diameter of perch***
7

8
9
10 158 Because the morphological differences between females and males can results from distinct
11
12 159 habitat use (i.e. ecological niche divergence; Shine 1989), we compared whether females
13
14 160 and males differ in perch height and diameter within each population, using both variables
15
16
17 161 as a proxy of habitat use. Prior to comparison, we corroborated whether perch height and
18
19 162 diameter satisfied the parametric tests assumptions. Because normality and
20
21 163 homoscedasticity of variances were not met, we used non-parametric Mann-Whitney test
22
23 164 (two tailed test for all analysis) for comparisons.
24
25

26
27 165 ***Sexual size dimorphism and allometric relationships***
28

29
30 166 Prior to analysis all trait values were log₁₀ transformed. Differences in body size were tested
31
32 167 using a two way ANOVA. Population, sex, and their interaction were used as categorical
33
34 168 variables, and SVL (our proxy of body size) as the response variable. To test if the
35
36 169 occupation of different habitat it is associated with changes in the magnitude of SD, we
37
38 170 performed (for females and males separately) major axis (MA) regression with the six
39
40 171 phenotypic variables versus SVL. We used the Wald test and the *T*-student statistic to
41
42 172 determine if allometric slopes were heterogeneous between females and males (for details
43
44 173 see Warton *et al.* 2006). Although other methods, like analysis of covariance (ANCOVA)
45
46 174 have been used for such purposes (Smith & Lemos-Espinal, 2003; Ramírez-Bautista *et al.*,
47
48 175 2016), we selected MA regression because this method is appropriate when the purpose of
49
50 176 line-fitting is not to predict Y from X, but to summarize the relationship between two
51
52 177 variables, describing how size variables are related through linear relationships on
53
54
55
56
57
58
59
60

1
2
3 178 logarithmic scales (Warton *et al.* 2006). The main advantage of this regression is that it
4
5 179 estimates and infers the lines (slopes) considering the residual values of X and Y, which
6
7
8 180 provides a more accurate estimate of allometric slope (Warton *et al.*, 2006). Additionally,
9
10 181 we compared if the allometric slope differed from isometry ($\beta = 1$) using an F statistic for
11
12 182 the phenotypic traits that diverged in slopes between females and males (for details of
13
14
15 183 calculation see Warton *et al.* 2006).

16
17
18 184 For variables where the allometric slopes were comparable (i.e. slopes were equal
19
20 185 and a common slope could be estimated), we determined changes among common axis and
21
22 186 changes in elevation, this latter test is analogous to ANCOVA. We used the Wald test with
23
24 187 chi-square (χ^2) for comparison analyses (for details see Warton *et al.* 2006). For all MA
25
26 188 analyses we used the program SMATR ver 2.0. In Appendix I we present the statistic
27
28 189 values for common axis and elevation comparisons.
29
30
31
32
33
34
35

36 191 **Results**

37
38
39 192 *Habitat use.* There was no divergence in female and male habitat use in the three
40
41 193 populations. The height and diameter perch for females and males did not differ in arboreal
42
43 194 (height: $U_{(1, 0.05)} = 483$, $P = 0.53$; diameter: $U_{(1, 0.05)} = 901.5$, $P = 0.64$), saxicolous (height: $U_{(1,$
44
45 195 $0.05)} = 950$, $P = 0.55$; diameter: $U_{(1, 0.05)} = 1918$, $P = 0.56$), and generalist-climbing (height: $U_{(1,$
46
47 196 $0.05)} = 800$, $P = 0.82$; diameter: $U_{(1, 0.05)} = 814.5$, $P = 0.90$) populations.
48
49
50
51

52 197 *Sexual size dimorphism.* Males were significantly larger than females ($F_{(1, 234)} = 60.32$,
53
54 198 $P < 0.0001$). Moreover, there were significant differences in body size among the three
55
56 199 populations ($F_{(2, 234)} = 26.54$, $P < 0.0001$). Post-hoc comparisons using the Tukey HSD test
57
58
59
60

1
2
3 200 indicated that the saxicolous population contained the largest individuals (adjusted mean \pm
4
5 201 SE; 1.80 ± 0.008), followed by generalist (1.78 ± 0.008) and arboreal populations ($1.75 \pm$
6
7
8 202 0.009). However, there were no interpopulation differences in the magnitude of body size
9
10 203 differences between females and males (Interaction Sex * Population: $F_{(2, 234)} = 1.24$, $P =$
11
12
13 204 0.29 , Fig. 1).

16 205 *Allometric relationships*

18
19 206 In the arboreal population four of the six traits showed a heterogeneous slope (Table 1 and
20
21 207 Fig. 2). Males had steeper allometric slopes than females for HW, HL, FLL and HLL (Fig.
22
23
24 208 2A to D), whereas males and females showed homogeneous slopes in TL and HH. Females
25
26 209 and males diverged along a common slope in both TL and HH (Table 2). The TL elevation
27
28 210 was greater in females, which indicate that females have larger TL with respect the body
29
30 211 size. There were no significant differences between sexes in elevation on HH (Table 3). In
31
32 212 contrast, females and males from the saxicolous population showed homogeneous slopes in
33
34
35 213 the six phenotypic traits (Table 1). In all traits we found significant changes among
36
37 214 common axes (Table 2). This indicated that even when males were larger than females in
38
39 215 overall size, the allometric relationship between phenotypic traits and SVL remains similar
40
41 216 for both sexes. We also found that four of six traits showed changes in elevation. Females
42
43 217 had greater TL values, whereas HL, FLM, and HLM showed higher values in males (Table
44
45 218 3). The generalist-climbing population showed a heterogeneous slope in TL (Fig. 2E), and
46
47
48 219 homogeneous slopes for the other five phenotypic traits (Table 1). For changes in common
49
50 220 slope, as well as in elevation, males were larger than females in the five phenotypic traits
51
52
53 221 (Table 2 and Table 3).
54
55
56
57
58
59
60

1
2
3 222 **Discussion**
4
5

6 223 Our results indicate that within the three populations of *S. grammicus* there are no
7
8 224 differences in habitat use between females and males. However, the saxicolous and arboreal
9
10 225 populations contain the largest and smallest lizards, respectively. Moreover, males are
11
12 226 larger than females, even though there are no interpopulation differences in the magnitude
13
14 227 of sexual size dimorphism between them. Perhaps the differences in body size between
15
16 228 populations could be explained by distinct habitat uses. Both females and males from
17
18 229 saxicolous populations may have lower mobility constraints than generalist or arboreal
19
20 230 lizards. These last two populations have similar allometric trends between them, suggesting
21
22 231 that, at some level, the selective pressures remains similar (see Table 1). However, because
23
24 232 habitat use of females and males do not differ, our results may suggest that selection on
25
26 233 fecundity and sexual selection rather than differences in ecological niche may be shaping
27
28 234 the morphological divergence between females and males.
29

30
31
32
33
34
35 235 The interplay between fecundity selection, sexual selection and habitat use pressures
36
37 236 could explain the allometric relationships we find in the arboreal population. In females,
38
39 237 fecundity selection (number or size of the offspring) can favor the evolution of elongated
40
41 238 bodies (Braña, 1996; Cox *et al.*, 2003; Jiménez-Arcos *et al.*, 2016), and the short limbs may
42
43 239 compensate for the climbing instability due to the extra weight of the offspring. Moreover,
44
45 240 in narrow substrates, elongated and flattened bodies and heads results in a low center of
46
47 241 gravity closer to substrate in both sexes (Losos, 1990b; Herrel *et al.*, 2001, 2002; Leyte-
48
49 242 Manrique *et al.*, 2017), reducing the risk of falling. Conversely, sexual selection may
50
51 243 explain why the allometric relationships on limbs and width and length of the head are
52
53
54
55
56
57
58
59
60

1
2
3 244 steeper in males than females. The head and limbs are involved in sexual display behavior,
4
5 245 principally for male-male combat for defense of mates and territory (Carpenter, 1978).
6
7

8
9 246 The selective pressures can operate in similar directions in the arboreal and
10
11 247 generalist-climbing populations, even though in the latter the habitat may impose less
12
13 248 locomotor constraints than in the arboreal environment. Thus, only generalist climbing
14
15 249 females show a hyper allometric relationship between SVL and the trunk length, suggesting
16
17 250 that selection on fecundity may favor a faster increase in the females' trunk length.
18
19 251 Conversely, in females from the saxicolous population where there are presumably no
20
21 252 climbing constraints on movement, fecundity selection perhaps has favored a general
22
23 253 increase in size. Although it is likely that ecological niche constraints are shaping inter
24
25 254 population differentiation, the generalist climbing and arboreal males show similar, but
26
27 255 steeper allometric trends than females, suggesting that these traits can be under sexual
28
29 256 selection. Larger trait size confers benefits due to sexual competition and/or female mate
30
31 257 choice (Bonduriansky & Day, 2003; Bonduriansky, 2007; Eberhard, Rodriguez &
32
33 258 Polihronakis, 2009). However, we stress that none of the allometric slopes in males are
34
35 259 steeper than one so perhaps the evolutionary response to sexual selection is constrained by
36
37 260 the niche (see Bonduriansky & Day, 2003; Bonduriansky, 2007), and that the allometric
38
39 261 relationships can be explained by other sources, including ontogenetic and phylogenetic
40
41 262 constraints (Butler, Sawyer, & Losos, 2007; Kaliontzopoulou *et al.*, 2015). Thus,
42
43 263 experimental studies are needed in order to test the relative impact of natural and sexual
44
45 264 selection on the evolution of *S. grammicus*.
46
47
48
49
50
51
52

53
54 265 The correlative evidence in our study suggests an interplay of fecundity and sexual
55
56 266 selection generating the divergence in body size between females and males. These results
57
58
59
60

1
2
3 267 are similar to those conducted in a comparative study on phrynosomatids, where males and
4
5 268 females show a differential correlative response associated to habitat use (Herrel *et al.*,
6
7
8 269 2002). Males possess larger limbs than females, which are associated with territoriality. In
9
10 270 the 20 species analyzed, all males perform sexual display behavior (push-ups), which
11
12 271 suggests that perhaps limbs are targets of sexual selection (Carpenter, 1978; Martins, 1994;
13
14 272 Herrel *et al.*, 2001, 2002). In *Anolis* lizards the magnitude of SD in size and shape changes
15
16 273 among ecomorphs (Butler *et al.*, 2000, 2007; Butler & Losos, 2002). Males usually show
17
18 274 fewer lamellae, smaller relative mass and relative body length than females (Butler *et al.*,
19
20 275 2007). Larger relative body length in females can be explained by fecundity selection. Even
21
22 276 when clutch size in *Anolis* is fixed to one egg, large differences in clutch number per
23
24 277 reproductive season can be associated with fecundity selection pressures. Large sizes in
25
26 278 male SVL and head and limb length may be associated with sexual selection pressures, as
27
28 279 sexual display behavior associated with territory defense is common among *Anolis* species
29
30 280 (Butler & Losos, 2002; Butler *et al.*, 2007). The evidence suggests that interplay between
31
32 281 fecundity and sexual selection is the main force explaining the phenotypic divergence
33
34 282 between females and males, and differences in habitat use are responsible for
35
36 283 interpopulation phenotypic diversification among both sexes.
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

285 **References**

- 286 **Anderson RA, Vitt LJ. 1990.** Sexual selection versus alternative causes of sexual
287 dimorphism in teiid lizards. *Oecologia* 84: 145–157.
- 288 **Andersson M. 1994.** *Sexual selection*. Princeton: Princeton University Press.
- 289 **Baeckens S, Martín J, García-Roa R, van Damme R. 2017.** Sexual selection and the
290 chemical signal design of lacertid lizards. *Zoological Journal of the Linnean Society* zlx075
- 291 **Bastiaans E. 2013.** Variation in Reproductive Behavior and Sexual Signals Within and
292 Among Populations of an Incipiently Speciating Lizard. Unpublished thesis, University of
293 California, Santa Cruz. Ph.D.
- 294 **Bastiaans E, Bastiaans MJ, Morinaga G, Castañeda-Gaytán JG, Marshall JC, Bane B,**
295 **Méndez-de la Cruz F, Sinervo B. 2014.** Female preference for sympatric vs. allopatric
296 male throat color morphs in the mesquite lizard (*Sceloporus grammicus*) species complex.
297 *PLoS ONE* 9: 44–48.
- 298 **Blanckenhorn WU. 2005.** Behavioral causes and consequences of sexual size dimorphism.
299 *Ethology* 111: 977–1016.
- 300 **Bonduriansky R. 2007.** Sexual selection and allometry: A critical reappraisal of the
301 evidence and ideas. *Evolution* 61: 838–849.
- 302 **Bonduriansky R. 2011.** Sexual Selection and Conflict as Engines of Ecological
303 Diversification. *The American Naturalist* 178: 729–745.
- 304 **Bonduriansky R, Day T. 2003.** The evolution of static allometry in sexually selected
305 traits. *Evolution* 57: 2450–2458.

- 1
2
3 306 **Braña F. 1996.** Sexual dimorphism in lacertid lizards : male head increase vs female
4
5
6 307 abdomen increase? *Oikos* 75: 511–523.
7
8
9 308 **Butler MA. 2007.** *Vive le difference!* Sexual dimorphism and adaptive patterns in lizards of
10
11 309 the genus *Anolis*. *Integrative and Comparative Biology* 47: 272–284.
12
13
14 310 **Butler MA, Losos JB. 2002.** Multivariate sexual dimorphism, sexual selection, and
15
16 311 adaptation in greater antillean *Anolis* lizards. *Ecological Monographs* 72: 541–559.
17
18
19
20 312 **Butler MA, Sawyer SA, Losos JB. 2007.** Sexual dimorphism and adaptive radiation in
21
22 313 *Anolis* lizards. *Nature* 447: 3–6.
23
24
25
26 314 **Butler M, Schoener TW, Losos JB. 2000.** The relationship between sexual size
27
28 315 dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* 54: 259–272.
29
30
31 316 **Carpenter CC. 1978.** Comparative Display Behavior in the genus *Sceloporus* (Iguanidae).
32
33 317 *Contributions in Biology and Geology to the Milwaukee Public Museum*: 1–71.
34
35
36
37 318 **Carpenter CC, Badham JA, Kimble B. 1970.** Behavior Patterns of Three Species of
38
39 319 *Amphibolurus* (Agamidae). *Copeia* 1970: 497–505.
40
41
42
43 320 **Cornwallis CK, Uller T. 2010.** Towards an evolutionary ecology of sexual traits. *Trends*
44
45 321 *in Ecology and Evolution* 25: 145–152.
46
47
48 322 **Cox RM, Butler MA, John-Alder HB. 2007.** The evolution of sexual size dimorphism in
49
50 323 reptiles. In: Fairbairn DJ,, In: Blanckenhorn WU,, In: Székely T, eds. *Sex, Size and Gender*
51
52 324 *Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford, U.K. Oxford Univ. Press.
53
54
55
56 325 **Cox RM, Skelly SL, John-Alder HB. 2003.** A comparative test of adaptive hypotheses for
57
58
59
60

- 1
2
3 326 sexual size dimorphism in lizards. *Evolution* 57: 1653–1669.
4
5
6 327 **Darwin C. 1871.** *The Descent of Man, and Selection in Relation to Sex*. London, UK: John
7
8 328 Murray.
9
10
11 329 **Eberhard WG, Huber BA, Rodriguez RL, Briceno DR, Salas I, Viterbo R. 1998.** One
12
13 330 Size Fits All? Relationships Between the Size and Degree of Variation in Genitalia and
14
15 331 Other Body Parts in Twenty Species of Insects and Spiders. *Evolution* 52: 415–431.
16
17
18 332 **Eberhard W, Rodriguez RL, Polihronakis M. 2009.** Pitfalls in understanding the
19
20 333 functional significance of genital allometry. *Journal of Evolutionary Biology* 22(3):435-45
21
22
23 334 **Fairbairn DJ. 1997.** Allometry for Sexual Size Dimorphism : Pattern and Process in the
24
25 335 Coevolution of Body Size in Males and Females. *Annual Review of Ecology and*
26
27 336 *Systematics* 28: 659–687.
28
29
30 337 **Fairbairn DJ, Blanckenhorn WU, Székely T. 2007.** *Sex, size & gender roles.*
31
32 338 *Evolutionary studies of sexual size dimorphism*. Oxford, U.K.: Oxford University Press.
33
34
35 339 **Frankino WA, Emlen DJ, Shingleton AW. 2009.** Experimental approaches to studying
36
37 340 the evolution of animal form: The Shape of Things to Come. In: Garland T., In: Rose M,
38
39 341 eds. *Experimental evolution: concepts, methods, and applications*. Berkeley and Los
40
41 342 Angeles, CA: University of California Press, 419–478.
42
43
44 343 **Garland TJ, Losos JB. 1994.** Ecological Morphology of Locomotor Performance in
45
46 344 Squamate Reptiles. In: Wainwright PC, In: Reilly S, eds. *Ecological Morphology:*
47
48 345 *Integrative Organismal Biology*. Chicago: University of Chicago, 240–302.
49
50
51 346 **Herrel A, Meyers JJ, Vanhooydonck B. 2001.** Correlations between habitat use and body
52
53
54
55
56
57
58
59
60

- 1
2
3 347 shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis.
4
5 348 *Biological Journal of the Linnean Society* 74: 305–314.
6
7
8
9 349 **Herrel A, Meyers JJ, Vanhooydonck B. 2002.** Relations between microhabitat use and
10
11 350 limb shape in phrynosomatid lizards. *Biological Journal of the Linnean Society* 77: 149–
12
13 351 163.
14
15
16
17 352 **Hover EL. 1985.** Differences in Aggressive Behavior Between Two Throat Color Morphs
18
19 353 in a Lizard, *Urosaurus ornatus*. *Copeia*: 933–940.
20
21
22 354 **Jiménez-Arcos VH, Sanabria-Urbán S, Cueva del Castillo R. 2016.** The interplay
23
24 355 between natural and sexual selection in the evolution of sexual size dimorphism in
25
26 356 *Sceloporus* lizards (Squamata: Phrynosomatidae). *Ecology and Evolution* 7: 905–917.
27
28
29
30 357 **Jiménez-Cruz E, Ramírez-Bautista A, Marshall JC, Lizana-Avia M, Nieto-Montes De**
31
32 358 **Oca A. 2005.** Reproductive Cycle of *Sceloporus grammicus* (Squamata: Phrynosomatidae)
33
34 359 From Teotihuacán, México. *The Southwestern Naturalist* 50: 178–187.
35
36
37
38 360 **Jones AG, Ratterman NL. 2009.** Mate choice and sexual selection: what have we learned
39
40 361 since Darwin? *Proceedings of the National Academy of Sciences of the United States of*
41
42 362 *America* 106 Suppl: 10001–10008.
43
44
45
46 363 **Kaliontzopoulou A, Carretero MA, Adams DC. 2015.** Ecomorphological variation in
47
48 364 male and female wall lizards and the macroevolution of sexual dimorphism in relation to
49
50 365 habitat use. *Journal of Evolutionary Biology* 28: 80–94.
51
52
53
54 366 **Kraaijeveld K, Kraaijeveld-Smit FJL, Maan ME. 2011.** Sexual selection and speciation:
55
56 367 the comparative evidence revisited. *Biological Reviews* 86: 367–377.
57
58
59
60

- 1
2
3 368 **Leyte-Manrique A, Hernández-Salinas U, Ramírez-Bautista A, Mata-Silva V,**
4
5 369 **Marshall J. 2017.** Habitat use in eight populations of *Sceloporus grammicus* (Squamata:
6
7 Phrynosomatidae) from the Mexican Plateau. *Integrative Zoology* 12: 198–210.
8
9
10
11 371 **Losos JB. 1990a.** Ecomorphology, performance capability, and scaling of West Indian
12
13 372 *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* 60: 369–388.
14
15
16
17 373 **Losos JB. 1990b.** The evolution of form and function: Morphology and Locomotor
18
19 374 performance in West Indian *Anolis* lizards. *Evolution* 44: 1189–1203.
20
21
22 375 **Losos JB, Butler M, Schoener TW. 2003.** Sexual Dimorphism in Body Size and Shape in
23
24 376 Relation to Habitat Use among Species of Caribbean *Anolis* Lizards. In: Fox S, McCoy J,
25
26 377 Baird T, eds. *Lizard Social Behavior*. Baltimore: Johns Hopkins Press, 356–380.
27
28
29
30 378 **Losos JB, Sinervo B. 1989.** The Effects of Morphology and Perch Diameter on Sprint
31
32 379 Performance of *Anolis* Lizards. *Journal of Experimental Biology* 145: 23–30.
33
34
35
36 380 **Maan ME, Seehausen O. 2011.** Ecology, sexual selection and speciation. *Ecology Letters*
37
38 381 14: 591–602.
39
40
41 382 **Martins EP. 1994.** Phylogenetic perspectives on the Evolution of lizard territoriality. In:
42
43 383 Vitt LJ,, In: Pianka ER, eds. *Lizard ecology: Historical and experimental perspectives*.
44
45 384 Princeton: Princeton University Press, 117–144.
46
47
48
49 385 **Melville J, Swain R. 2000.** Evolutionary Relationships Between Morphology, Performance
50
51 386 and Habitat Openness in the Lizard Genus *Niveoscincus* (Scincidae: Lygosominae).
52
53 387 *Biological Journal of the Linnean Society* 70: 667–683.
54
55
56
57 388 **Mirth CK, Frankino WA, Shingleton AW. 2016.** Allometry and size control: What can
58
59
60

- 1
2
3 389 studies of body size regulation teach us about the evolution of morphological scaling
4
5 390 relationships? *Current Opinion in Insect Science* 13: 93–98.
6
7
8
9 391 **Network TMCS. 2012.** What do we need to know about speciation? *Trends in Ecology*
10
11 392 *and Evolution* 27: 27–39.
12
13
14 393 **Olberding JP, Herrel A, Higham TE, Garland T. 2016.** Limb segment contributions to
15
16 394 the evolution of hind limb length in phrynosomatid lizards. *Biological Journal of the*
17
18 395 *Linnean Society* 117: 775–795.
19
20
21
22 396 **Panhuis TM, Butlin R, Zuk M, Tregenza T. 2001.** Sexual selection and speciation.
23
24 397 *Trends in ecology & evolution (Personal edition)* 16: 364–371.
25
26
27
28 398 **Pélabon C, Firmat C, Bolstad GH, Voje KL, Houle D, Cassara J, Rouzic A Le,**
29
30 399 **Hansen TF. 2014.** Evolution of morphological allometry. *Annals of the New York Academy*
31
32 400 *of Sciences* 1320: 58–75.
33
34
35
36 401 **Perry G, Levering K, Girard I, Garland T. 2004.** Locomotor performance and social
37
38 402 dominance in male *Anolis cristatellus*. *Animal Behaviour* 67: 37–47.
39
40
41 403 **Petrie M. 1988.** Intraspecific variation in structures that display competitive ability: large
42
43 404 animals invest relatively more. *Animal Behaviour* 36: 1174–1179.
44
45
46
47 405 **Petrie M. 1992.** Are all secondary sexual display structures positively allometric and, if so,
48
49 406 why? *Animal Behaviour* 43: 173–175.
50
51
52
53 407 **Pincheira-Donoso D, Hunt J. 2015.** Fecundity selection theory: Concepts and evidence.
54
55 408 *Biological Reviews* 2015: 1–16.
56
57
58
59
60

- 1
2
3 409 **Ramírez-Bautista A, Hernández-Salinas U, Cruz-Elizalde R, Lozano A, Rodríguez-**
4
5 410 **Romero F. J. 2016.** Sexual dimorphism and reproductive traits over time in *Sceloporus*
6
7 411 *aeneus* (Squamata: Phrynosomatidae), based on a population in the Transmexican Volcanic
8
9 412 Belt, Mexico. *Salamandra* 52: 197–203.
- 10
11
12
13 413 **Ramírez-Bautista A, Stephenson BP, Lozano A, Uribe-Rodríguez H, Manrique AL.**
14
15 414 **2012.** Atypical reproductive cycles in a population of *Sceloporus grammicus* (Squamata:
16
17 415 Phrynosomatidae) from the Mexican Plateau. *Ecology and Evolution* 2: 1903–1913.
- 18
19
20
21 416 **Ruckstuhl KE, Neuhaus P. 2005.** *Sexual Segregation in Vertebrates. Ecology of the Two*
22
23 417 *Sexes*. Cambridge: Univ. Press Cambridge.
- 24
25
26
27 418 **Safran RJ, Scordato ESC, Symes LB, Rodríguez RL, Mendelson TC. 2013.**
28
29 419 Contributions of natural and sexual selection to the evolution of premating reproductive
30
31 420 isolation: A research agenda. *Trends in Ecology and Evolution* 28: 643–650.
- 32
33
34
35 421 **Scales JA, Butler MA. 2016.** Adaptive evolution in locomotor performance: How selective
36
37 422 pressures and functional relationships produce diversity. *Evolution* 70: 48–61.
- 38
39
40
41 423 **Scordato ESC, Symes LB, Mendelson TC, Safran RJ. 2014.** The role of ecology in
42
43 424 speciation by sexual selection: A systematic empirical review. *Journal of Heredity* 105:
44
45 425 782–794.
- 46
47
48
49 426 **Selander RK. 1966.** Sexual dimorphism and differential niche utilization in birds. *The*
50
51 427 *Condor* 68: 113–151.
- 52
53
54
55 428 **Serrano-Meneses MA, Székely T. 2006.** Sexual size dimorphism in seabirds: Sexual
56
57 429 selection, fecundity selection and differential niche-utilisation. *Oikos* 113: 385–394.
- 58
59
60

- 1
2
3 430 **Shine R. 1989.** Ecological Causes for the Evolution of Sexual Dimorphism: A Review of
4
5 431 the Evidence. *The Quarterly Review of Biology* 64: 419–461.
6
7
8
9 432 **Sinervo B, Losos JB. 1991.** Walking the tight rope: arboreal sprint performance among
10
11 433 *Sceloporus occidentalis* lizard populations. *Ecology* 72: 1225–1233.
12
13
14 434 **Slatkin M. 1984.** Ecological Causes of Sexual Dimorphism. *Evolution* 38: 622–630.
15
16
17
18 435 **Smith G, Lemos-Espinal J. 2003.** Body size, sexual dimorphism, and clutch size in two
19
20 436 populations of the lizard *Sceloporus ochoteranae*. *Southwestern Naturalist* 48: 123–126.
21
22
23 437 **Stillwell RC, Shingleton AW, Dworkin I, Frankino WA. 2016.** Tipping the scales:
24
25 438 Evolution of the allometric slope independent of average trait size. *Evolution* 70: 433–444.
26
27
28
29 439 **Voje KL. 2016.** Scaling of Morphological Characters across Trait Type, Sex, and
30
31 440 Environment. *The American Naturalist* 187: 89–98.
32
33
34 441 **Warton DI, Wright IJ, Falster DS, Westoby M. 2006.** Bivariate line-fitting methods for
35
36 442 allometry. *Biological Reviews* 81: 259–291.
37
38
39
40 443 **West-Eberhard MJ. 1983.** Sexual Selection, Social Competition, and Speciation. *The*
41
42 444 *Quarterly review of biology* 58: 155–183.
43
44
45 445 **Zaaf A, Van Damme R. 2001.** Limb proportions in climbing and ground-dwelling geckos
46
47 446 (Lepidosauria, Gekkonidae): A phylogenetically informed analysis. *Zoomorphology* 121:
48
49 447 45–53.
50
51
52
53 448
54
55
56
57 449
58
59
60

1
2
3 450 **Figure Legends**
4

5 451 Figure 1. Comparison of body size (SVL) in three populations of *S. grammicus*: A) Males
6
7 452 were larger than females considering all the data of the three populations together. B)
8
9 453 Interpopulation size comparison with females and males together. Saxicolous (SAX) was
10
11 454 the largest population, followed by generalist (GEN) and arboreal (ARB) populations. C)
12
13 455 Interaction of sex*population. Males were larger than females in the three populations,
14
15 456 without changes in the magnitude of sexual size dimorphism in body size among three
16
17 457 populations.
18
19
20
21
22

23 458

24
25
26 459 Figure 2. Allometric relationships for the five traits where the slopes of females and males
27
28 460 are significantly heterogeneous in the arboreal population (A to D), and for one trait (E) in
29
30 461 the generalist population. The dashed and solid lines represent allometric relationship for
31
32 462 females and males respectively. Open and filled symbols represent values of females and
33
34 463 males respectively. Abbreviation: t_w = Wald test using *T*-student statistic. Only phenotypic
35
36 464 traits that showed significantly heterogeneous slopes are depicted.
37
38
39
40

41 465
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

466 **Tables**

467 Table 1. Allometric slope values for six phenotypic traits versus snout-vent length (SVL) among three populations of *Sceloporus*
 468 *grammicus*. Values in parentheses indicate 95% confidence intervals of the slope. * = Significantly different from isometry ($\beta = 1$). **
 469 = Significant slope heterogeneity between females and males. TL: trunk length, HW: head width, HL: head length, HH: head height,
 470 FLM: fore limb length, and HLM: hind limb length.

Population	TL		HW		HH		HL		FLM		HLM	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Arboreal	1.08	1.06	0.77*	1.05	0.82	0.82*	0.65*	0.80*	0.61*	0.89	0.60*	0.87*
	(1.00-1.18)	(0.94-1.19)	(0.64-0.90)	(0.89-1.26)	(0.60-1.09)	(0.67-0.99)	(0.58-0.72)	(0.72-0.89)	(0.52-0.72)	(0.77-1.02)	(0.50-0.71)	(0.76-0.99)
	$P = 0.77$		$P = 0.004^{**}$		$P = 0.99$		$P = 0.01^{**}$		$P = 0.001^{**}$		$P = 0.001^{**}$	
Saxicolous	1.1	0.89	1.09	1.11	0.83*	0.101	0.72*	0.82*	0.70*	0.77	0.66*	0.90
	(0.96-1.26)	(0.70-1.08)	(0.71-1.71)	(0.90-1.36)	(0.69-0.99)	(0.69-1.48)	(0.65-0.80)	(0.71-0.95)	(0.56-0.85)	(0.58-1.01)	(0.52-0.82)	(0.67-1.19)
	$P = 0.91$		$P = 0.95$		$P = 0.31$		$P = 0.15$		$P = 0.53$		$P = 0.09$	
Generalist climbing	1.40*	0.95	0.70*	0.76	0.74*	0.64*	0.68*	0.80*	0.60*	0.79	0.63*	0.75*
	(1.23-1.60)	(0.84-1.06)	(0.60-0.81)	(0.69-1.00)	(0.61-0.89)	(0.47-0.84)	(0.61-0.92)	(0.70-0.92)	(0.44-0.79)	(0.60-1.02)	(0.50-0.77)	(0.62-0.90)
	$P = 0.001^{**}$		$P = 0.14$		$P = 0.36$		$P = 0.05$		$P = 0.15$		$P = 0.19$	

471

472

473

474

475 Table 2. Mean values for fitted axis scores (F). The empty cells correspond to heterogeneous slopes where no comparison can be
 476 made. * = significant changes among common slope. Data are mean of $F \pm 1$ SE. TL: trunk length, HW: head width, HL: head length,
 477 HH: head height, FLM: fore limb length, and HLM: hind limb length.

Population	TL		HW		HH		HL		FLM		HLM	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Arboreal	3.38 ±0.02	3.44 ±0.02	---	---	2.36 ±0.01	2.44 ±0.02	---	---	---	---	---	---
	<i>P</i> = 0.04				<i>P</i> < 0.001							
Saxicolous	3.48 ±0.01	3.60 ±0.01	2.96 ±0.01	3.11 ±0.01	2.48 ±0.01	2.60 ±0.008	2.64 ±0.01	2.75 ±0.008	2.81 ±0.01	2.93 ±0.007	2.97 ±0.01	3.08 ±0.008
	<i>P</i> < 0.001		<i>P</i> < 0.001		<i>P</i> < 0.001		<i>P</i> < 0.001		<i>P</i> < 0.001		<i>P</i> < 0.001	
Generalist climbing	---	---	2.57 ±0.01	2.67 ±0.08	2.34 ±0.01	2.42 ±0.01	2.58 ±0.07	2.67 ±0.01	2.76 ±0.01	2.84 ±0.01	2.89 ±0.07	2.98 ±0.08
			<i>P</i> < 0.001		<i>P</i> < 0.001		<i>P</i> < 0.001		<i>P</i> < 0.001		<i>P</i> < 0.001	

478

479

480

481

482

483 Table 3. Mean values for residual axis scores (R). Changes in elevation are analogous to analysis of covariance (Warton *et al.* 2006).

484 The cells with dashes correspond to heterogeneous slopes where no comparison can be made. * = significant changes in elevation

485 based on common slope. Data are mean of $R \pm 1$ SE. TL: trunk length, HW: head width, HL: head length, HH: head height, FLM: fore

486 limb length and HLM: hind limb length.

Population	TL		HW		HH		HL		FLM		HLM	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Arboreal	-0.32 ±0.002	-0.35 ±0.003	---	---	-0.63 ±0.005	-0.62 ±0.02	---	---	---	---	---	---
	$P < 0.001^*$				$P = 0.053$							
Saxicolous	-0.37 ±0.003	-0.39 ±0.003	-0.87 ±0.007	-0.86 ±0.003	-0.70 ±0.003	-0.69 ±0.02	-0.19 ±0.002	-0.17 ±0.002	0.15 ±0.003	0.18 ±0.003	0.31 ±0.003	0.33 ±0.003
	$P = 0.003^*$		$P = 0.35$		$P = 0.22$		$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$	
Generalist climbing	---	---	-0.25 ±0.003	-0.21 ±0.003	-0.44 ±0.003	-0.41 ±0.004	-0.13 ±0.002	-0.11 ±0.003	0.21 ±0.004	0.24 ±0.004	0.38 ±0.003	0.42 ±0.003
			$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$	

487

488

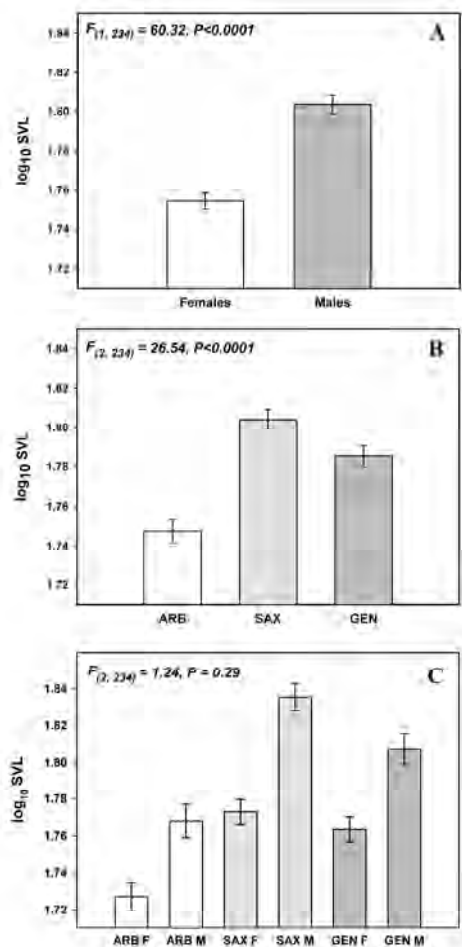


Figure 1. Comparison of body size (SVL) in three populations of *S. grammicus*: A) Males were larger than females considering all the data of the three populations together. B) Interpopulation size comparison with females and males together. Saxicolous (SAX) was the largest population, followed by generalist (GEN) and arboreal (ARB) populations. C) Interaction of sex*population. Males were larger than females in the three populations, without changes in the magnitude of sexual size dimorphism in body size among three populations.

297x420mm (300 x 300 DPI)

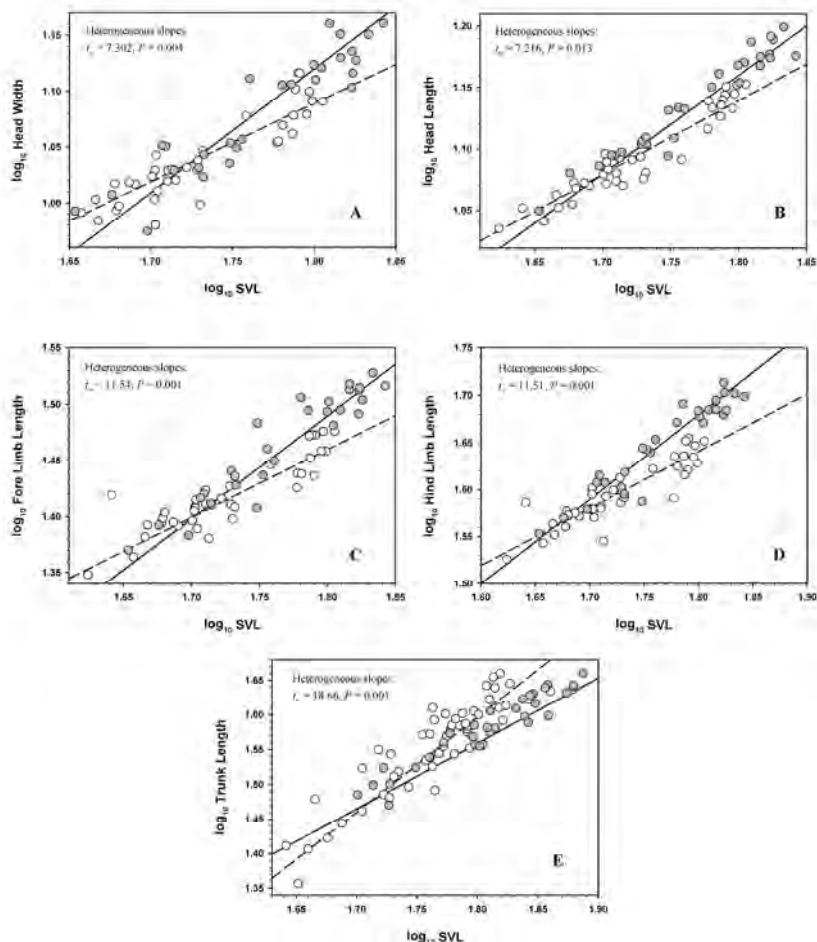


Figure 2. Allometric relationships for the five traits where the slopes of females and males are significantly heterogeneous in the arboreal population (A to D), and for one trait (E) in the generalist population. The dashed and solid lines represent allometric relationship for females and males respectively. Open and filled symbols represent values of females and males respectively. Abbreviation: tw = Wald test using T-student statistic. Only phenotypic traits that showed significantly heterogeneous slopes are depicted.

297x420mm (300 x 300 DPI)

1 Appendix 1

2 Table A1. Wald test values using an F statistic for comparing if slope differs from isometry ($H_0: \beta = 1$) for females and males using
 3 major axis regression. d.f. = degrees of freedom. HW: head width, HL: head length, HH: head height, FLM: fore limb length and
 4 HLM: hind limb length. * = Significantly different from isometry.

Trait / Population	d.f.	TL		HW		HH		HL		FLM		HLM	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Arboreal	♀ (1, 36)	3.72	0.06	10.93	0.002*	2.03	0.16	63.55	<0.001*	39.497	<0.001*	39.96	<0.001*
	♂ (1, 26)	1.04	0.32	0.40	0.53	4.73	0.04*	19.33	<0.001*	3.057	0.09	5.19	0.03*
Saxicolous	♀ (1, 48)	1.88	0.18	0.18	0.67	4.71	0.03*	38.15	<0.001*	13.597	<0.001*	14.24	<0.001*
	♂ (1, 39)	0.55	0.46	1.01	0.32	0.005	0.94	7.54	0.009*	3.809	0.06	0.60	0.44
Generalist climbing	♀ (1, 48)	27.97	<0.001*	22.68	<0.001*	10.52	0.002*	61.42	<0.001*	14.276	<0.001*	20.66	<0.001*
	♂ (1, 31)	0.98	0.33	4.05	0.053	11.28	0.002*	11.35	0.002*	3.467	0.07	10.41	0.003*

1
2
3
4
5 10 Table A2. Values of common slopes estimated with MA regression. All the Wald statistics were estimated with a critical P -value of α
6
7 11 = 0.05, one tailed test using the T -student distribution and 1 degree of freedom (Warton *et al.* 2006). The cells with dashes correspond
8
9 12 to significantly heterogeneous slope. HW: head width, HL: head length, HH: head height, FLM: fore limb length and HLM: hind limb
10
11
12 length.
13

Population	TL			HW			HH			HL			FLL			HLL		
	β_{comm}	t_w	P	β_{comm}	t_w	P	β_{comm}	t_w	P	β_{comm}	t_w	P	β_{comm}	t_w	P	β_{comm}	t_w	P
Arboreal	1.08	0.1	0.78	---	---	---	0.82	0.001	0.99	---	---	---	---	---	---	---	---	---
Saxicolous	1.09	0.01	0.91	1.1	0.003	0.95	0.86	1.02	0.31	0.75	1.97	0.15	0.72	0.4	0.53	0.74	2.91	0.09
Generalist climbing	---	---	---	0.75	2.12	0.14	0.71	0.77	0.36	0.72	3.93	0.054	0.69	2.12	0.15	0.7	1.67	0.19

14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49

Table A3. Statistic values for Wald test using chi-square (χ^2) evaluating changes among common axis for the six phenotypic traits. The degrees of freedom were similar (d.f. = 1) for all the variables. * = Significant changes among common axis. The cells with dashes correspond to significantly heterogeneous slope. HW: head width, HL: head length, HH: head height, FLM: fore limb length and HLM: hind limb length.

Population	TL		HW		HH		HL		FLM		HLM	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Arboreal	4.11	0.04*	---		13.33	< 0.001	---		---		---	
Saxicolous	42.70	< 0.001	64.63	< 0.001	61.23	< 0.001	45.22	< 0.001	73.81	< 0.001	72.29	< 0.001
Generalist climbing	---		28.15	< 0.001	23.47	< 0.001	21.95	< 0.001	22.18	< 0.001	25.59	< 0.001

Table A4. Statistic values for Wald test using chi-square (χ^2) to evaluate changes in elevation based on a common slope for the six phenotypic traits. The degrees of freedom were the same (d.f. = 1) for all the variables. * = Significantly changes in elevation. The cells with dashes correspond to significantly heterogeneous slope. HW: head width, HL: head length, HH: head height, FLM: fore limb length and HLM: hind limb length.

Population	TL		HW		HH		HL		FLM		HLM	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Arboreal	51.11	< 0.001*	---		3.74	0.053	---		---		---	
Saxicolous	8.67	0.003	0.87	0.35	1.50	0.22	74.15	< 0.001*	20.51	< 0.001*	15.77	< 0.001*
Generalist climbing	---		72.56	< 0.001*	21.23	< 0.001*	57.82	< 0.001*	16.18	< 0.001*	49.14	< 0.001*

Literatura citada

- Alfaro-Juantorena, L.A. & Jiménez-Arcos, V.H., 2017. *Leiocephalus cubensis* (Cuban Curlytail Lizard). Sexual display behavior. *Herpetological Review*, 48(4), pp.2016–2017.
- Anderson, R.A. & Vitt, L.J., 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia*, 84, pp.145–157.
- Andersson, M., 1994. Sexual selection. *Princeton*.
- Andersson, M. & Simmons, L.W., 2006. Sexual selection and mate choice. *Trends in Ecology and Evolution*, 21(6), pp.296–302.
- Bell, E.L., Smith, H.M. & Chiszar, D.C., 2003. an Annotated List of the Species-Group Names Applied To the Lizard Genus *Sceloporus*. *Acta Zoologica Mexicana*, 174, pp.103–174.
- Blanckenhorn, W.U., Meier, R. & Teder, T., 2007. Rensch's rule in insects: patterns among and within species. In D. J. Fairbairn, W. U. Blanckenhorn, & T. Székely, eds. *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism*. Oxford, U.K.: Oxford Univ. Press, pp. 60–70.
- Bonduriansky, R., 2011. Sexual Selection and Conflict as Engines of Ecological Diversification. *The American Naturalist*, 178(6), pp.729–745.
- Braña, F., 1996. Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase? *Oikos*, 75(3), pp.511–523.
- Butler, M.A. & Losos, J.B., 2002. Multivariate sexual dimorphism, sexual selection, and adaptation in greater antillean *Anolis* lizards. *Ecological Monographs*, 72(4), pp.541–559.
- Butler, M., Schoener, T.W. & Losos, J.B., 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution*, 54(1), pp.259–272.
- Carpenter, C.C., 1978. Comparative Display Behavior in the genus *Sceloporus* (Iguanidae). *Contributions in Biology and Geology to the Milwaukee Public Museum*, (18), pp.1–71.
- Carpenter, C.C., Badham, J.A. & Kimble, B., 1970. Behavior Patterns of Three Species of *Amphibolurus* (Agamidae). *Copeia*, 1970(3), pp.497–505.
- Cornwallis, C.K. & Uller, T., 2010. Towards an evolutionary ecology of sexual traits. *Trends in Ecology and Evolution*, 25(3), pp.145–152.
- Cox, R.M., Butler, M.A. & John-Alder, H.B., 2007. The evolution of sexual size dimorphism in reptiles. In D. J. Fairbairn, W. U. Blanckenhorn, & T. Székely, eds.

- Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford, U.K.: Oxford Univ. Press.
- Cox, R.M., Skelly, S.L. & John-Alder, H.B., 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, 57(7), pp.1653–1669.
- Cueva del Castillo, R. & Fairbairn, D.J., 2011. Macroevolutionary patterns of bumblebee body size: detecting the interplay between natural and sexual selection. *Ecology and Evolution*, 2(1), pp.46–57.
- Darwin, C., 1871. *The Descent of Man, and Selection in Relation to Sex*, London, UK: John Murray.
- Fairbairn, D.J. 1997. Allometry for Sexual Size Dimorphism: Pattern and Process in the Coevolution of Body Size in Males and Females. *Annual Review of Ecology and Systematics*, 28(1997), pp.659–687.
- Fairbairn, D.J. 2013. *Odd Couples Extraordinary Differences between the Sexes in the Animal Kingdom*. Princeton, NJ, Princeton University Press.
- Fairbairn, D.J., Blanckenhorn, W.U. & Székely, T., 2007. *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism*, Oxford, U.K.: Oxford Univ. Press.
- Felsenstein, J., 1985. Phylogenies and the Comparative Method. *The American Naturalist*, 125(1), pp.1–15.
- Fitch, H.S., 1978. Sexual size differences in the genus *Sceloporus*. *University of Kansas Science Bulletin the University of Kansas Science Bulletin*, 51(13), pp.441–461.
- Fitch, H.S., 1985. Variation in clutch and litter size in new world reptiles. *Miscellaneous Publications of the Museum of Natural History of the University of Kansas*, 76, pp.1–76.
- Foellmer, M.W. & Moya-Laraño, J., 2007. Sexual size dimorphism in spiders: patterns and processes. In D. J. Fairbairn, W. U. Blanckenhorn, & T. Székely, eds. *Sex, size & gender roles. Evolutionary studies of sexual size dimorphism*. Oxford, U.K.: Oxford Univ. Press, pp. 38–49.
- Harvey, P.H. & Pagel, M.D., 1991. *The comparative method in evolutionary biology*, Oxford, U.K.: Oxford Series in Ecology and Evolution.
- Husak, J.F. & Fox, S.F., 2008. Sexual selection on locomotor performance. *Evolutionary Ecology Research*, 10(2), pp.213–228.
- Jones, A.G. & Ratterman, N.L., 2009. Mate choice and sexual selection: what have we learned since Darwin? *Proceedings of the National Academy of Sciences of the United States of America*, 106 Suppl, pp.10001–10008.
- Köhler, G. & Heimes, P., 2002. *Stachelleguane*, Germany: Herpeton Verlag.
- Kraaijeveld, K., Kraaijeveld-Smit, F.J.L. & Maan, M.E., 2011. Sexual selection and

- speciation: the comparative evidence revisited. *Biological Reviews*, 86, pp.367–377.
- Lambert, S.M. & Wiens, J.J., 2013. Evolution of viviparity: A phylogenetic test of the cold-climate hypothesis in phrynosomatid lizards. *Evolution*, 67(9), pp.2614–2630.
- Lappin, A.K., Brandt, Y. Husak, J.F., Macedonia, J.M. & Kemp, D.J. 2006. Gaping Displays Reveal and Amplify a Mechanically Based Index of Weapon Performance. *The American Naturalist*, 168(1), pp. 100-113.
- Leaché, A.D., Banbury, B.L., Linkem, C.W. & Nieto-Montes de Oca, A. 2016. Phylogenomics of a rapid radiation: is chromosomal evolution linked to increased diversification in north american spiny lizards (Genus *Sceloporus*)? *BMC evolutionary biology*, 16(1), p.63-74.
- Leaché, A.D., 2010. Species trees for spiny lizards (Genus *Sceloporus*): Identifying points of concordance and conflict between nuclear and mitochondrial data. *Molecular Phylogenetics and Evolution*, 54(1), pp.162–171.
- Losos, J.B., Butler, M. & Schoener, T.W., 2003. Sexual Dimorphism in Body Size and Shape in Relation to Habitat Use among Species of Caribbean *Anolis* Lizards. In S. Fox, J. McCoy, & T. Baird, eds. *Lizard Social Behavior*. Baltimore: Johns Hopkins Press, pp. 356–380.
- Maan, M.E. & Seehausen, O., 2011. Ecology, sexual selection and speciation. *Ecology Letters*, 14(6), pp.591–602.
- Martins, E.P., 1994. Phylogenetic perspectives on the Evolution of lizard territoriality. In L. J. Vitt & E. R. Pianka, eds. *Lizard ecology: Historical and experimental perspectives*. Princeton: Princeton University Press, pp. 117–144.
- Martins, E.P. & Hansen, T.F., 1997. Phylogenies and the comparative method a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist*, 149(4), pp.646–667.
- Méndez-de la Cruz, F.R., Villagrán-Santa Cruz, M. & Andrews, R.M., 1998. Evolution of Viviparity in the Lizard Genus *Sceloporus*. *Herpetologica*, 54(4), pp.521–532.
- Olsson, M., Shine R., Wapstra, E., Ujvari, B. & Madsen, T. 2002. Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution*, 56(7), pp.1538–1542.
- Panhuis, T.M., Butlin R., Zuk, M. & Tregenza, T. 2001. Sexual selection and speciation. *Trends in Ecology & Evolution*, 16(7), pp.364–371.
- Pincheira-Donoso, D., Hodgson, D.J. & Tregenza, T., 2008. The evolution of body size under environmental gradients in ectotherms: why should Bergmann’s rule apply to lizards? *BMC evolutionary biology*, 8, p.68.
- Pincheira-Donoso, D. & Hunt, J., 2015. Fecundity selection theory: Concepts and evidence. *Biological Reviews*, 2015, pp.1–16.

- Pincheira-Donoso, D. & Tregenza, T., 2011. Fecundity Selection and the Evolution of Reproductive Output and Sex-Specific Body Size in the *Liolaemus* Lizard Adaptive Radiation. *Evolutionary Biology*, 38(2), pp.197–207.
- Qualls, C.P. & Shine, R., 1995. Maternal body-volume as a constraint on reproductive output in lizards: evidence from the evolution of viviparity. *Oecologia*, 103(1995), pp.73–78.
- Rensch, B., 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner Zoologische Beiträge*, 1, pp.58–69.
- Rodríguez-Romero, F.J., Méndez-de la Cruz, F.R., Hernández-Gallegos, O. & Velázquez-Rodríguez, A.S. 2010. Fenología reproductora de alta montaña en dos especies de lacertilios emparentados (Squamata: Phrynosomatidae). In O. Hernández-Gallegos, F. R. Méndez-de la Cruz, & F. J. Méndez-Sánchez, eds. *Reproducción en reptiles: morfología, ecología y evolución*. Toluca: Universidad Autónoma del Estado de México, p. 169.
- Scharf, I. & Meiri, S., 2013. Sexual dimorphism of heads and abdomens: Different approaches to “being large” in female and male lizards. *Biological Journal of the Linnean Society*, pp.665–673.
- Scordato, E.S.C., Symes, L.B., Mendelson, T.C. & Safran, R.J. 2014. The role of ecology in speciation by sexual selection: A systematic empirical review. *Journal of Heredity*, 105(S1), pp.782–794.
- Serrano-Meneses, M.A. & Székely, T., 2006. Sexual size dimorphism in seabirds: Sexual selection, fecundity selection and differential niche-utilisation. *Oikos*, 113(3), pp.385–394.
- Shine, R., 1989. Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence. *The Quarterly Review of Biology*, 64(4), pp.419–461.
- Sites, J.W., Archie, J.W., Cole, C.J. & Flores-Villela, O. 1992. A Review of Phylogenetic Hypotheses for Lizards of the Genus *Sceloporus* (Phrynosomatidae) - Implications for Ecological and Evolutionary Studies. *Bulletin of the American Museum of Natural History*, (213), pp.1–110.
- Slatkin, M., 1984. Ecological Causes of Sexual Dimorphism. *Evolution*, 38(3), pp.622–630.
- Smith, H.M., 1939. The Mexican and Central American lizards of the genus *Sceloporus*. *Field Mus. Nat. Hist., Zool. Ser.*, 26(1–397).
- Stillwell, R., Blanckenhorn, W.U., Teder, T., Davidowitz, G. & Fox, C.W. 2010. Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: from physiology to evolution. *Annu Rev Entomol*, 55, pp.227–245.
- Stuart-Fox, D.M. & Ord, T.J., 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society B: Biological Sciences*, 271(1554), pp.2249–2255.

- Sun, Y.Y., Yu, D., Jing, Y., Tian-Bao, F. Chi-Xian, L. & Xiang, L. 2012. Is the Evolution of Viviparity Accompanied by a Relative Increase in Maternal Abdomen Size in Lizards? *Evolutionary Biology*, 39(3), pp.388–399.
- Watson, C.M., Makowsky, R. & Bagley, J.C., 2014. Reproductive mode evolution in lizards revisited: Updated analyses examining geographic, climatic and phylogenetic effects support the cold-climate hypothesis. *Journal of Evolutionary Biology*, 27(12), pp.2767–2780.
- Webb, T.J. & Freckleton, R.P., 2007. Only half right: Species with female-biased Sexual Size Dimorphism consistently break Rensch’s rule. *PLoS ONE*, 2(9).
- West-Eberhard, M.J., 1983. Sexual Selection, Social Competition, and Speciation. *The Quarterly review of biology*, 58(2), pp.155–183.
- Wiens, J.J., Kuczynski, C.A., Arif, S. & Reeder, T.W. 2010. Phylogenetic relationships of phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*. *Molecular Phylogenetics and Evolution*, 54(1), pp.150–161.
- Wiens, J.J., Reeder, T.W. & Nieto Montes de Oca, A., 1999. Molecular Phylogenetics and Evolution of Sexual Dichromatism among Populations of the Yarrow’s Spiny Lizard (*Sceloporus jarrovi*). *Evolution*, 53(6), pp.1884–1897.

Discusión y conclusiones generales

El dimorfismo sexual puede resultar del balance entre la selección natural y la selección sexual. Una vez que los efectos filogenéticos son controlados, nuestros resultados muestran un mayor impacto relativo de la selección sexual en la divergencia en talla en el género *Sceloporus* (Capítulo 1). La regla de Rensch se refiere al incremento en la magnitud del dimorfismo sexual a medida que aumenta la talla corporal promedio. Cuando la talla corporal es mayor en machos, la magnitud del dimorfismo sexual se incrementa. Cuando el dimorfismo en talla es sesgado a hembras, asociado a presiones de selección en fecundidad, se esperaría que la selección sexual reduzca la magnitud del dimorfismo sexual (Rensch 1950; Fairbairn 1997). En el caso de las lagartijas, se ha reportado que la selección intrasexual es la principal causa de dimorfismo sexual en talla sesgado a machos (Ord et al. 2001; Cox et al. 2003; Cox et al. 2007). Las peleas entre machos son comunes y ligadas a defensa de territorio y/o recursos, donde mayor tamaño puede incrementar la probabilidad de apareamiento (Lopez et al. 2002). En *Sceloporus*, la dominancia y comportamiento territorial son comunes en diversas especies del género, y la conducta de despliegue es ligada principalmente a enfrentamientos entre machos (Carpenter 1978; Martins 1993; Martins 1994). Aunque en lagartijas, y reptiles en general, los estudios en los que se analizan las preferencias femeninas son limitados (Ptacek 2000), la talla también puede ser sujeta a elección de pareja (Lappin et al. 2006), por lo que la selección intersexual puede estar involucrada en favorecer machos de mayor tamaño (Censky 1997). En cualquier caso, la historia evolutiva dentro del género *Sceloporus* sugiere un mayor rol diversificador de la selección sexual sobre la selección en fecundidad. Es importante recalcar que en este trabajo se exploró el patrón de dimorfismo sexual resultante de presiones de selección

natural (i.e. fecundidad) y sexual. Son necesarios estudios de experimentales y de selección que midan el impacto de ambas fuerzas sobre los rasgos fenotípicos analizados.

La selección en fecundidad favorece un incremento en cantidad y/o calidad de la nidada o camada en función de un aumento en el tamaño corporal de hembras (Darwin 1871; Cox et al. 2007; Pincheira-Donoso & Hunt 2015). Aun cuando el efecto de la selección en fecundidad sobre la evolución del dimorfismo en talla en *Sceloporus* es menor, puede explicar la evolución de la talla corporal femenina, tanto en especies ovíparas como vivíparas (Jiménez-Arcos et al. 2017). El que las especies con diferente modo reproductor dentro del género *Sceloporus* presenten tallas similares puede asociarse a la transición de la oviparidad a la viviparidad. Durante la transición de modo reproductor se ha sugerido que un prolongado periodo de retención uterino de los huevos es un paso inicial y transicional a la viviparidad (Shine 1985; Demarco 1993). Ambientes templados y áridos se han correlacionado con la capacidad de retención uterina en lagartijas (Méndez-de la Cruz et al. 1998; Calderón-Espinosa et al. 2006), especialmente en phrynosomatidos (Lambert & Wiens 2013). El género *Sceloporus* alcanza su mayor diversidad en las zonas áridas de México y Estados Unidos, así como las zonas templadas en el trópico de México (sistemas montañosos de México; Smith 1939; Sites et al. 1992; Wiens et al. 2013). Es probable que estos ambientes hayan favorecido la retención de huevos y un incremento global en la talla de las hembras de especies ovíparas. Esto podría potencialmente reducir las diferencias en talla en las hembras con diferente modo reproductor, independientemente del tiempo de gestación.

Actualmente tenemos un entendimiento profundo de como la selección natural y sexual moldean los atributos fenotípicos (Kraaijeveld et al. 2011; Maan & Seehausen 2011;

Safran et al. 2013; Scordato et al. 2014; Gomes et al. 2018). La divergencia entre sexos puede dar un indicio de diferencias en las fuerzas selectivas actuando sobre atributos fenotípicos (Bonduriansky & Day 2003; Bonduriansky 2007). No obstante, la interacción, balance e importancia relativa de ambas fuerzas genera interacciones complejas difíciles de explorar (Jones & Ratterman 2009; van Doorn et al. 2009; Network 2012; Gomes et al. 2018). *Sceloporus grammicus* (Capítulo 2) es un ejemplo de esta interacción, los resultados muestran como la magnitud del dimorfismo sexual puede cambiar en función del contexto ecológico, en rasgos sujetos a selección natural o sexual.

La diferencia en las pendientes alométricas de machos y hembras de la población arborícola de *S. grammicus* sugiere que la restricción de movimiento puede tener un impacto en la magnitud del dimorfismo sexual en extremidades, con machos presentando extremidades más largas que las hembras, lo cual puede ser resultado de selección sexual (Herrel et al. 2001; Herrel et al. 2002; Losos 2009). En las otras poblaciones, quizá perchas de mayor diámetro reducen las restricciones en movimiento y favorecen extremidades más largas en ambos sexos, patrón ecomorfológico documentado en diversas lagartijas (Losos 1990; Melville & Swain 2000; Herrel et al. 2001; Herrel et al. 2002; Stuart-Fox & Moussalli 2007; Da Silva & Tolley 2013). Solamente la longitud del tronco de hembras en la población generalista presentó una pendiente significativamente diferente de 1 (hiperalometría), lo que sugiere que quizá ocupar diferentes perchas y una menor restricción de movimiento a menor altura favorece un incremento general en la talla. La evidencia correlativa sugiere que algunos rasgos están bajo diferentes fuerzas selectivas con un efecto antagónico, como en lagartijas arborícolas (sobre tamaño de extremidades y cabeza en machos) o sinérgico (mayor longitud de tronco) en función del contexto

ecológico. Estudios experimentales y de selección son necesarios para determinar la contribución relativa de ambas fuerzas selectivas en la divergencia fenotípica.

Considerando los resultados de este trabajo en conjunto, la evolución del dimorfismo sexual a nivel de especies puede asociarse a la interacción entre la selección natural y sexual. A nivel interpoblacional, la divergencia fenotípica puede ser asociada a las condiciones ecológicas particulares de cada población, concordando con la teoría ecológica (Schluter 2001; Schoener 2011), pero la divergencia entre machos y hembras (i.e. dimorfismo sexual) es asociada a la interacción de la selección en fecundidad y sexual. Además, la reconstrucción de estados de carácter ancestral sugiere que a lo largo del tiempo evolutivo el patrón de dimorfismo sexual se origina desde el ancestro de *Sceloporus*.

El género *Sceloporus* exhibe la mayor riqueza de especies en México y es actualmente el género de vertebrados terrestres más diverso en nuestro país. Prácticamente es encontrado en todos los tipos de vegetación. Su gran diversidad morfológica, ecológica y conductual sugieren que la selección natural y sexual han tenido un papel central en la divergencia fenotípica. Patrones similares de diversidad fenotípica han sido reportados para los géneros *Anolis* (Losos 2009) y *Liolaemus* (Pincheira-Donoso et al. 2015), ambos grupos de lagartijas considerados como ejemplos de radiación adaptativa. Es probable que *Sceloporus* represente también un ejemplo de una radiación adaptativa (Sites et al. 1992; Wiens et al. 2010; Leache et al. 2016). Sin embargo, aún resta información por ser obtenida. Durante el desarrollo de esta tesis, notamos que elementos básicos de historia natural, ecología y reproducción son desconocidos, especialmente en especies con distribución limitada a México. Estudios futuros deben encaminarse en obtener información de historia natural, fuente de cualquier hipótesis en evolución y ecología (Endler 2015).

Estudios experimentales evaluando la significancia adaptativa de los rasgos fenotípicos, tanto por selección natural, sexual y diferentes condiciones ecológicas son necesarios para determinar los mecanismos que han conducido la divergencia y diversificación del género de vertebrados terrestres más diverso de México.

Literatura citada

- Bonduriansky, R. & Day, T., 2003. The evolution of static allometry in sexually selected traits. *Evolution*, 57(11), pp.2450–2458.
- Bonduriansky, R., 2007. Sexual selection and allometry: A critical reappraisal of the evidence and ideas. *Evolution*, 61(4), pp.838–849.
- Calderón-Espinosa, M.L., Andrews, R.M. & Méndez de la Cruz, F.R., 2006. Evolution of Egg Retention in the *Sceloporus spinosus* Group: Exploring the Role of Physiological, Environmental, and Phylogenetic Factors. *Herpetological Monographs*, 20, p.147.
- Carpenter, C.C., 1978. Comparative Display Behavior in the genus *Sceloporus* (Iguanidae). *Contributions in Biology and Geology to the Milwaukee Public Museum*, (18), pp.1–71.
- Censky, E.J., 1997. Female mate choice in the non-territorial lizard *Ameiva plei* (Teiidae). *Behavioral Ecology and Sociobiology*, 40(4), pp.221–225.
- Cox, R.M., Butler, M.A. & John-Alder, H.B., 2007. The evolution of sexual size dimorphism in reptiles. In D. J. Fairbairn, W. U. Blanckenhorn, & T. Székely, eds. *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford, U.K.: Oxford Univ. Press.
- Cox, R.M., Skelly, S.L. & John-Alder, H.B., 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, 57(7), pp.1653–1669.
- Da Silva, J.M. & Tolley, K.A., 2013. Ecomorphological variation and sexual dimorphism in a recent radiation of dwarf chameleons (*Bradypodion*). *Biological Journal of the Linnean Society*, 109(1), pp.113–130.
- Darwin, C., 1871. *The Descent of Man, and Selection in Relation to Sex*, London, UK: John Murray.
- Demarco, V., 1993. Estimating Egg Retention Times in Sceloporine Lizards. *Journal of Herpetology*, 27(4), pp.453–458.
- Endler, J.A. 2015. Writing scientific papers, with special reference to *Evolutionary Ecology*. *Evolutionary Ecology*, 29(4): pp. 465-478.
- Fairbairn, D.J., 1997. Allometry for Sexual Size Dimorphism: Pattern and Process in the Coevolution of Body Size in Males and Females. *Annual Review of Ecology and Systematics*, 28(1997), pp.659–687.
- Gomes, V., Carretero, M.A. & Kaliontzopoulou, A., 2018. Run for your life, but bite for your rights? How interactions between natural and sexual selection shape functional morphology across habitats. *Science of Nature*, 105(1–2).
- Herrel, A., Meyers, J.J. & Vanhooydonck, B., 2001. Correlations between habitat use and

- body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biological Journal of the Linnean Society*, 74(April), pp.305–314.
- Herrel, A., Meyers, J.J. & Vanhooydonck, B., 2002. Relations between microhabitat use and limb shape in phrynosomatid lizards. *Biological Journal of the Linnean Society*, 77(1), pp.149–163.
- Jiménez-Arcos, V.H., Sanabria-Urbán, O.S. & Cueva del Castillo, R. 2017. The interplay between natural and sexual selection in the evolution of sexual size dimorphism in *Sceloporus* lizards (Squamata: Phrynosomatidae). *Ecology and Evolution*. 7: 905-917.
- Jones, A.G. & Ratterman, N.L., 2009. Mate choice and sexual selection: what have we learned since Darwin? *Proceedings of the National Academy of Sciences of the United States of America*, 106 Suppl, pp.10001–10008.
- Lambert, S.M. & Wiens, J.J., 2013. Evolution of viviparity: A phylogenetic test of the cold-climate hypothesis in phrynosomatid lizards. *Evolution*, 67(9), pp.2614–2630.
- Lappin, A.K., Brandt, Y. Husak, J.F., Macedonia, J.M. & Kemp, D.J. 2006. Gaping Displays Reveal and Amplify a Mechanically Based Index of Weapon Performance. *The American Naturalist*, 168(1), pp. 100-113.
- Leaché, A.D., Banbury, B.L., Linkem, C.W. & Nieto-Montes de Oca, A. 2016. Phylogenomics of a rapid radiation: is chromosomal evolution linked to increased diversification in north american spiny lizards (Genus *Sceloporus*)? *BMC evolutionary biology*, 16(1), p.63-74.
- Lopez, P., Muñoz, A. & Martin, J., 2002. Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. *Behavioral Ecology and Sociobiology*, 52(4), pp.342–347.
- Losos, J.B., 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs*, 60(3), pp.369–388.
- Losos, J.B., 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*, Berkley, USA: University of California Press.
- Maan, M.E. & Seehausen, O., 2011. Ecology, sexual selection and speciation. *Ecology Letters*, 14(6), pp.591–602.
- Martins, E.P., 1993. A comparative study of the evolution of *Sceloporus* push-up displays. *The American Naturalist*, 142(6), pp.994–1018.
- Martins, E.P., 1994. Phylogenetic perspectives on the Evolution of lizard territoriality. In L. J. Vitt & E. R. Pianka, eds. *Lizard ecology: Historical and experimental perspectives*. Princeton: Princeton University Press, pp. 117–144.
- Melville, J. & Swain, R., 2000. Evolutionary Relationships Between Morphology, Performance and Habitat Openness in the Lizard Genus *Niveoscincus* (Scincidae: Lygosominae). *Biological Journal of the Linnean Society*, 70(4), pp.667–683.

- Méndez-de la Cruz, F.R., Villagrán-Santa Cruz, M. & Andrews, R.M., 1998. Evolution of Viviparity in the Lizard Genus *Sceloporus*. *Herpetologica*, 54(4), pp.521–532.
- Network, T.M.C.S., 2012. What do we need to know about speciation? *Trends in Ecology and Evolution*, 27(1), pp.27–39.
- Ord, T.J., Blumstein, D.T. & Evans, C.S., 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of Biological Sciences*, 268(1468), pp.737–744.
- Pincheira-Donoso, D. & Hunt, J., 2015. Fecundity selection theory: Concepts and evidence. *Biological Reviews*, 2015, pp.1–16.
- Ptacek, M.B., 2000. The role of mating preferences in shaping interspecific divergence in mating signals in vertebrates. *Behavioural Processes*, 51(1–3), pp.111–134.
- Rensch, B., 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner Zoologische Beiträge*, 1, pp.58–69.
- Safran, R.J., Scordato, E.S.C., Symes, L.B., Rodríguez, R.L. & Mendelson, T.C. 2013. Contributions of natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. *Trends in Ecology and Evolution*, 28(11), pp.643–650.
- Schoener, T.W. 2011. The Newest Synthesis: Understanding the Interplay of Evolutionary and Ecological Dynamics. *Science*, 331, pp.426–429.
- Schutler, D. 2001. Ecology and the origins of species. *Trends in Ecology and Evolution*, 16(7), pp.372–380.
- Scordato, E.S.C. et al., 2014. The role of ecology in speciation by sexual selection: A systematic empirical review. *Journal of Heredity*, 105(S1), pp.782–794.
- Shine, R., 1985. The evolution of viviparity in reptiles: an ecological analysis. In C. Gans & F. Billet, eds. *Biology of the Reptilia*. New York: Wiley.
- Sites, J.W. et al., 1992. A Review of Phylogenetic Hypotheses for Lizards of the Genus *Sceloporus* (Phrynosomatidae) - Implications for Ecological and Evolutionary Studies. *Bulletin of the American Museum of Natural History*, (213), pp.1–110.
- Smith, H.M., 1939. The Mexican and Central American lizards of the genus *Sceloporus*. *Field Mus. Nat. Hist., Zool. Ser.*, 26(1–397).
- Stuart-Fox, D. & Moussalli, A., 2007. Sex-specific ecomorphological variation and the evolution of sexual dimorphism in dwarf chameleons (*Bradypodion* spp.). *Journal of Evolutionary Biology*, 20(3), pp.1073–1081.
- van Doorn, S.G., Edelaar, P. & Weissing, F.J., 2009. On the Origin of Species by Natural and Sexual Selection. *Science*, 326(5960), pp.1704–1707.
- Wiens, J.J., Kuczynski, C.A., Arif, S. & Reeder, T.W. 2010. Phylogenetic relationships of

phrynosomatid lizards based on nuclear and mitochondrial data, and a revised phylogeny for *Sceloporus*. *Molecular Phylogenetics and Evolution*, 54(1), pp.150–161.

Wiens, J.J., Kozak, K.H. & Silva, N., 2013. Diversity and niche evolution along aridity gradients in north american lizards (Phrynosomatidae). *Evolution*, 67(6), pp.1715–1728.