Universidad Autónoma de Tlaxcala

Posgrado en Ciencias Biológicas

Influencia del ambiente térmico sobre la demografía y conducta de la lagartija *Sceloporus grammicus*.

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTOR EN CIENCIAS BIOLÓGICAS

Presenta

Miguel Adrián Domínguez Godoy

Codirectores

Aníbal Helios Díaz de la Vega Pérez
y
Robyn Elizabeth Hudson

Tlaxcala, Tlax. Enero, 2021

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PRESENTE

Los abajo firmantes, miembros del jurado evaluador del proyecto de tesis que **Miguel Adrián Domínguez Godoy** realiza para la obtención del grado de **Doctor en Ciencias Biológicas**, expresamos que, habiendo revisado la versión final del documento de tesis, damos la aprobación para que ésta sea impresa y defendida en el examen correspondiente. El título que llevará es **"Influencia del ambiente térmico sobre la demografía y conducta de la lagartija *Sceloporus grammicus*".**

Sin otro particular, aprovechamos para enviarle un cordial saludo.

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TLAXCALA, TLAX., NOVIEMBRE 30 DE 2020

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RESUMEN

La temperatura corporal es importante para todos los seres vivos, pues de ella dependen todos los procesos fisiológicos necesarios para su funcionamiento. A diferencia de los endotermos, los ectotermos son incapaces de generar calor por vías metabólicas, por lo tanto, dependen completamente de la temperatura ambiental para regular la temperatura corporal y realizar sus funciones vitales. En los reptiles existe un intervalo de temperatura corporal dentro del cual pueden llevar a cabo sus funciones biológicas y fisiológicas de manera óptima. Ya que la temperatura ambiental fluctúa espacial y temporalmente, los organismos recurren a la termorregulación (i.e., proceso por medio del cual, mantienen en homeostasis su temperatura corporal) para obtener la temperatura corporal adecuada y compensar las diferencias con la temperatura ambiental. A través del índice de calidad térmica es posible evaluar la magnitud de la discrepancia entre la temperatura ambiental disponible y la temperatura corporal preferida por los organismos. A medida que la calidad térmica del ambiente disminuye, se reduce el tiempo disponible para realizar otras tareas indispensables (i.e. defensa del territorio, conductas antidepredatorias, búsqueda de parejas, forrajeo). En esta tesis, estudié la asociación de la calidad térmica con la probabilidad de supervivencia, la presión de depredación y la conducta agresiva de *Sceloporus grammicus* en un gradiente altitudinal de alta montaña en donde la temperatura ambiental disminuye drásticamente. Encontré que la probabilidad de supervivencia aumenta a medida que la calidad térmica disminuye por la baja temperatura. Asimismo, observé que la presión de depredación es menor en el sitio más frío y elevado y que la conducta de agresividad de los organismos que habitan este sitio disminuye. *Sceloporus grammicus* posee diversas adaptaciones fisiológicas, morfológicas y conductuales que le permiten hacer frente a las condiciones de temperatura extremas que imperan en ambientes de alta montaña. En conjunto, estos resultados sugieren que la calidad térmica es un factor ecológico clave en la ecología de los reptiles ectotermos ya que nos permite interpretar los resultados con base en los requerimientos térmicos de las especies y a los costos asociados a la termorregulación.

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1. INTRODUCCIÓN

El termino ecología fue acuñado por Ernst Haeckel (1834-1919), quien lo definió como "la ciencia que estudia la relación entre los organismos y su ambiente” (Goodland, 1975). Sin embargo, la palabra ambiente es un término complejo con un amplio significado. De acuerdo con su raíz etimológica, el ambiente (del latín *ambiens* = que rodea) se puede entender como absolutamente todo lo que está alrededor de un organismo (i.e. la suma de factores bióticos y abióticos). Por lo tanto, estudiar el ambiente y su interacción con los seres vivos, es uno de los mayores retos en la biología (Green et al. 2005).

A pesar de las dificultades metodológicas, ha sido posible estudiar las variaciones asociadas con la disponibilidad de recursos y la duración de las condiciones ambientales (Hernández-Salinas et al. 2010). Por ejemplo, variaciones intraespecíficas en la morfología (Herrel et al. 2001; Bickel y Losos, 2002; Herrel et al. 2002) y en diferentes rasgos de historias de vida (e.g. fecundidad, tasa de crecimiento, edad a la reproducción, longevidad), han sido documentadas en invertebrados (Brown, 1985; Jackson y Moltschaniwskyj, 2002; Queirós et al. 2013), peces (Caselle et al. 2011; Herrera et al. 2016; Dunbrack y Green, 2017; Estlander et al. 2017), anfibios (Trenham et al. 2000; Morrison y Hero 2003), aves (Koenig, 1984; Sedinger et al. 1995; Dunn y Winkler, 2010), mamíferos (Ralls y Harvey, 1985; Sæther y Heim, 1993; Gilpatrick y Perryman, 2008; Sassi et al. 2018) y también en reptiles (Dunham, 1982; Wapstra y Swain, 2001; Mesquita y Colli, 2003; Angilletta et al. 2004; Ramírez-Bautista et al. 2011). Por otro lado, sabemos que las características bióticas (Graves y Duvall, 1995; Parrish y Eldestein-Keshet, 1999) y abióticas del ambiente (Venier y Fahring, 1996) determinan la distribución espacial de los organismos. La interacción con otros animales también repercute sobre la conducta de los individuos, por ejemplo, la presencia de depredadores potenciales influye sobre la territorialidad (Joshi et al. 1995), en la conducta antidepredatoria (Lima y Bednekoff, 1999) y el tamaño de grupo (Hill y Lee, 1998). Asimismo, la presencia de conespecíficos puede determinar el tamaño del ámbito hogareño (Dussault, 2005) y la territorialidad (Gray et al. 2002). De manera interesante, se ha encontrado que incluso el ambiente parental experimentado antes del nacimiento influye sobre la conducta de las crías a largo plazo, por ejemplo, la presencia de los padres es importante para el aprendizaje del canto en aves (Freeberg, 2004) y el ambiente experimentado por la madre durante la gestación altera la fisiología y conducta de las crías en mamíferos (Kaiser y Sachser, 1998).

Entre todos los factores ambientales que interactúan con los organismos, la temperatura es uno de los más importantes (Clarke et al. 2013). A medida que la temperatura ambiental y corporal incrementa, la energía cinética en las reacciones bioquímicas es mayor y acelera la tasa de los procesos metabólicos, por lo tanto, una temperatura adecuada, es imprescindible para llevar a cabo los procesos metabólicos que mantienen el crecimiento y la reproducción en todos los organismos (Gillooly et al. 2001). Existen límites térmicos, conocidos como temperaturas críticas mínimas (TC_{min}) y máximas (TC_{max}), por debajo y por encima de los cuales las funciones biológicas son afectadas negativamente, comprometiendo la supervivencia de los animales (Huey 1982; Black et al. 2019). En este sentido, para cada especie existe un intervalo de temperatura que maximiza la tasa de eficiencia de los procesos fisiológicos (i.e. T_{sel}: temperatura seleccionada; Hertz et al. 1993). Para mantener la temperatura corporal cerca de la T_{sel} y lejos de las temperaturas críticas los animales recurren a la termorregulación, que es un proceso por medio del cual mantienen en homeostasis su temperatura corporal (Angilletta, 2009). Este proceso difiere ampliamente entre los vertebrados y de acuerdo con las diferencias que presentan se pueden dividir en dos grandes grupos (Cowles 1962): endotermos, animales cuya temperatura corporal es determinada por el calor producido durante el metabolismo celular (e.g. algunos peces, mamíferos y aves) y ectotermos, animales cuya temperatura corporal es determinada por una fuente de calor externa (e.g. peces, anfibios y reptiles).

Debido a su incapacidad para generar calor metabólico, los organismos ectotermos, como los reptiles, muestran una mayor dependencia de fuentes externas de calor para realizar sus funciones fisiológicas y conductuales, por lo que la temperatura ambiental es un factor indispensable (Adolph y Porter, 1993; Avery et al. 1982). Para los reptiles, es importante controlar su temperatura corporal para regular la tasa de crecimiento (Pincheira-Donoso et al. 2008), la velocidad a la que se desarrollan los embriones, el éxito de eclosión (Du y Ji, 2003), la eficiencia digestiva (Harwood 1979; Chen et al. 2003) y el desempeño locomotor (Zajitschek et al. 2012) y en algunas especies para determinar el sexo de las crías (Ji et al. 2006). En condiciones ideales, cuando la temperatura ambiental se acerca a la T_{sel}, los costos de la termorregulación disminuyen (Hertz et al. 1993). Sin embargo, debido a que la temperatura ambiental varía espacial y temporalmente, los reptiles recurren a estrategias conductuales (e.g. selección de microhábitats adecuados, exposición al sol o a la sombra, ajustes posturales), mecanismos fisiológicos (e.g. ajustes en la frecuencia cardiaca, evapotranspiración) o morfológicos (e.g. reflectancia cutánea) para regular su temperatura corporal en ambientes térmicamente fluctuantes (Angilletta y Angilletta, 2009; Black et al. 2019).

Los costos de la termorregulación están determinados por la calidad térmica del ambiente, es decir, por el grado de discrepancia entre la temperatura operativa ambiental y la T_{sel} (Hertz et al. 1993). De acuerdo con el modelo costo-beneficio propuesto por Huey y Slatkin (1976), las lagartijas emplearán una estrategia termoconformista (i.e. la temperatura corporal cambia y es aproximadamente la misma que la del ambiente) cuando los costos de la termorregulación superen a los beneficios. No obstante, se ha encontrado que la mayoría de las lagartijas son termorreguladores activos a pesar de los costos de la termorregulación (Blouin-Demers y Nadeau, 2005; Besson y Cree, 2010). Sin embargo, se desconocen los efectos de la calidad térmica sobre distintos aspectos de la ecología de los reptiles, debido a que la mayoría de las investigaciones se han enfocado en estudiar el efecto de la temperatura, y otras variables ambientales, dejando de lado los requerimientos térmicos de las especies. En este sentido, el uso de variables ambientales en combinación con los requerimientos fisiológicos de las especies (e.g. calidad térmica) puede ser una herramienta útil para entender mejor la relación entre los organismos y su ambiente, particularmente en condiciones adversas. En esta tesis propongo una serie de hipótesis para probar el efecto de la calidad térmica del ambiente, sobre la probabilidad de supervivencia, la depredación y la conducta de *Sceloporus grammicus* en tres sitios con diferentes atributos térmicos, en un ambiente de alta montaña.

2. OBJETIVO

Evaluar el efecto de la calidad térmica sobre la supervivencia, la depredación y la conducta de *Sceloporus grammicus* en tres sitios con diferentes atributos térmicos, en un ambiente de alta montaña.

OBJETIVOS PARTICULARES

Capítulo 1 – Determinar si la exposición a ambientes con baja calidad térmica, por periodos cortos de tiempo, influye en la probabilidad de supervivencia de las lagartijas.

Capítulo 2 – Determinar si las presiones de depredación difieren entre tres poblaciones de *S. grammicus* que habitan a diferentes elevaciones en un sistema de alta montaña y si el morfotipo de color y el sexo, resultan en presiones de depredación diferencial.

Capítulo 3 – Determinar si existe una asociación entre la conducta agresiva de *S. grammicus* y la calidad térmica del sitio de procedencia.

3. HIPÓTESIS

Capítulo 1 – Habitar sitios con baja calidad térmica incrementa los costos de la termorregulación y las horas de restricción, por lo tanto, disminuye la probabilidad de supervivencia de los individuos.

Capítulo 2 – 1) Debido a la baja riqueza de depredadores potenciales a mayor elevación, existe una relación negativa entre las presiones de depredación y la elevación. 2) Existen presiones de depredación diferencial asociadas al morfotipo de color gular y al sexo, por lo tanto, los individuos más activos y conspicuos son más propensos a sufrir el ataque de un depredador, independientemente del sitio que habiten.

Capítulo 3 – El tiempo asignado a la conducta agresiva está comprometido con el tiempo dedicado a adquirir y mantener una temperatura corporal óptima, por lo tanto, los individuos procedentes de sitios con baja calidad térmica son menos agresivos.

4. ESPECIE DE ESTUDIO

Sceloporus grammicus, conocida como lagartija del Mesquite, es una lagartija de talla media, perteneciente a la familia Phrynosomatidae. Se distribuye en el sureste de Texas en EUA y desde Chihuahua a Oaxaca en México (Fig. 1), y es la lagartija de mayor distribución en México. Principalmente es una lagartija de hábitos arborícolas y saxícolas (i.e. vive en rocas). Habita en la mayoría de las regiones desérticas y montañosas del país (Hall 1973; Ramírez-Bautista et al. 2004), en bosques de pino, encino y junípero, y matorral xerófilo a elevaciones que van de los ~100 a los 4,400 msnm (Sites, 1982; Lemos-Espinal y Ballinger, 1995; Marshall et al. 2006), aunque también es común observarla en asentamientos urbanos.

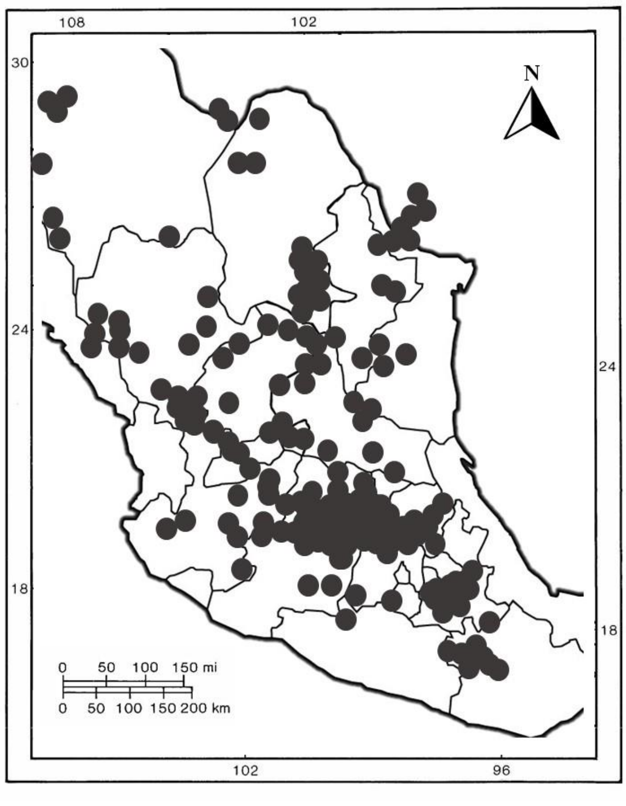

Fig. 1. Mapa de distribución de *Sceloporus grammicus*. Modificado de Sites et al. 1988.

Es una especie vivípara. La gametogénesis, el cortejo y el apareamiento ocurren en otoño, la gestación transcurre en invierno y los partos en primavera (Jiménez et al. 2005). Debido a su amplia distribución geográfica (altitudinal y latitudinalmente) y su presencia en una amplia gama de ambientes (desde conservados hasta zonas urbanas), exhiben una gran variación en sus patrones reproductivos entre poblaciones (Ramírez-Bautista et al. 2004; Jiménez et al. 2005; Ramírez-Bautista et al. 2009; Hernández-Salinas et al. 2010). Son lagartijas pequeñas y generalmente presentan dimorfismo sexual en su longitud hocico cloaca, con machos más grandes que las hembras (Ramírez-Bautista et al. 2004; Jiménez et al. 2005; Ramírez-Bautista et al. 2009). Dorsalmente son de color gris pálido con manchas oscuras que atraviesan toda su espalda hasta la cola, las hembras tienen el vientre de color blanco o anaranjado, mientras que los machos adultos exhiben un par de parches ventrales de color azul turquesa, ubicados a cada lado del abdomen (Dixon y Lemos-Espinal et al. 2010). Como en otras especies del género *Sceloporus*, esta lagartija presenta una característica pigmentación en las escamas gulares, que en esta especie pueden ser de color amarillo, anaranjado, gris o las combinaciones amarillo-gris, amarillo-anaranjado y anaranjado-gris (i.e. polimorfismo; Fig. 2), aunque en algunas poblaciones el morfotipo gris es sustituido por el color azul en los machos (Fig. 2; Bastiaans et al. 2013). Este atributo de color ha sido motivo de estudio, en esta (Bastiaans et al. 2013) y en otras especies (Sinervo y Lively, 1996; San-José et al. 2014), debido a su asociación con distintos rasgos conductuales y fisiológicos (McKinnon y Pierotti, 2010). Además, *S. grammicus* presenta una gran variabilidad cromosómica, con ocho razas cariotípicas (de 32 a 46 cromosomas en estado diploide), por lo que ha sido considerada como un ejemplo de especiación en progreso (Marshall et al. 2006).

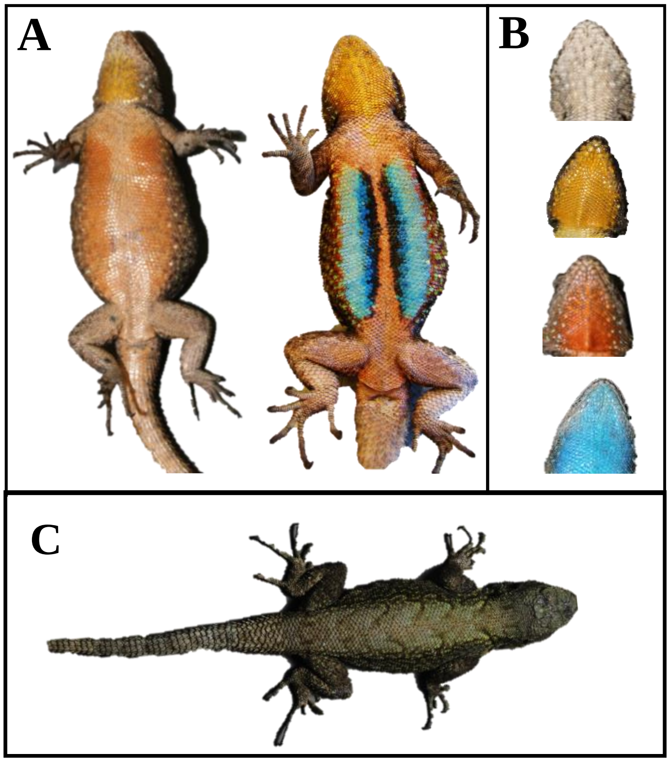

Fig. 2. Características morfológicas de *Sceloporus grammicus*. A) Comparación ventral entre una hembra (parches anaranjados) y un macho (parches azules) adultos. B) Representación de los diferentes morfotipos gulares. C) Vista dorsal de un individuo adulto.

5. SITIO DE ESTUDIO

El Parque Nacional La Malinche (PNLM), decretado como un área natural protegida desde 1938, es el quinto parque nacional de mayor extensión en el país, con una superficie total de 45 852.45 ha. Este parque está formado por un volcán inactivo, conocido como La Malinche, o Matlalcuéyetl, que significa “La de las faldas azules”. Se ubica en la zona central oriente de México y forma parte de la Faja Volcánica Transmexicana. Además de ser la quinta montaña más alta (4,460 msnm) del país, es parte importante de la biodiversidad del país (Fernández y López-Domínguez, 2005; Méndez de la Cruz et al. 2018), sin embargo, también es una de las zonas con mayor deforestación en la Faja Volcánica Trasmexicana (Espejel-Rodríguez et al. 2001).

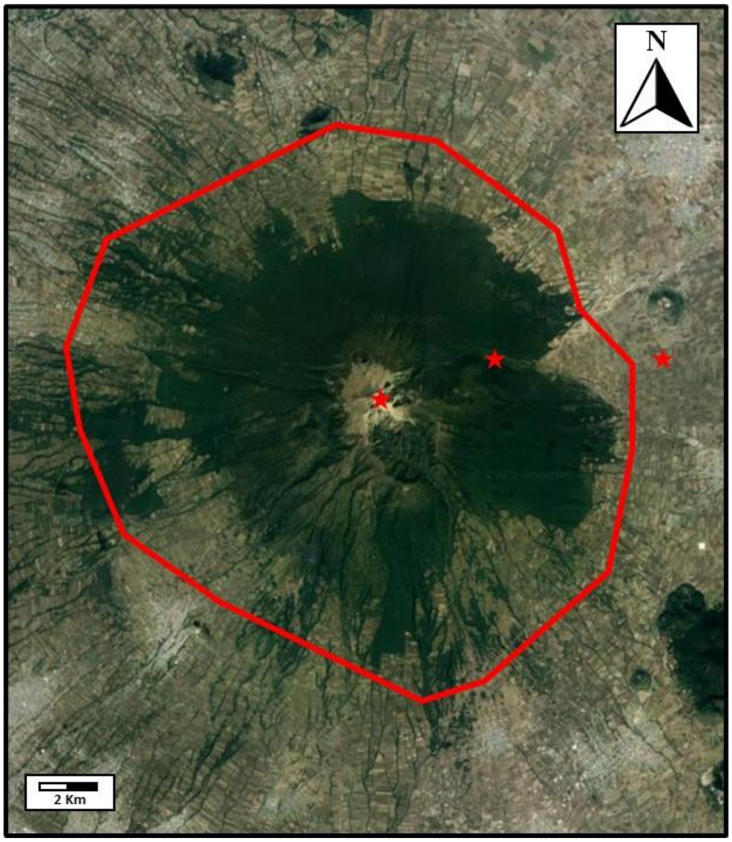

Fig. 3. Delimitación del polígono del Parque Nacional La Malinche. Las estrellas representan cada uno de los sitios delimitados para los muestreos. De izquierda a derecha: sitio más elevado (4150 msnm), sitio intermedio (3100 msnm) y sitio bajo (2600 msnm).

Para realizar estos estudios, se establecieron tres cuadrantes de muestreo, en tres elevaciones diferentes, en la ladera oeste del volcán La Malinche. El sitio de menor elevación (4.8 ha) se localizó a 2600 msnm (Lat: 19.2454, Lon: -97.9266; Datum WGS 84) en una ex-hacienda rodeada de campos de maíz, arbustos y pastizales (Fig. 4A). El sitio intermedio (4.7 ha) se localizó a 3100 msnm (Lat: 19.2596, Lon: -97.9796) en los alrededores de la Estación Científica de La Malinche. Este sitio está rodeado por bosque de coníferas (*Pinus montezumae* y *Abies religiosa*) y pastizales (Fig. 4B). Finalmente, el sitio de mayor elevación (4.9 ha) se localizó a 4150 msnm (Lat: 19.2401, Lon: -98.0344), y se caracteriza por su suelo rocoso, la ausencia de vegetación arbórea y por la presencia de pastos alpinos y algunos arbustos de *Juniperus monticola* (Fig. 4C) (Villers et al. 2006). La temperatura promedio disminuye significativamente al aumentar la elevación, por lo tanto, varía entre los sitios de estudio. La temperatura promedio (± D.E.) del sitio más bajo es de 13.20 ± 6.69 °C, mientras que en el sitio intermedio es de 9.31 ± 5.5 °C y la temperatura más baja se registró en el sito de mayor elevación 6.02 ± 4.7 °C. Asimismo, la humedad relativa varía entre las tres elevaciones. La humedad relativa es de 66.68 ± 22.09% en el sitio más bajo, de 77.25 ± 21.35% en el sitio intermedio, y de 67.74 ± 29.93% en el sitio de mayor elevación. Como resultado de las características topográficas, el tipo de vegetación y el descenso en la temperatura media ambiental, el índice de calidad térmica aumenta, lo que significa que la calidad térmica disminuye altitudinalmente, de 9.35 en el sitio a 2600 msnm, de 12.13 en el sitio a 3100 msnm y de 18.93 en el sitio de 4150 msnm (Díaz de la Vega-Pérez et al. 2019).

Fig. 4. Sitios de muestreo en el Parque Nacional La Malinche. A) 2600 msnm; B) 3100 msnm; C) 4150 msnm.

6. PRESENTACIÓN DE ESTUDIOS REALIZADOS

Para entender cómo el ambiente térmico influye, a través de las restricciones energéticas de la termorregulación, en la supervivencia y la conducta de *S. grammicus*, plantee tres estudios complementarios.

En el primer capítulo "Living on the edge: Lower thermal quality but greater survival probability at a high altitude mountain for the mesquite lizard (*Sceloporus grammicus*)" estudié el efecto de la calidad térmica sobre la probabilidad de supervivencia de *S. grammicus* en tres elevaciones diferentes. Encontré que la calidad térmica influye en la probabilidad de supervivencia de *S. grammicus*. Sin embargo, contario a nuestra predicción, la probabilidad de supervivencia aumentó a medida que la calidad térmica disminuía. En concreto, por cada unidad adicional de desviación en la oferta térmica ambiental, con respecto a la temperatura seleccionada por estas lagartijas, la supervivencia aumentó aproximadamente 1.01%. Las probabilidades de supervivencia variaron de 0.80 a 0.90 en el sitio de menor elevación (2600 msnm), de 0.76 a 0.87 en el sitio de elevación media (3100 msnm) y de 0.90 a 0.94 en el sitio de mayor elevación (4150 msnm). Estos resultados sugieren que, en ambientes de baja calidad térmica, la lagartija del mezquite emplea estrategias termorreguladoras (e.g. conductuales, fisiológicas y/o morfológicas) para disminuir su gasto metabólico y la exposición a los depredadores, maximizando la supervivencia. Estos hallazgos resaltan la relevancia de la calidad térmica del hábitat para determinar la probabilidad de supervivencia de los ectotermos.

En el capítulo 2 "Lower predation with increasing altitude in the mesquite lizard *Sceloporus grammicus*" evalué la presión de depredación sobre *S. grammicus* en los tres sitios de muestreo por medio de tres métodos complementarios: ataques en modelos de lagartija construidos con plastilina, la frecuencia de autotomía de la cola y la estimación de la riqueza de posibles depredadores. Encontré que la presión de depredación es menor en el sitio más elevado. Este hallazgo fue consistente entre nuestros tres métodos de evaluación. Ninguno de los modelos colocados en el sitio de mayor elevación presentó marcas relacionadas con un intento de depredación, a diferencia de los sitios más bajos. Asimismo, en el sitio de mayor elevación el número de lagartijas con autotomía fue menor, lo que coincide con el bajo número de depredadores potenciales observado. Una menor depredación a mayor elevación podría deberse al efecto combinado entre la baja riqueza de depredadores y una menor visibilidad de las lagartijas, debido al menor contraste con el sustrato y a una menor actividad locomotora, de forrajeo y de la conducta social, debido a la restricción térmica del sitio.

Finalmente, en el capítulo 3 "Too cool to fight: Males from low thermal quality environments are less aggressive" estudié las implicaciones conductuales ocasionadas por las restricciones térmicas del ambiente. Para analizar el efecto a largo plazo de la calidad térmica sobre el comportamiento agresivo de *S. grammicus* realicé confrontaciones agresivas entre machos de tres localidades con distinta calidad térmica. Encontré que las lagartijas del sitio con menor calidad térmica (i.e. el de menor temperatura) son menos agresivas (i.e. conductas agresivas de menor intensidad y menos frecuentes), en comparación con las lagartijas que habitan en los sitios con calidad térmica media y alta. Al mismo tiempo, observé que las lagartijas pasan más tiempo compartiendo la percha (i.e. el recurso por el que supuestamente compiten). Contrario a otros estudios, no encontré una asociación entre el color del morfotipo gular y la agresividad en ningún sitio. Los resultados sugieren que el comportamiento agresivo en ambientes de baja calidad térmica compite con la termorregulación. Mientras que la falta de asociación entre el color del morfotipo y la agresividad puede ser indicativo de otros atributos asociados al morfotipo, como estrategias para sobreponerse en ambientes extremos de alta montaña.

Considero que los trabajos próximos deberán enfocarse en determinar si las asociaciones observadas en estos estudios, entre la calidad térmica, la supervivencia y la agresividad, se mantienen en sistemas en donde la calidad térmica disminuye por un aumento en la temperatura ambiental. Del mismo modo, queda pendiente determinar los efectos de la calidad térmica en especies termoconformistas, en las cuales, los ambientes térmicos podrían tener distintas repercusiones. Por otro lado, se desconoce el papel que desempeñan los diferentes morfotipos de color, es decir, si existen estrategias conductuales o atributos fisiológicos asociados con la coloración gular en esta especie. Por lo cual, será importante continuar con estudios a largo plazo para conocer las dinámicas poblacionales y las posibles estrategias asociadas con cada morfotipo de color en esta especie, principalmente en ambientes térmicamente restrictivos.

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8. CAPÍTULO 1

Living on the edge: Lower thermal quality but greater survival probability at a high altitude mountain for the mesquite lizard (*Sceloporus grammicus*)

RESUMEN EN ESPAÑOL

El análisis de captura-recaptura de 20 meses, con 1,001 lagartijas del mezquite (*Sceloporus grammicus*) marcadas, sugiere que la variación en la calidad térmica en tres elevaciones influye en la probabilidad de supervivencia. Cada unidad adicional de desviación de la temperatura seleccionada por estas lagartijas en experimentos de laboratorio previos (i.e. disminución de la calidad térmica) significó un aumento de aproximadamente 1.01% en la probabilidad de supervivencia. Las probabilidades de supervivencia variaron de 0.80 a 0.90 en el sitio de menor elevación (2600 msnm), de 0.76 a 0.87 en el sitio de elevación medio (3100 msnm) y de 0.90 a 0.94 en el sitio de mayor elevación (4150 msnm). Estos resultados sugieren que, en ambientes de baja calidad térmica, las lagartijas del mezquite pueden emplear estrategias termorreguladoras (e.g. conductuales, fisiológicas y/o morfológicas) para disminuir su gasto metabólico y la exposición a los depredadores, maximizando la supervivencia. Estos hallazgos resaltan la relevancia de la calidad térmica del hábitat para determinar la probabilidad de supervivencia de los ectotermos.

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Living on the edge: Lower thermal quality but greater survival probability at a high altitude mountain for the mesquite lizard (*Sceloporus grammicus*)

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ABSTRACT

A 20-month recapture analysis of 1001 individually marked mesquite lizards (*Sceloporus grammicus*) suggests that variation in thermal quality across three altitudes influences survival probability. Each additional unit of deviation from the temperature selected by these lizards in previous laboratory experiments (i.e. decreased thermal quality) meant an increase of roughly 1.01% in survival probability. Survival probabilities ranged from 0.80 to 0.90 at the lowest elevation site (2600 m), from 0.76 to 0.87 at the middle elevation site (3100 m) and from 0.90 to 0.94 at the highest elevation site (4150 m). These results suggest that in poor thermal quality environments mesquite lizards may employ thermoregulatory strategies (behavioral, physiological and/or morphological) to decrease their metabolic expenditure and their exposure to predators, maximizing survival. These findings highlight the relevance of thermal quality of the habitat in determining survival probability of ectotherms.

1. Introduction

Temperature is one of the most important environmental factors for living organisms because it affects the kinetic activity of molecules and thus determines the biochemical processes necessary for the vital functions of organisms (Cossins and Bowler, 1987). Consequently, fitness of organisms will depend on their body temperature, as well as their ability to reach and maintain their temperature within an optimal range (Davenport, 2012). Physiological, morphological, behavioral and life history traits of ectotherms are strongly dependent on the ambient temperature, because their capacity to generate metabolic heat is practically null (Avery, 1982; Adolph and Porter, 1993).

All non-avian reptiles are ectotherms, and temperature regulates their embryonic development, hatching success and growth (Du and Ji, 2003; Pincheira et al., 2008). It also influences their digestive efficiency (Chen et al., 2003), locomotor performance (Zajitschek et al., 2012), thermoregulatory behavior (Myres and Eells, 1968), and often determines the sex of embryos (Ji et al., 2006), and possibly cognitive abilities in the early stages of development (Amiel et al., 2014). Therefore, the thermal environment (i.e. spatial-temporal distribution of thermal resources) is critical for the evolution of life histories in reptiles, and also for their fitness at individual and population levels (Adolph and Porter, 1993). In wide-spread species distributed across environments with differing temperatures, for example lizard species that occur along altitudinal gradients, the thermal environment may lead to changes in foraging behavior, territorial and sexual displays, or changes in mobility patterns across habitats (Lemos-Espinal and Ballinger, 1995a; Gvoždík, 2002). At the physiological level, the decrease in ambient temperature at higher altitudes may induce changes such as increased erythrocyte number and lower hematocrit level (González-Morales et al., 2017), diminished running performance (Van Damme et al., 1989), and increased melanin levels in integument structures in lizards (Reguera et al., 2014). Non-avian reptile life histories are also influenced by variation in the thermal environment the animals experience along

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altitudinal gradients, as colder temperatures at higher altitudes are associated with delayed sexual maturation and the production of smaller broods (Rohr, 1997). Importantly, changes in physiology, behavior, and life history traits associated with thermal variation can be adaptive in response to thermal stress (Angilletta, 2001; Jaramillo-Alba et al., 2020).

Non-avian reptiles need to maintain their body temperature within a specific temperature range in order to adequately accomplish necessary physiological processes and ecological activities (e.g. mating, feeding; Huey, 1982; Adolph and Porter, 1993; Meek, 1995). For lizards, however, thermoregulation is a time-consuming activity that is energetically costly because the energy and time needed for it may compromise the time or energy that otherwise can be devoted to foraging, acquiring and maintaining a territory, mating and to avoiding predators (McConnachie and Alexander, 2004). According to the cost-benefit model proposed by Huey and Slatkin (1976) for lizards, the thermal quality of the environment determines the costs of thermoregulation. Thermal quality is the degree of discrepancy between the temperatures available in a given environment and the body temperatures that animals prefer (Hertz et al., 1993). According to this model, if the cost associated with thermoregulating in a given environment is low, ectotherm reptiles will be thermoregulators (i. e. body temperature is maintained within a preferred temperature); if this cost is too high, then they will be thermoconformers (i.e. body temperature changes and is approximately equal to ambient temperature). Intriguingly, some lizards are not thermoconformers despite the high energetic costs or highly compromised time budgets that low thermal quality environments may impose (Blouin-Demers and Nadeau, 2005; Sears and Angilletta, 2015; Díaz de la Vega-Pérez et al., 2019). Unless these, reptiles buffer the costs of thermoregulating in low thermal quality environments by other physiological, behavioral, morphological or life history mechanisms, their fitness may be critically reduced. Buffering mechanisms, like the use of shelters, have been documented in some lizards that can mitigate survival costs of thermoregulation by reducing their activity times and thus their exposure to predators (Pianka and Pianka, 1970; Formanowicz et al., 1990). However, remaining in shelters for longer periods imposes fitness costs (Sinervo et al., 2010) by the reduction in opportunities to forage (Downes, 2001).

Survival costs of facing suboptimal environmental temperatures may have conservation implications in lizards of the genus *Sceloporus*, since predictive models suggest that this group may experience demographic collapse, and hence increased risk of extinction, if hours of restriction (i. e. hours with suboptimal environmental temperatures) are greater than 3.85 h during their reproductive period (Sinervo et al., 2010). However, it is still an open question to what extent exposure to low thermal quality environments (and its drivers, i.e. extremely low or extremely high temperatures) during short periods of time (e.g. months) influences survival of free-ranging lizards. In the present study we aim to help fill this gap in knowledge by estimating the influence of variation in thermal quality on survival probability of the mesquite lizard at three elevations on a mountainous ecosystem. The mesquite lizard (*Sceloporus grammicus*, Wiegmann, 1828) is a thigmothermic species (i.e. body temperature is closely correlated with substrate temperature) with narrow thermal preferences ($T_p = 30.1 \pm 4.6$ °C at 2600 m, 30 ± 4.5 °C at 3100 m and 31.1 ± 3.7 °C at 4150 m) in different environments (Díaz de la Vega-Pérez et al., 2019). Due to its wide altitudinal and latitudinal distribution, the mesquite lizard is a good model to study the effect of the thermal environment on survival. Earlier studies suggest that survival in mesquite lizards increases with altitude, as annual survival probability may be as low as 0.23 at lower elevations, in an oak-pine forest located at 2700 m (Ortega-Rubio et al., 1999), and increases to 0.41–0.68 at higher elevations, in a pine forest located at 3200 m (Zuñiga-Vega et al., 2008). In contrast, a study performed at higher elevations than the previous one in high mountain ecosystems (from 3700 to 4400 m) showed an inverse relationship between annual survival probability and elevation (Lemos-Espinal et al., 1998). Therefore, if there is a positive or negative relationship between altitude and survival in a mountainous ecosystem remains to be seen, as well as the underlying mechanisms that may explain altitudinal variation in survival probability in this species and other ectotherms.

We hypothesized that inhabiting sites with low thermal quality will increase the costs of thermoregulation and hours of restriction, limit metabolic function, and ultimately affect the survival chances of individuals. Specifically, we predicted a positive relationship between survival probability and thermal quality of the habitat, independent of the site. Accordingly, we expected that at higher elevations an increase in the number of hours with suboptimal temperatures (i.e. a higher number of hours of thermal restriction for lizards; Díaz de la Vega-Pérez et al., 2019), would result in lower survival probability, because to spend time in retreats for longer periods imposes fitness costs (Downes, 2001).

The mesquite lizard is the most widespread lizard species in Mexico, ranging from southeastern Texas in the USA to Oaxaca in Mexico (Sites et al., 1992; Lemos-Espinal and Ballinger, 1995a). Mesquite lizards are insectivorous and occur from ~100 to 4400 m above sea level (m a.s.l.) (Sites, 1982; Lemos-Espinal and Ballinger, 1995a; Marshall et al., 2006), and in a wide variety of habitats, from deserts and shrublands (e.g. xerophytic, crasicaule, submontane) to forests (e.g. pine, oak) and mountainous ecosystems at higher altitudes (Lemos-Espinal et al., 1998). It is an arboreal lizard, although it may be saxicolous depending on the landscape and other site conditions. Mesquite lizards are viviparous; gametogenesis, courtship, and mating occur in autumn, gestation takes place in winter, and parturition in spring (Pérez-Mendoza et al., 2013). This species shows great variation in growth times, for example, minimum size (snout-vent length) at sexual maturity ranges from 39 to 44 mm, mature individuals being smaller at high elevations (Lemos-Espinal and Ballinger, 1995b; Lemos-Espinal et al., 1998; Jiménez-Cruz et al., 2005).

2. Material and methods

2.1. Study sites

The study was conducted from January 2017 to August 2018 in La Malinche National Park, an inactive volcano located in the Mexican states of Tlaxcala and Puebla, covered by patches of coniferous (*Pinus* and *Abies*) and oak (*Quercus*) forest patches and grassland. We established three sites on the eastern slope of the volcano. The high elevation site (4.9 ha) was located at 4150 m a.s.l. (Lat: 19.2401, Lon: -98.0344; Datum WGS84) and was characterized by rocky alpine grassland and scattered shrubs of *Juniperus monticola* (Fig. 1a). The middle elevation site (4.7 ha) was located at 3100 m a.s.l. (Lat: 19.2596, Lon: -97.9796) around La Malinche Scientific Station. This site was mainly covered by coniferous trees (*Pinus montezumae* and *Abies religiosa*) and abundant bunchgrass (Fig. 1b). The low elevation site (4.8 ha) was located at 2600 m a.s.l. (Lat: 19.2454, Lon: -97.9266), where lizards inhabit an abandoned hacienda surrounded by maize fields, shrubs, and herbaceous plants (Fig. 1c) (Villers et al., 2006).

2.2. Field methods

2.2.1. Environmental and operative temperature

In order to characterize the thermal environment, we recorded both the air temperature and the relative humidity, as well as the operative temperature (T_o), that is, the predicted thermal equilibrium of non-regulating ectotherms (Hertz et al., 1993), at each of the sampling sites, from January 2017 to August 2018.

To estimate the average air temperature and relative humidity, we placed an environmental temperature/humidity recorder (data logger HOBO® Pro v2 U23-002) at each site, 150 cm from the ground at a typical perch site of the lizards in the shade, for the whole 20-month period. Additionally, following Hertz et al. (1993), we estimated the T_o at each site using biophysical models attached to two temperature recorders (HOBO® pro v2-U23-003). Each recorder was attached to two such sensors (i.e. thermocouples) installed inside biophysical models (i.

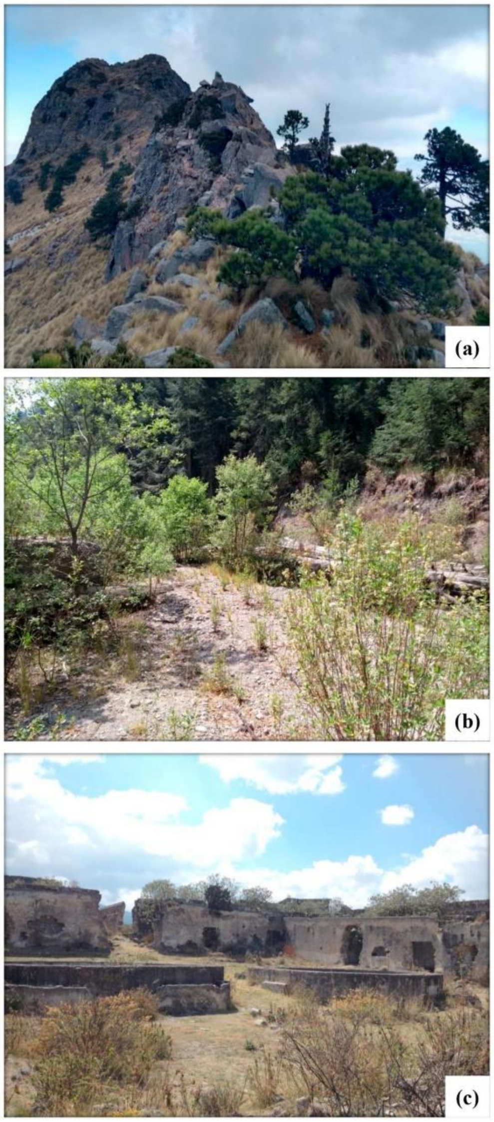

Fig. 1. Sampling sites in La Malinche National Park: a) 4150 m a.s.l., b) 3100 m a.s.l., c) 2600 m a.s.l.

e. four models by site). The biophysical models were pipes (7 cm long x 1.5 cm wide) of polyvinyl chloride (PVC), the ends of which were sealed with cork. Each model was painted with gray primer and calibrated following Lara-Reséndiz et al. (2014) and Díaz de la Vega-Pérez et al. (2019) (Fig. S1). We deployed each biophysical model at typical perch sites under different conditions of sun and shade used by lizards (i.e. rock walls and trees at 2600 m and at 3100 m, and among volcanic rocks and shrubs at 4150 m). We moved each model to different perch sites during the sampling period at least three times a year to increase the representativeness of the microhabitat. We recorded the T_o from the biophysical models over the whole 20-month period, every 30 min during the periods of activity reported for *S. grammicus* (Díaz de la Vega-Pérez et al., 2019) from 09:00 to 18:00 h at 2600 m, from 08:00 to 17:00 h at 3100 m, and from 10:00 to 18:00 h at 4150 m (Fig. S2).

2.2.2. *Lizard sampling*

From January 2017 to August 2018, three to four people visited each site every 60 days. In total, each site was sampled 11 times during the period of study. Each day, sampling took place during the activity period of the lizards. Immediately after capture we recorded the lizard's body temperature (T_b) in the cloaca, using a digital thermometer (Fluke 52 II). All lizards were captured by hand or using a noose. We recorded each capture site using a hand-held GPS unit (Garmin®, Oregon 360) in order to release the lizards where they were caught. We identified the sex of lizards according to the presence (in males) of enlarged post-cloacal scales and ventral blue patches. We used a numerical system for individual identification (Fig. S3) based on that proposed by Medica et al. (1971). We marked each lizard with an individual combination of small spots, made with a surgical cauterizer (Bovie Change-A-Tip® Del 1) over the limbs. We used this new marking method instead of toe clipping because it is a less invasive procedure (Ekner et al., 2011), and survival in this species may decrease due to toe clipping (Olivera-Tlahuel et al., 2017). After cauterization, we applied cicatrizing powder (Kwik Stop® Styptic Powder) to prevent infections. All lizards were released alive and in good condition at their capture sites after manipulation. Recaptures of marked individuals were also recorded at the three sites during all the 11 sampling occasions. Lizards were captured and manipulated with permission of the Secretaría de Medio Ambiente y Recursos Naturales (permit numbers SGPA/DGVS/15396/15 and SGPA/DGVS/007736/18). We followed all applicable institutional and national guidelines in Mexico for the care and use of animals.

2.3. *Sample sizes*

2.3.1. *Temperature records*

Across the 20-month study period, a total of 28,239, 28,898, and 22,026 environmental temperature/humidity records were obtained at the low, middle and high elevation sites, respectively. For the same period 41,454, 21,823, and 50,696 operative temperature records were obtained from the biophysical models installed at the low, middle and high elevation sites, respectively. The operative temperature data set was subsequently used to calculate the thermal quality indices (see *2.4*).

2.3.2. *Marked lizards*

Across the 11 sampling occasions, a total of 421, 242, and 338 captures were made of 298 (130 male and 168 female), 145 (60 male and 85 female), and 215 (101 male and 114 female) marked individuals, captured at the low, middle and high elevation sites, respectively. Subsequently, for each marked lizard, a catch history was generated, to be analyzed using the program MARK (see *2.5.2*).

2.4. *Computation of thermal quality index*

To assess the thermal quality of each site we used the procedure proposed by Hertz et al. (1993) to calculate an index of thermal quality (d_e) as the mean deviation of T_o from the inter-quartile range of the previously reported preferred body temperature for *S. grammicus* (T_{set} = IQR 28.1–33.3 °C at 2600 m, IQR 27.9–32.7 °C at 3100 m and IQR 29.6–33.5 °C at 4150 m; Díaz de la Vega-Pérez et al., 2019). To calculate d_e we used the equation: $d_e = T_{set}$ (low limit) - T_o when $T_o < T_{set}$, when $T_o > T_{set}$, then d_e was calculated as: $d_e = T_o$ - T_{set} (high limit). Additionally, to assess how well the lizards in each habitat deal with the variation in environmental quality, we calculated the thermal accuracy index (d_b) as the mean deviation of T_b from the inter-quartile range of the preferred body temperature, by means of the equation

$d_b = T_{set}$ (low limit) - T_b when $T_b < T_{set}$, when $T_b > T_{set}$, then d_b was calculated as: $d_b = T_b$ - T_{set} (high limit). Values of d_e and d_b far from zero indicate low thermal quality and accuracy (greater deviation from the mean temperature selected by lizards in laboratory trials), and values close to zero denote high thermal quality and accuracy for a given site (small deviation from the mean temperature experimentally selected by lizards; Hertz et al., 1993). It should be noted that the thermal quality of each site was estimated at 60-day intervals, that is, the time between sampling occasions. Thus, we obtained a total of 10 thermal quality indices for each site. In addition, for a better interpretation of the thermal quality index, we used the T_{set} and the non-lethal temperature thresholds (i.e. the thermal limits: CT_{min} = minimum critical temperature and CT_{max} = maximum critical temperature) estimated for mesquite lizards (Díaz de la Vega-Pérez et al., 2019). These thermal limits were used to determine the operative temperature distributed around the T_{set}, and therefore the degree to which the thermal quality index was influenced by operative temperatures lower than the CT_{min} or higher than the CT_{max}.

2.5. Data treatment and analysis

2.5.1. Thermal environment

To test for differences in air temperature, relative humidity and thermal quality among sites we used an Analysis of Variance (ANOVA), when data satisfied the requirements for parametric tests. Otherwise non-parametric Kruskal-Wallis tests were used. Post hoc pair-wise comparisons were implemented to test for significant differences between groups, using Tukey tests (parametric) or Dunn's tests (non-parametric), which included the Bonferroni correction for multiple comparisons. The significance value for all statistical tests was set at $p < 0.05$.

2.5.2. Capture-recapture analyses

To estimate lizard survival probability and recapture probability, we carried out a capture-recapture analysis. We analyzed the 20-month capture-recapture data using Cormack-Jolly-Seber models (Lebreton et al., 1992) as implemented using the program MARK (White and Burnham, 1999). We used a maximum-likelihood procedure and a multi-model inference approach to estimate two parameters: apparent survival (ϕ) and recapture rate (ρ). Apparent survival probability (ϕ) is the probability that a marked lizard that is in the population at time i is still alive and in the population at time i+1. This implies that true mortality and permanent emigration are confounded. The recapture probability (ρ) is defined as the probability of sighting a marked individual that is alive and in the population at time i (Lebreton et al., 1992). To avoid fitting an unnecessarily large number of models to the data, we first looked for the best parametrization for the recapture probability (ρ) following Lebreton et al. (1992) and Doherty et al. (2012). Using this procedure, we first tested different sources of variation for ρ (sex, site, time, and their additive and interactive effects) while maintaining the survival parameter varying across time, sites, and sexes. Because the thermal quality was estimated in the period prior to each sampling occasion (i.e. 60 days), we did not test for the effect of thermal quality on recapture rate. We selected the model that best fitted variation in ρ using the Akaike Information Criterion corrected for small sample sizes (AICc). A difference in the AICc scores between the top-ranked model and any given model larger than two AICc units (ΔAICc > 2) suggests a real difference between competing models in their fit to the data (Sugiura, 1978). In addition, we calculated w_i as an estimate of the relative support for each model and calculated weighted average estimates using the subset of the best-fitting models that, together, had a cumulative w_i of approximately 0.95 (Burnham and Anderson, 2004). A single model had strong support in our data with an Akaike weight (w_i) of 0.61 (Table 1). This top-ranked model considered variation in ρ across the three different sampling sites. The second best-fitting model differed by less than two AICc units from the top-ranked model and had weaker support in our data ($w_i = 0.34$; Table 1). The remaining models differed by more than two AICc units from the top-ranked model and thus had less support in our data ($w_i < 0.034$; Table 1). Adding the effect of sex in the second best-fitting model did not improve model fit, and therefore in all the subsequent models examining variation in ϕ we assumed among-site variation in ρ without distinguishing between males and females.

Table 1
Model selection results for the best parameterization of recapture probability (p) of mesquite lizards at three different sites located at 2600, 3100, and 4150 m a.s.l. in La Malinche National Park. Notations: AICc = Akaike information criterion adjusted for small sample sizes; ΔAICc = difference in the value of the AIC from the model having the lowest AIC; w_i = Akaike weight for each particular model and model deviance; K = number of parameters.

Model	AICc	ΔAICc	*wi*	K	Deviance
ϕ (Time*Site*Sex) p (Site)	2165.87	0	0.61	63	2030.35
ϕ (Time*Site*Sex) p (Site + Sex)	2167.00	1.13	0.34	64	2029.17
ϕ (Time*Site*Sex) p (Site*Sex)	2167.15	5.57	0.034	66	2029.14
ϕ (Time*Site*Sex) p (Site + Time)	2178.57	12.69	<0.001	72	2022.02
ϕ (Time*Site*Sex) p (Site + Sex + Time)	2180.93	15.06	<0.001	73	2022.02
ϕ (Time*Site*Sex) p (.)	2190.53	24.66	0	61	2059.63
ϕ (Time*Site*Sex) p (Sex)	2190.70	24.83	0	62	2057.49
ϕ (Time*Site*Sex) p (Time)	2200.25	34.38	0	70	2048.42
ϕ (Time*Site*Sex) p (Sex + Time)	2202.60	36.73	0	71	2048.42
ϕ (Time*Site*Sex) p (Site*Time)	2211.76	45.89	0	90	2011.79
ϕ (Time*Site*Sex) p (Sex*Time)	2224.05	58.18	0	80	2048.43
ϕ (Time*Site*Sex) p (Time*Site*Sex)	2288.96	123.09	0	120	2012.20

We then tested the potential impact of the thermal quality index (d_e) on survival probability, fitting competing linear models using the program MARK. We considered models in which ϕ varied as a function of sex, site and d_e, as well as the additive and the interactive effects of these variables on ϕ. In total, we fitted 12 competing models, including an intercept-only model (i.e. null model). We selected the model with the best fit to our data using the AICc and calculated weighted average estimates using the subset of the best-fitting models that, together, had a cumulative w_i of approximately 0.95 (Burnham and Anderson, 2004).

Because thermal quality experienced across the 20-month study period cannot account for all the temporal variation in survival, we also built a model that represented overall temporal variation in the survival probability across the three different sampling sites (i.e. reference model). This model included the interactive effect between sex, site and time affecting ϕ and, as in all previous models, the effect of site on ρ. Then, we used the F statistic proposed by Grosbois et al. (2008) to test whether the particular combination of explanatory variables selected by AICc accounted for a statistically significant proportion of the observed temporal variation in survival probability across all sampling sites. Furthermore, we calculated the proportion of the temporal variation in lizards' survival probability as estimated by our reference model that can be explained by the ecological covariates selected by AICc (i.e. the thermal quality and site). To do this, we used a measure of effect size based on the proportion of deviance explained by our top-ranked model (R^2_Dev; Grosbois et al., 2008). This quantity is equivalent to a coefficient of determination and estimates the importance of ecological covariates in eliciting temporal variation in survival. An R^2_Dev larger than 0.20 indicates that the explanatory variables selected by AICc are considered as influential (Grosbois et al., 2008).

3. Results

3.1. Thermal quality along the mountain ecosystem

The air temperature across the 20-month study period was statistically different among the three sampling sites (Kruskal-Wallis: $H_2 = 17500.75$, $p < 0.001$) being warmest at the low elevation site, intermediate at the middle elevation site, and coldest at the high elevation site (average ± SD temperatures: 13.20 ± 6.69 °C at 2600 m, 9.31 ± 5.5 °C at 3100 m, and 6.02 ± 4.7 °C at 4150 m). Relative humidity was also statistically different among the three sampling sites (Kruskal-Wallis: $H_2 = 2475.21$, $p < 0.001$), being higher at the middle elevation site, intermediate at the high elevation site, and low at the low elevation site (average ± SD relative humidity: 66.68 ± 22.09% at 2600 m, 77.25 ± 21.35% at 3100 m, and 67.74 ± 29.93% at 4150). Thermal quality was also significantly different among the three sites (ANOVA: $F_{2,27} = 118.65$, $p < 0.001$), being significantly lower at the high elevation site compared to the two other sites (average thermal quality ± CI at 95%, at 2600 m: 8.7 CI [7.44, 9.99 °C], at 3100 m: 11.04 CI [10.08, 12.01 °C], at 4150 m: 19.81 CI [18.85, 20.64 °C]). The degree of overlap between T_o and T_{set} was 10.9% at 2600 m and 8.5% at 3100 m, whereas at 4150 m, only 1% of the observed T_o overlapped with the T_{set}. Most operative temperatures recorded at the three sites were well below T_{set} (percentage of temperature values below T_{set} at 2600: 82.2%, at 3100: 83.2%, at 4150 m 96.2%). From all operative temperatures recorded at 2600, 3100, and 4150 m, 14.9%, 20.7%, and 51.8% were below the CT_{min}, whereas only 1.39%, 0.87%, and 1.5% were above the CT_{max}, respectively (Table 2 and Figs. 2 and 3). Similarly, d_b indexes were different among populations ($H_2 = 19.72$, $p < 0.001$; Table S1), thermal accuracy index was significantly lower at the high elevation site compared to the two other sites (median thermal accuracy index ± IQR at 2600 m: 0.83 IQR [0.71, 1.27], at 3100 m: 1.12 IQR [0.77, 1.57], at 4150 m: 5.15 IQR [3.58, 6.64]).

3.2. Survival probability

The average recapture probability ± SE was 0.18 ± 0.02 at 2600 m, 0.40 ± 0.04 at 3100 m, and 0.17 ± 0.02 at 4150 m (Fig. S4).

Thermal quality of the sites influenced lizard survival probability: survival probabilities increased as thermal quality decreased. Two models had statistical support in our data. The model including an additive effect of site and thermal quality on apparent survival was the top-ranked model and had a relative support of $w_i = 0.60$ (Table 3). The second best-fitting model included the additive effects of sex, site and thermal quality; this model differed by two AICc units from the top-ranked model and had weaker support in our data ($w_i = 0.22$; Table 3). All other tested models differed by more than four AICc units from the top-ranked model and thus had even less support in our data ($w_i < 0.08$; Table 3).

We estimated lizard survival probability over the 20-month sampling period (estimated from our best supported model; Table S2) and the expected association between thermal quality and survival at the three sites. According to the top-ranked model, survival probability was affected by thermal quality. As thermal quality decreased, lizard survival probability increased. Each additional unit of deviation from the selected temperature for these lizards (i.e. decreased thermal quality) meant an increase of roughly 1.01% in survival probabilities (Fig. 2). Altitudinally, survival probability ranged from 0.80 to 0.90 at the lowest elevation site (2600 m), from 0.76 to 0.87 at the middle elevation site (3100 m) and from 0.90 to 0.94 at the highest elevation site (4150 m). The highest elevation site thus presented the highest survival probability, while the middle elevation site presented the lowest (Fig. 2). The additive effect of site and thermal quality was statistically significant ($F_{3,8} = 6.45$, $p < 0.001$), and explained roughly 42% of the total within-site temporal variation in survival probability (R^2_Dev = 0.42).

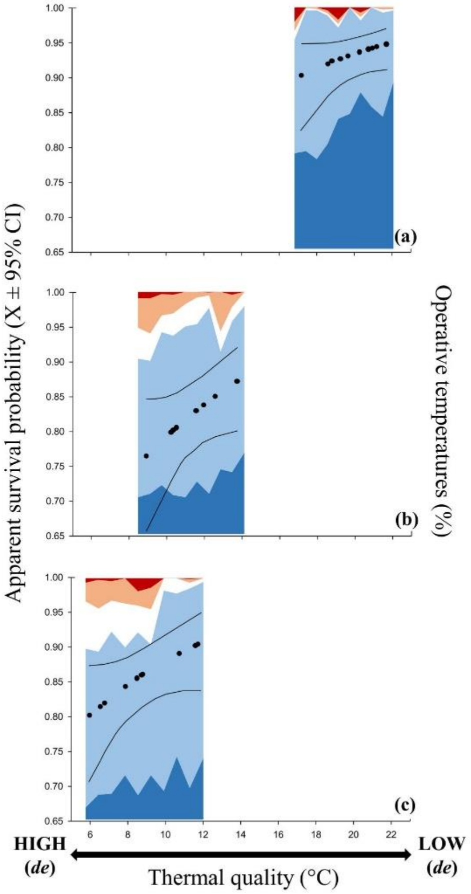

Fig. 2. Apparent survival probability estimated at three different elevations. Points represent estimated relationships between survival and thermal quality. The shaded areas indicate the percentage of operative temperature between sampling occasions. White represents the safety area (T_{set} = no thermoregulatory effort). Red and blue represent temperatures higher and lower than the T_{set}, respectively; dark shading represents temperatures beyond the critical maximum and minimum. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Average percentage of T_o lower than the CT_{min} ($<CT_{min}$), temperatures between the CT_{min} and T_{set} ($<T>$), within the selected temperature (T_{set}), temperatures between the T_{set} and CT_{max} ($>T<$) and higher than CT_{max} ($>CT_{max}$).

Site m a.s.l.	$< CT_{min}$	$< T >$	T_{set}	$> T <$	$> CT_{max}$
2600	14.92	67.23	10.95	5.48	1.39
3100	20.78	62.45	8.51	7.36	0.87
4150	51.8	44.44	1.07	1.16	1.5

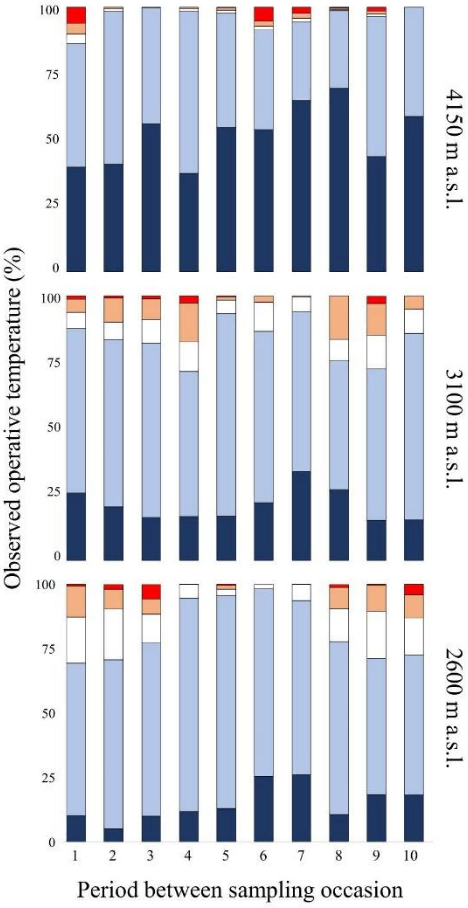

Fig. 3. Percentage of operative temperature between sampling periods. The shaded areas indicate the percentage of operative temperature between sampling occasions. White represents the safety area (T_{set} = no thermoregulatory effort). Red and blue represent temperatures higher and lower than the T_{set}, respectively; dark shading represents temperatures beyond the critical maximum and minimum. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

This study reports two main results. First, thermal quality and survival probability of mesquite lizards varied across three sites located at different altitudes across a mountain terrain. Thermal quality was lowest at the high elevation site, intermediate at the middle elevation site and high at the lowest elevation site. However, the lowest survival probability was recorded at the middle elevation site and the highest survival probability was recorded at the high elevation site. Second, irrespective of the site, survival probability increased as thermal quality decreased.

Contrary to our prediction, the survival probability of lizards was higher at the high elevation site where thermal quality was lower, and at all the three sites, survival probability increased as the thermal quality decreased. This result suggests that regardless of the particularities of each site, such as elevation, type of vegetation, environmental temperature, potential predators, and availability of food and shelter, thermal quality had a similar impact on lizard survival. We therefore conclude that thermal quality is a key ecological factor that may operate similarly at different spatial scales and strongly influences population dynamics of ectotherms.

Table 3
Model selection results for the best parameterization of survival probability of mesquite lizards at three different sites located at 2600, 3100, and 4150 m a.s.l. in La Malinche National Park. Notations: AICc = Akaike information criterion adjusted for small sample sizes; ΔAICc = difference in the value of the AIC from the model having the lowest AIC; w_i = Akaike weight for each particular model and model deviance; K = number of parameters.

Model	AICc	ΔAICc	w_i	K	Deviance
ϕ (Site + d_e) p (Site)	2086.2	0	0.60	7	2072.08
ϕ (Site + Sex + d_e) p (Site)	2088.2	2.0	0.22	8	2072.08
ϕ (Site*d_e) p (Site)	2090.2	4.0	0.081	9	2072.03
ϕ (d_e) p (Site)	2090.7	4.6	0.059	5	2080.78
ϕ (Sex + d_e) p (Site)	2090.7	6.6	0.021	6	2080.78
ϕ (Sex*d_e) p (Site)	2094.7	8.7	0.008	7	2080.78
ϕ (Site*Sex*d_e) p (Site)	2102.5	16.3	<0.001	15	2072.03
ϕ (Site) p (Site)	2253.7	167.5	<0.001	6	2076.07
ϕ (Site + Sex) p (Site)	2255.8	169.6	<0.001	7	2076.07
ϕ (Site*Sex) p (Site)	2259.8	173.6	<0.001	9	2076.07
ϕ (Sex) p (Site)	2278.0	191.8	<0.001	5	2100.39
ϕ (.) p (Site) *Null model*	2278.9	192.7	<0.001	4	2103.17
ϕ (Site*Sex*Time) p (Site) *Reference model*	2165.87	0	0	63	2030.35

Higher survival probability at the high elevation site where thermal quality was lower may have been due (at least partially) to a decreased predation probability (Domínguez-Godoy et al., in press) and an increase in the hours of restriction due to low temperatures and the consequent reduction in lizards' activity. As thermal quality decreases, costs of thermoregulation are expected to increase (DeWitt, 1967; Huey and Slatkin, 1976), and thus lizards may be forced to spend longer periods of time inside thermal retreats, which has been shown to impose fitness costs (Downes, 2001). Nonetheless, time spent in shelters during hours of thermal restriction due to low temperature may help to increase survival probability through 1) reduced exposure to predators (Pianka and Pianka, 1970; Formanowicz et al., 1990; Domínguez-Godoy et al., in press), and 2) reduced metabolic expenditure (Steffen and Appel, 2012), as effective strategies to cope with thermally-stressing environments (Andersson et al., 2010; Martín and López, 2010; Scheffers et al., 2014) that may favor survival (Martín et al., 2003; Souter et al., 2004; Amo et al., 2007). Additionally, the high probability of survival, coupled with a high population density (see A1 and Table S3), suggests that the high elevation site presents suitable conditions for *S. grammicus* (Eaton et al., 2002).

Our results suggest that coping with low thermal quality can have different costs, depending on the temperature that restricts the activity of the lizards. At the physiological level, body temperature, even at rest, relates positively with oxygen consumption, respiratory rate (Piercy et al., 2015), heart rate (Gatten, 1974), digestive efficiency (Harwood, 1979), and water loss (Dmi'el, 1972). Therefore, as the cost of body maintenance can compromise part of the energy budget (Congdon et al., 1982), the exposure to environmental temperatures higher than preferred body temperatures translates into impaired embryonic development (Du and Ji, 2003), accelerated telomere shortening (Zhang et al., 2018) and reduced survival (Sinervo et al., 2010). Meanwhile, lower metabolic rates at lower temperatures may explain why survival probability can be greater where thermal quality is lower due to low temperatures (Dmi'el, 1972; Piercy et al., 2015).

Despite the low thermal quality, the thermal accuracy index suggests that mesquite lizards inhabiting higher elevations exhibit characteristics that may aid them in coping with low temperatures. These include smaller body sizes (Díaz de la Vega-Pérez et al., 2019) and higher dorsal melanism (Clusella-Trullas et al., 2009; Díaz de la Vega-Pérez et al., unpublished data) that may help them to increase heating rates (Ashton and Feldman, 2003), as well as decreased activity, e.g. reduced behavioral displays and reduced food consumption (Marquet et al., 1989; Lemos-Espinal and Ballinger, 1995a; Zamora-Camacho et al., 2013), enabling them to heat up faster, thereby decreasing basking time. Additionally, they maintain higher resting metabolic rates (Plasman et al., 2020) that may help them to faster recovery from extreme low temperatures (Williams et al., 2016), and to be active at lower temperatures (Berg et al., 2017). We suggest these characteristics may promote survival of mesquite lizards at higher altitudes and thus may be considered as strategies to cope with the associated low thermal quality.

Our findings are consistent with earlier studies that reported a positive relationship between the probability of survival and elevation, and where the authors also attributed this to a decrease in predation pressure at higher altitudes (Adolph and Porter, 1993). However, some previous studies in *S. grammicus* carried out at similar elevations (3700 and 4400 m) to those analyzed here, have reported that survival tends to be higher at lower elevations compared to higher elevations (Lemos-Espinal et al., 1998). These contrasting results may be partially explained by the toe clipping method because it has negative effects on survival (Olivera-Tlahuel et al., 2017) and can have a different effect depending on the environment the animals inhabit (Herrel, 2002). Together with our results, these studies suggest that lizards with warmer thermal preferences that inhabit cooler, higher elevations are subject to strong thermal and energy restriction, with behavioral and life history consequences, as has been documented in this and other lizard species (Shine, 2005; Pérez-Mendoza and Zúñiga-Vega, 2014).

Despite the behavioral (Andrews et al., 1997; López and Martín, 2002) and ecophysiological (Shine, 1980) variations between males and females that could imply differential survival costs, our results suggest that the impact of thermal quality and site on survival probability do not differ between the sexes. Our results are consistent with previous reports showing that some populations of *S. grammicus* do not exhibit sexual differences in survival (Pérez-Mendoza et al., 2013, 2014). The absence of sex differences in the impact of thermal quality and altitude on survival probability could be explained, at least in part, by the absence of sex differences in predation probabilities (Schwarzkopf and Shine, 1992; Domínguez-Godoy et al., in press).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2020.102757.

Credit author statement

Aníbal Díaz de la Vega-Pérez: Writing- Reviewing and Editing, Conceptualization, Funding acquisition, Methodology. Miguel Domínguez-Godoy: Writing- Reviewing and Editing, Conceptualization, Formal analysis, Investigation, Funding acquisition, Methodology. Sergio Ancona: Writing- Reviewing and Editing, Conceptualization. Robyn Hudson: Writing- Reviewing and Editing, Conceptualization. Hibrahim Pérez-Mendoza: Writing- Reviewing and Editing, Conceptualization.

Author contributions

MD, AD and SA originally formulated the idea. MD and AD developed methodology and conducted the fieldwork. MD analyzed the thermal data and conducted the capture-recapture analysis. MD, AD, SA, RH and HP wrote the manuscript.

Declarations of competing interest

The authors declare no conflict of interests.

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SUPPLEMENTARY MATERIAL

Fig. S1. Pair of biophysical models (7 cm long x 1.5 cm wide) attached to temperature recorders (HOBO ® pro v2-U23-003): a) Temperature recorders with two sensors, installed inside biophysical models; b) biophysical models installed in situ, one exposed and one inside the rocks.

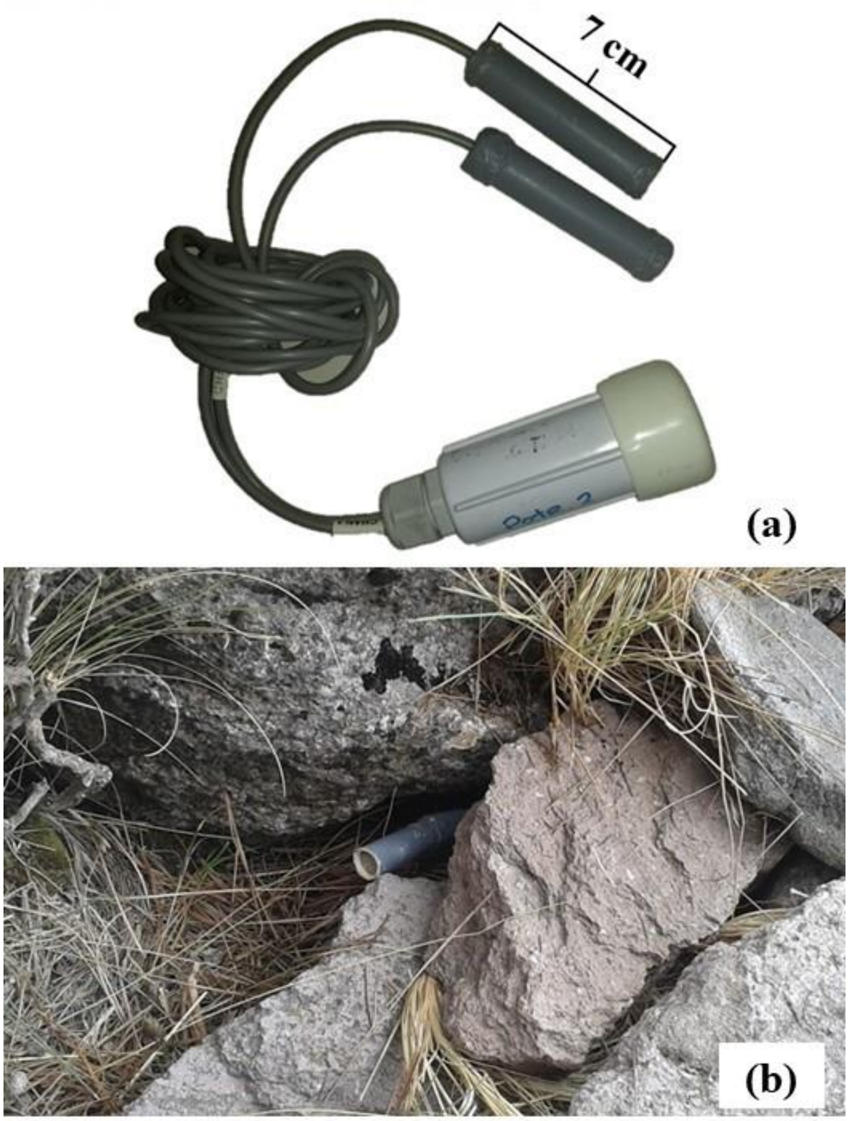

Fig. S2. Average monthly operative temperature (± SD) for two different years of capture/recapture study, by elevation (c: 2,600, b: 3,100 and a: 4,150 m a.s.l.). Dashed lines represent the upper (CT_{max}) and lower (CT_{min}) critical thermal limits. Red line represents the T_{set}

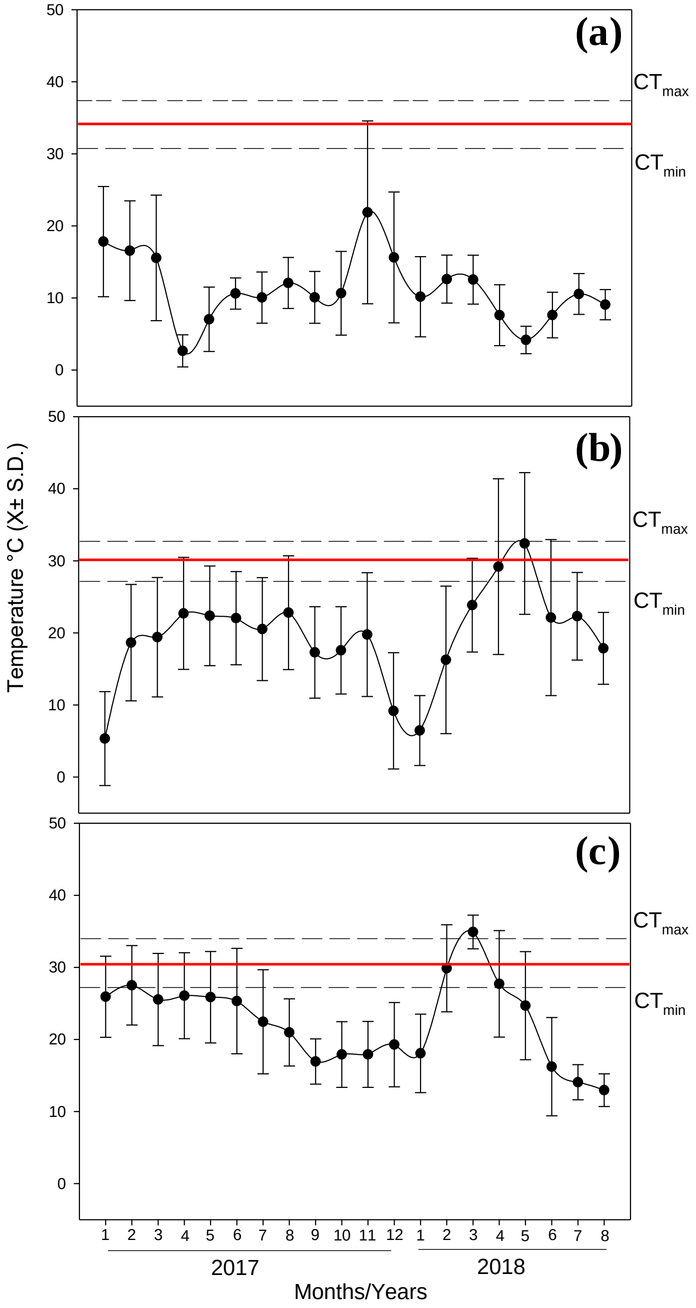

Fig. S3. Ventral view of the identification numerical system based on the one proposed by Medica et al. (1971). Each point represents a cauterization mark.

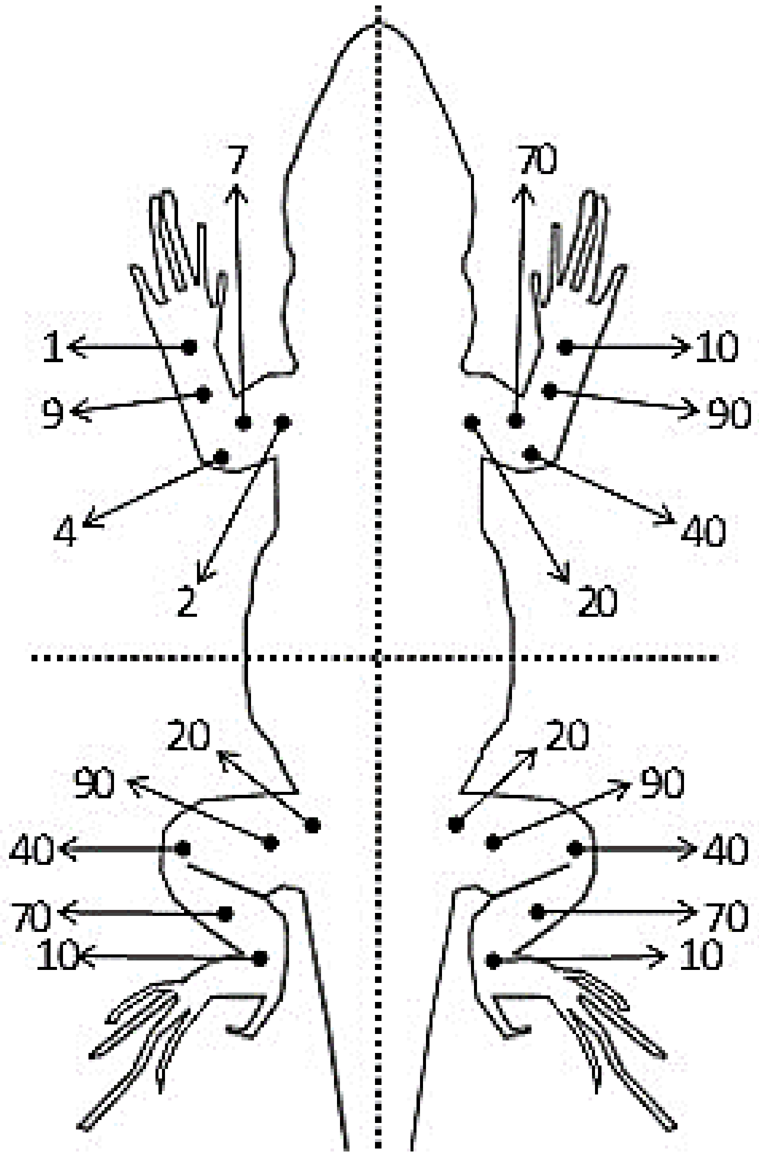

Fig. S4. Estimated recapture probabilities (± SE) for each elevation site (2,600, 3,100 and 4,150 m a.s.l.).

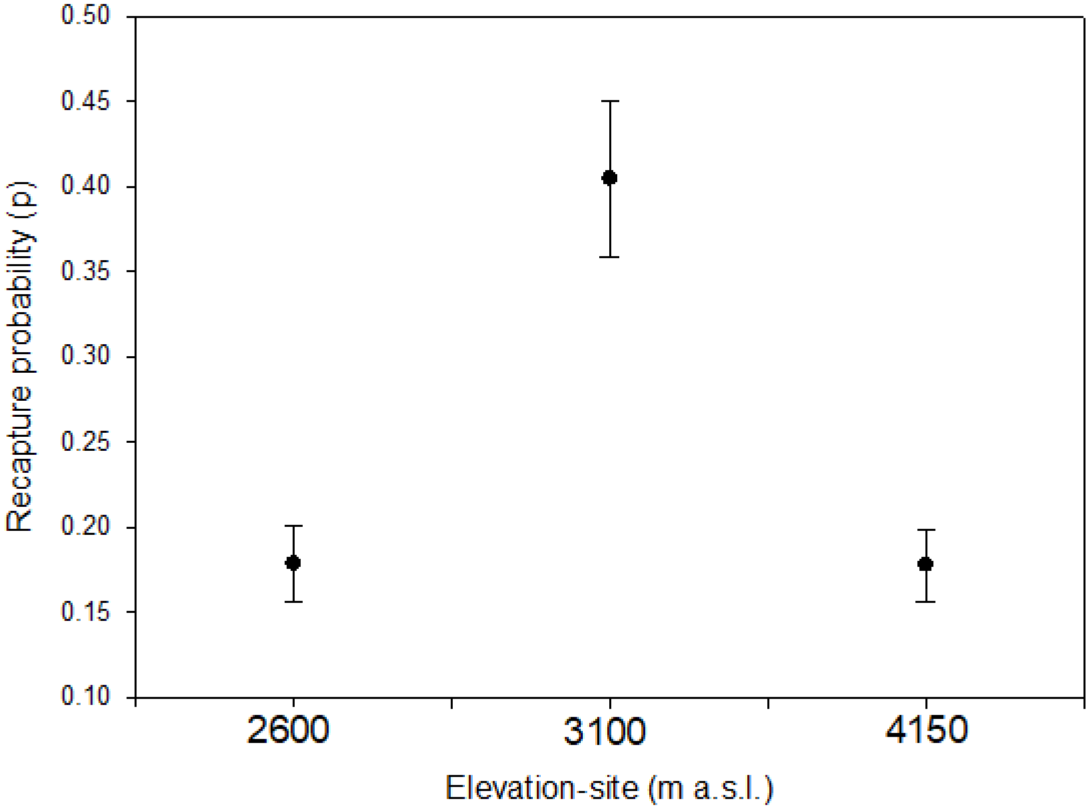

Table S1. Estimated lizard survival rates, based on the best supported model [φ (Site + d_e) p(Site)].

Site (m a.s.l.)	**Estimate**	**SE**	**LCI**	**UCI**
2600	0.815	0.035	0.734	0.875
2600	0.802	0.043	0.703	0.873
2600	0.856	0.021	0.810	0.892
2600	0.862	0.020	0.817	0.898
2600	0.904	0.026	0.839	0.945
2600	0.906	0.026	0.839	0.947
2600	0.893	0.023	0.836	0.931
2600	0.820	0.033	0.746	0.876
2600	0.844	0.023	0.792	0.885
2600	0.862	0.020	0.816	0.897
3100	0.850	0.025	0.791	0.894
3100	0.797	0.030	0.731	0.850
3100	0.800	0.029	0.737	0.851
3100	0.762	0.047	0.658	0.842
3100	0.837	0.024	0.783	0.879
3100	0.829	0.024	0.776	0.871
3100	0.872	0.030	0.799	0.921
3100	0.837	0.024	0.784	0.880

3100	0.762	0.047	0.657	0.842
3100	0.804	0.027	0.743	0.853
4150	0.906	0.028	0.832	0.950
4150	0.923	0.017	0.880	0.952
4150	0.940	0.013	0.907	0.961
4150	0.929	0.015	0.892	0.954
4150	0.932	0.014	0.897	0.956
4150	0.934	0.014	0.900	0.957
4150	0.944	0.013	0.910	0.965
4150	0.951	0.014	0.913	0.972
4150	0.926	0.016	0.885	0.953
4150	0.945	0.013	0.911	0.967

9. CAPÍTULO 2

Lower predation with increasing altitude in the mesquite lizard *Sceloporus grammicus*

RESUMEN EN ESPAÑOL

Evalué la presión diferencial de la depredación en la lagartija *Sceloporus grammicus* en tres sitios de muestreo a lo largo de un gradiente de alta montaña, utilizando tres métodos: ataques en modelos de lagartija construidos con plastilina, la frecuencia de autotomía de la cola y la estimación de la riqueza de posibles depredadores. Colocamos un total de 720 modelos de lagartijas en cada sitio de muestreo (2600, 3100 y 4150 msnm) durante 6 días en la estación reproductiva y durante 6 días en la estación no reproductiva. Cada día coloqué 60 modelos, n = 30 que representan cada sexo y que comprenden n = 10 para cada uno de los tres morfotipos de color gular (gris, amarillo y anaranjado), sobre las perchas de lagartijas observadas previamente. Adicionalmente, en cada sitio realicé 20 muestreos de marcaje-recaptura desde el 2014 hasta el 2019 para determinar el número de individuos con autotomía de la cola, asimismo, realicé observaciones para estimar la riqueza de posibles depredadores, estas observaciones se complementaron con la literatura disponible. Esperaba 1) un efecto inverso de la elevación sobre la presión de la depredación debido a una posible disminución en la riqueza de los depredadores potenciales con la elevación, y 2) una presión de depredación diferencial acorde al sexo y al color del morfotipo gular, debido a las diferencias conductuales y en la conspicuidad morfológica. Estos hallazgos respaldan la disminución de la presión de depredación con la altitud de acuerdo con los tres métodos de evaluación. Sin embargo, no encontré evidencia de un efecto del sexo o del morfotipo de color gular sobre la presión de la depredación, ni por el número de ataques en los modelos de plastilina ni por la frecuencia de la autotomía de la cola. Una menor depredación a mayor elevación podría deberse al efecto combinado de una menor riqueza de depredadores y a una menor visibilidad de las lagartijas, causado por un menor contraste con el sustrato y a una menor actividad locomotora, de forrajeo y de la conducta social, debido a la restricción térmica.

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Lower predation with increasing altitude in the mesquite lizard *Sceloporus grammicus*

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Abstract.—We evaluated differential predation pressure on the lizard *Sceloporus grammicus* at 3 sampling sites along a high-mountain gradient, using 3 methods of assessment: attacks on plasticine lizard models, frequency of lizard tail autotomy, and estimation of the richness of potential predators. We placed a total of 720 lizard models at each sampling site (2600, 3100, and 4150 m asl) on 6 d during the reproductive season and on 6 d during the nonreproductive season. Each day we placed 60 models ($n = 30$ for each sex, with each sex having 10 each of 3 gular color morphotypes [gray, yellow, and orange]) at lizards' previously observed basking sites. Additionally, we conducted 20 mark-recapture sampling visits at each site from 2014 to 2019 to determine the number of individuals with tail autotomy; we also made observations to estimate the richness of potential predators and supplemented our observations with information from the available literature. We expected (1) an inverse effect of altitude on predation pressure due to a possible decrease in the richness of potential predators with altitude, and (2) differential predation pressure according to sex and gular morphotype due to differential behavioral and morphological conspicuity. Our findings support a decrease in predation pressure with altitude according to our 3 methods of assessment. However, we did not find evidence for an effect of sex or color of gular morphotype on predation pressure, neither from the number of attacks on the plasticine models nor from the frequency of tail autotomy. Lower predation with increasing altitude could be due to the following combined effects: lower richness of predators, lower visibility of lizards because of less contrast of their bodies with the substrate, and reduced locomotor, foraging, and social movements due to thermal restriction.

Resumen.—Evaluamos la presión diferencial de la depredación en la lagartija *Sceloporus grammicus* en tres sitios de muestreo a lo largo de un gradiente de alta montaña, utilizando tres métodos: ataques en modelos de lagartija construidos con plastilina, la frecuencia de autotomía de la cola y la estimación de la riqueza de posibles depredadores. Colocamos un total de 720 modelos de lagartijas en cada sitio de muestreo (2600, 3100 y 4150 m snm) durante 6 días en la estación reproductiva y durante 6 días en la estación no reproductiva. Cada día colocamos 60 modelos, $n = 30$ que representan cada sexo y que comprenden $n = 10$ para cada uno de los tres morfotipos de color gular (gris, amarillo y anaranjado), sobre las perchas de lagartijas observadas previamente. Adicionalmente, en cada sitio realizamos 20 muestreos de marcaje-recaptura desde 2014 hasta 2019 para determinar el número de individuos con autotomía de la cola, asimismo, realizamos observaciones para estimar la riqueza de posibles depredadores, estas observaciones se complementaron con la literatura disponible. Nosotros esperábamos (1) un efecto inverso de la elevación sobre la presión de la depredación debido a una posible disminución en la riqueza de los depredadores potenciales con la elevación, y (2) una presión de depredación diferencial acorde al sexo y al color del morfotipo gular, debido a las diferencias conductuales y en la conspicuidad morfológica. Nuestros hallazgos respaldan la disminución de la presión de depredación con la altitud de acuerdo con nuestros tres métodos de evaluación. Sin embargo, no encontramos evidencia de un efecto del sexo o del morfotipo de color gular sobre la presión de la depredación, ni por el número de ataques en los modelos de plastilina ni por la frecuencia de la autotomía de la cola. Una menor depredación a mayor elevación podría deberse al efecto combinado de una menor riqueza de depredadores y a una menor visibilidad de las lagartijas, causado por un menor contraste con el sustrato y a una menor actividad locomotora, de forrajeo y de la conducta social, debido a la restricción térmica.

Predation is the relationship between 2 organisms in which one organism (i.e., the predator) detects, attacks, and sometimes kills and consumes another organism (i.e., the prey)

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for nutritional purposes (Begon et al. 2006). This interaction has been compared to an arms race between the predator and its prey (Dawkins and Krebs 1979), one that affects the morphology and behavioral patterns of both contestants (Langerhans 2006, Steffen 2009), and therefore can be considered one of the strongest selective forces of evolution (Bengtson 2002).

The initiation and outcome of such interactions are affected by decision-making of the prey and predator (Lima and Dill 1990), by antipredator strategies of the prey (McElroy 2019), by predator and prey movement, and by the population density of the species involved (Sih 1984). The predator-prey relationship can also be affected by abiotic characteristics of the environment (Smee 2010). For example, at high altitudes relative humidity and solar radiation increase, while other abiotic factors such as atmospheric pressure and ambient temperature decrease (Körner 2007, Sáenz-Romero et al. 2010). At the same time, changes in environmental conditions are accompanied by variation in species richness, including that of predators (Rahbek 1995), generally with a decrease in richness as elevation increases (Sánchez-Cordero 2001, Grytnes and Vetaas 2002, McCain and Grytnes 2010). Together, such variation in environmental conditions and species richness generates differences in biotic interactions, as in, for example, intraspecific competition (Terborgh and Weske 1975), parasitism (Veijalainen et al. 2014), and predation (Hillyer and Silman 2010).

Ectotherms such as lizards depend on warmth from the environment for all behavioral and physiological activities (Hertz et al. 1993, Blouin-Demers and Weatherhead 2001, Lourdais et al. 2004, Andrews and Schwarzkopf 2012). However, behavioral thermoregulation involves a trade-off with other activities such as foraging, mating, and antipredator behavior (McConnachie and Alexander 2004); in these senses, the thermal quality of the environment determines the cost of thermoregulation (Lara-Reséndiz et al. 2014, Díaz de la Vega-Pérez et al. 2019a). Along altitudinal gradients, lizards experience different thermal environments and are thus subject to different degrees of thermal restriction.

Lizards inhabiting sites with suboptimal environmental temperature (i.e., cooler or warmer than the lizards' metabolic optimum) are less active during the restrictive periods of the day (Vidal et al. 2010). However, more active lizards occupying more favorable thermal environments may incur a greater risk of predation due to increased detectability (Pianka and Pianka 1970, Formanowicz et al. 1990, Schwarzkopf and Shine 1992, Carter et al. 2010). For example, whereas lizards inhabiting cool environments (e.g., high altitudes) show few behavioral displays and feeding attempts (Marquet et al. 1989, Lemos-Espinal and Ballinger 1995a), those in warm environments engage for long periods in foraging (Cooper 2000, Downes 2001), basking, and territorial or courtship behavior (e.g., sexual displays and males fighting for mates) (Marler and Moore 1988, Cooper 1999) but incur a higher risk of predation due to increased detectability by predators. The risk of predation may further increase with prey mobility and conspicuity (Smallwood 1989), as when, for example, territorial, dominance, or courtship behavior is accompanied by colorful displays (Endler 1978). A sexual bias in predation pressure on lizards has been suggested (Costantini et al. 2007) because of behavioral differences between the sexes. Additionally, individuals with greater visual contrast with their environment due to body coloration than their conspecifics may also experience greater predation (Huhta et al. 2003, Van Gossum et al. 2004, Hawlena 2009), and it has been suggested that colorful males are more readily detected and experience higher predation than less colorful males or females (Husak et al. 2006). It has also been suggested that predation pressure may modify antipredator behavior (Huey and Pianka 1981), foraging mode (Downes 2001, Martín et al. 2003), and morphological characteristics of lizards (Shepard 2007).

In this context, plasticine lizard models, lizard tail autotomy, estimation of the richness of potential predators, and direct estimates of killed individuals have been widely used to determine predation pressure under natural conditions (Munger 1986, Shepard 2007, Steffen 2009, Bateman et al. 2017, Purger et al. 2017, Keehn and Feldman 2018). However, because each of these techniques alone provides limited (Bateman et al. 2017), or in some cases inaccurate or biased, information (Medel et al. 1988), we evaluated predation pressure on the mesquite lizard *Sceloporus grammicus*

Wiegmann 1828 at 3 study sites, each with different thermal quality, by using a multimethodological approach.

Sceloporus grammicus is a generalist species with a wide distribution from southeastern Texas, USA, and Chihuahua to Oaxaca, Mexico, and is the most widely distributed lizard in Mexico. It is an arboreal and saxicolous species, inhabiting pine and oak woodlands, as well as juniper scrub, xerophilous scrub, and urban areas at elevations ranging from ~100 to 4600 m asl (Sites 1982, Lemos-Espinal and Ballinger 1995a, Marshall et al. 2006). *Sceloporus grammicus* is a polymorphic species in which both sexes exhibit orange, yellow, or gray gular color morphs; meanwhile, in some populations the gray morph in males is replaced by a blue morph (Bastiaans et al. 2014). Interestingly, different aggressive behavior patterns are associated with each color morph (i.e., yellow and blue are more aggressive; Bastiaans et al. 2013). In addition, *S. grammicus* exhibits sexual dimorphism: males have blue patches on their belly and enlarged post-cloacal scales, and males are also bigger than females (Díaz de la Vega-Pérez et al. 2019a). Interestingly, with increasing altitude *S. grammicus* shows a decrease in snout–vent length (SVL) (Lemos-Espinal and Ballinger 1995b, Lemos-Espinal et al. 1998, Jiménez-Cruz et al. 2005, Ramírez-Bautista et al. 2011), and lower body mass, but no sexual difference in SVL at 4150 m asl (Díaz de la Vega-Pérez et al. 2019a).

Based on the above information, we proposed 2 hypotheses: (1) a negative relation between predation pressure and altitude due to the lower richness of potential predators with increasing altitude, and (2) differential predation pressure associated with morphotype and sex due to differential conspicuity. Accordingly, our aims were to determine whether predation pressure differed among 3 populations of *S. grammicus* living at different altitudes in a high mountain system and whether color morphotype and sex result in differential predation pressure in an intra- and interpopulation comparison. To meet these aims we used 3 approaches at each of the 3 sampling sites: frequency of predation attempts (attacks) on plasticine lizard models, frequency of lizard tail autotomy, and richness of potential lizard predators. We predicted (1) that as altitude increased, the number of lizard models with evidence of attack, the number of lizards with evidence of tail autotomy, and the richness of potential predators would decrease, and (2) that the most brightly colored morphotypes (i.e., orange and yellow gular coloration) would be predated more in both sexes at all 3 study sites.

METHODS

Study Site

The study was conducted on the extinct volcano of La Malinche National Park located between the central Mexican states of Tlaxcala and Puebla. We determined three 5-ha study sites along a gradient on the eastern slope of the volcano. The highest site was at 4150 m asl (19°14.417′N, 98°02.068′W), had an annual mean ambient temperature of 6.86 °C (SD = 3.89), and is characterized by rocky volcanic outcrops, *Juniperus monticola* shrubs, and alpine grassland. Here the lizards inhabit crevices among the rocky outcrops (Fig. 1A). The middle site was at 3100 m asl (19°14.637′N, 97°59.452′W), had a mean ambient temperature of 11.94 °C (SD = 11.33), and is characterized by patches of oak (*Quercus* sp.) and pine (*Pinus hartwegii*) and induced grassland. Here the lizards inhabit small rock walls, dead trees, and crevices among boulders (Fig. 1B). The lowest site was at 2600 m asl (19°14.707′N, 97°55.603′W), had a mean ambient temperature of 14.69 °C (SD = 6.59), and is a degraded habitat due to agricultural activities and cattle grazing. Here the lizards mainly inhabit the walls of an abandoned hacienda that is surrounded by maize fields (Fig. 1C).

Lizard Models

We made models of *S. grammicus* from nontoxic plasticine (Crayola®, model 57-0380-052), using 2-part clay molds of representative preserved specimens chosen based on the mean snout–vent length (SVL) (low-elevation site, male 63 mm and female 56 mm; middle-elevation site, male 62 mm and female 51 mm; high-elevation site, male and female 50 mm), which varies with sex and altitude in adult lizards (Díaz de la Vega-Pérez et al. 2019a).

We used gray plasticine as the base color for the models, which we then hand-painted with nontoxic, water-based body paint (Nylo Digital®, Colonia El Patrimonio, Puebla, Mexico). To select the colors of the paint, we measured the spectral reflectance of the dorsal

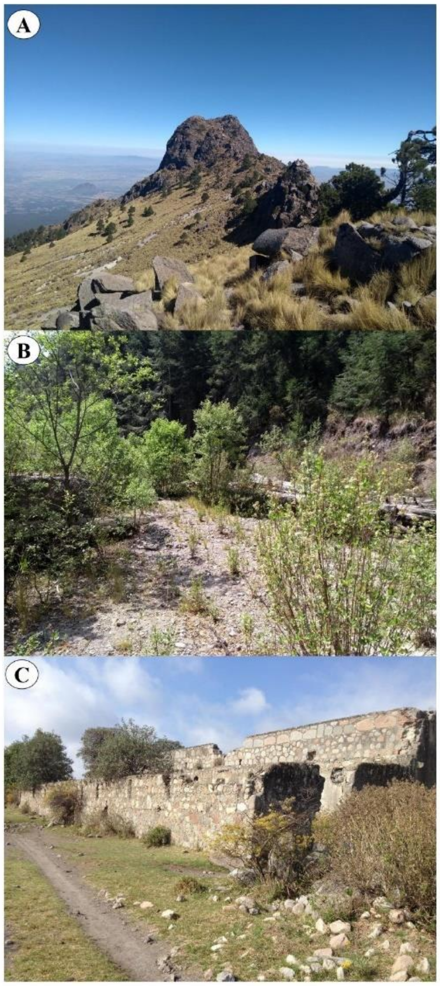

Fig. 1. Study sites at La Malinche National Park in Central Mexico: ***A,*** 4150 m above sea level (asl). ***B,*** 3100 m asl. ***C,*** 2600 m asl.

and gular region of 2 live lizards using a spectrophotometer (Jaz EL-200, Ocean Optics, Dunedin, FL). The lizards' color was measured at 32 °C, which is the lizards' preferred body temperature at all 3 altitudes and is presumably adequate for performing most of their physiological and behavioral functions (Hertz et al. 1993, Díaz de la Vega-Pérez et al. 2019a). We painted the dorsum of each model uniformly brown, adding black horizontal stripes to simulate the pattern of *S. grammicus*. To represent the 3 gular morphotypes, we used yellow and orange paint for the corresponding morphs as determined by spectrophotometry, but we did not paint the gular region of the gray morph. We used a total of 2160 models: 720 per site, 360 females and 360 males, comprising 120 of each gular morphotype.

Fieldwork

LIZARD MODELS.—We placed the models in the field at 2 times of year: from September to December 2018, representing the mating season, and from February to April 2019, when in this viviparous species, females are pregnant. We visited each site at regular intervals, 3 times for 2 consecutive days (i.e., 6 d during the reproductive season and 6 d during the nonreproductive season). On each experimental day, we simultaneously distributed 60 models (30 males and 30 females, comprising 10 of each color morph) at each study site. Models were placed in open areas previously identified as basking sites (Domínguez-Godoy et al., personal observations) and in a display posture with the gular patch exposed in order to increase visibility to potential predators (Fig. 2). The lizard activity period varied altitudinally: 09:00 to 18:00 at the low-elevation site; 08:00 to 17:00 at the middle-elevation site; and 10:00 to 18:00 at the high-elevation site (Díaz de la Vega-Pérez et al. 2019a). Therefore, the models were left in place from 10:00 to 16:00, corresponding to the lizards' highest activity period. After 16:00, the models were removed to avoid nocturnal "predation" and an overestimation of predation pressure (these lizards are not active after dark). We considered an "attack" on a model to be by a predator if the model showed peck marks, disappeared, or was displaced from the perch site (Fig. 3; Purger et al. 2017, Calderon-Chalco and Putman 2019). Each damaged or missing model was replaced by a similar one early on the second day of monitoring.

TAIL AUTOTOMY.—As a further estimation of predation pressure, we conducted a mark-recapture study over 4 years (September 2014 to February 2019), visiting each study site 20 times at approximately 2-month intervals. We captured lizards by hand or noose (collecting permits SGPA/DGVS/15396/15 and SGPA/DGVS/007736/18), determined their sex by the presence (males) or absence (females) of

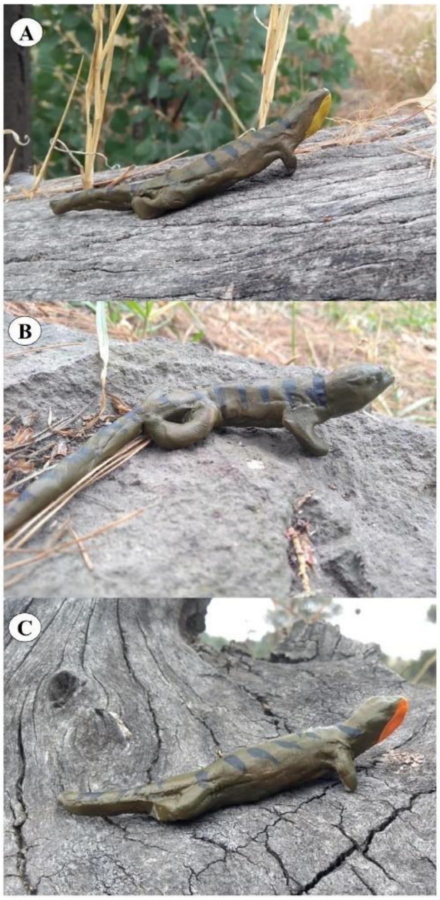

Fig. 2. Examples of the plasticine lizard models positioned in display posture exposing the gular region. ***A***, Yellow morph. ***B***, Gray morph. ***C***, Orange morph.

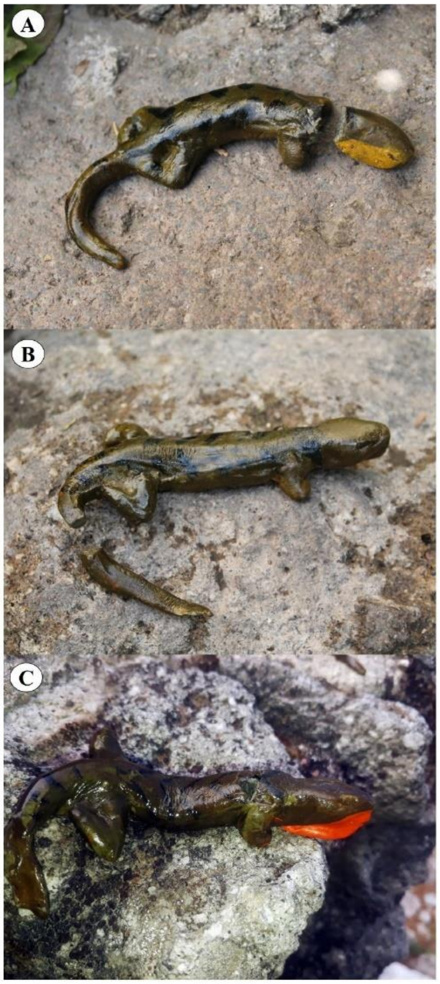

Fig. 3. Examples of attacks on plasticine lizard models. ***A***, To the neck. ***B***, To the tail. ***C***, To the dorsum.

enlarged post-cloacal scales, gular morphotype, and evidence of tail autotomy (i.e., broken tails and regenerated tails). We marked the captured lizards, using a surgical cauterizer (Bovie Change-A-Tip® Del 1) to avoid repeated measures of the same individuals (Medica et al. 1971, Ekner et al. 2011) and applying Kwik-Stop® antiseptic powder to avoid infection. We recorded the presence of tail autotomy as a natural defensive response to predation (Kelehear and Webb 2006, Bateman and Flemming 2009, 2011). Lizards were then released at their place of capture.

Richness of potential predators.—We monitored the presence of potential vertebrate predators (mammals, birds, and snakes) from September 2014 to February 2019 at each study site and its surrounds during visits to register tail autonomy. This effort was augmented by reports from the literature (Domínguez-Godoy et al. 2017, Méndez-de la Cruz et al. 2018, Díaz de la Vega-Pérez et al. 2019b, Gómez-Campos et al. 2019).

TABLE 1. Attack frequency on lizard models by site and season.

Season	Site	Number missing or with predation marks
Autumn	4150 m	0
	3100 m	6
	2600 m	14
Winter	4150 m	0
	3100 m	2
	2600 m	9

Statistical Analysis

We used a generalized linear model (GLM) with Poisson distribution to determine whether predation pressure on the lizards differed with altitude. First, we used as predictors the frequency of apparent predation attempts on the models as a response variable by site (low, middle, and high elevation), sex (male and female), gular color morph (gray, yellow, and orange), and their interactions, with multiple comparisons post hoc tests (package "*emmeans*"). Additionally, we performed a GLM with binomial distribution to determine if the frequency of tail autotomy differed by altitude. We used the presence or absence of tail regeneration as a response variable, using study site, sex, gular color morph, and their interactions as predictors. Tukey's post hoc tests adjusted for multiple comparisons were made using the package *lsmeans* in R version 3.6.0 (R Core Team 2019). Model selection was carried out by stepwise deletion of nonsignificant terms ($P > 0.05$), starting from the complete model containing all variables considered and their interactions. The statistical analyses were performed with the *lme4* package in R version 3.6.0 (R Core Team 2019).

RESULTS

Attack Frequency on Models

Although the overall frequency of "attacks" on the models was low (Table 1), we found significant differences in attack frequency according to study site (chi-square test: $X^2_{2,16} = 16.96$, $P < 0.001$). The post hoc tests showed differences between the low-elevation site (95% CI, 3.35 to 6.96) and the middle- (95% CI, 1.38 to 3.94) and high-elevation sites (95% CI, 0.44 to 2.23), but not between the middle- and high-elevation sites (Fig. 4A). The lowest study site presented the highest frequency of attacks, with 23 instances, compared to the middle and the highest sites with 8 and 0 instances, respectively. Although sample size was small, the frequency of attacks was not associated with sex ($X^2_1 = 1.66$) or color morphotype ($X^2_1 = 5.27$) and there was no effect of the interaction between site and morphotype ($X^2_2 = 3.03$), sex and morphotype ($X^2_2 = 1.03$), site and sex ($X^2_2 = 1.17$), or site, sex, and morphotype ($X^2_4 = 0.98$). Although we did not test the effect of the reproductive season on model predation, we found that 60% and 75% of the attacks, at the low- and the middle-elevation sites, respectively, occurred during the reproductive season.

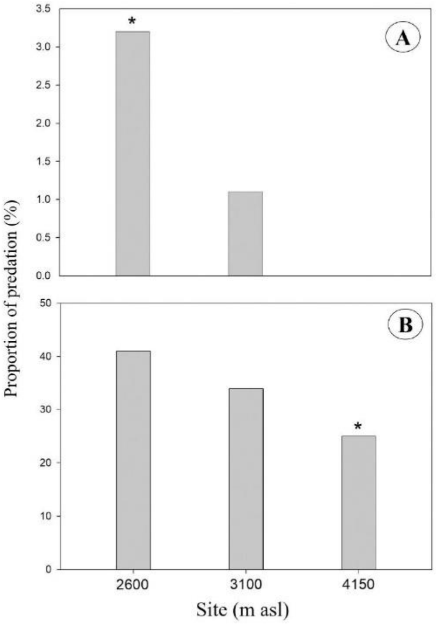

Fig. 4. Proportion of models or lizards showing evidence of attempted predation. **A**, Plasticine lizard models. **B**, Lizards with tail autotomy. Asterisks denote the significant differences in predation on lizard models between the middle and the highest sites, and in tail autotomy of lizards between the highest and lower sites, according to the post hoc analysis (see text for statistics).

Attacks on models were recorded only at the low- and middle-elevation sites. We found that at the low-elevation site, around 30% of the predator attacks on the models were aimed at the tail, 30% at the dorsal region, 13% at the legs, and 17% at the head and neck, while the remaining 9% corresponded to models that

TABLE 2. Tail autotomy frequency of lizards at the 3 study sites.

Site/Sex	Percent tail autotomy	*n*
4150 m	25%	113
Male	11%	51
Female	13%	62
3100 m	34%	106
Male	15%	46
Female	19%	60
2600 m	41%	233
Male	18%	105
Female	22%	128

TABLE 3. Potential lizard predators observed at each study site.

Predators	2650 m	3100 m	4150 m
Mammals			
Canis latrans	X	X	
Lynx rufus		X	X
Mustela frenata	X	X	
Birds			
Accipiter cooperii	X		
Buteo jamaicensis	X	X	X
Falco sparverius	X	X	X
Geococcyx velox	X	X	
Lanius ludovicianus	X		
Sialia mexicana	X	X	X
Corvus corax	X	X	X
Snakes			
Crotalus ravus	X	X	
Crotalus triseriatus		X	
Thamnophis scalaris	X	X	X

were missing or displaced from the perch site. Meanwhile, at the middle-elevation site, we found that 38% and 25% of the predator attacks were aimed at the legs and cephalic region, respectively. In contrast to the lowest site, only 12% of the predator attacks were aimed at the tail and 12% at the dorsal region, and 12% of models were missing or displaced from the perch site.

Tail Autotomy

We found a significant effect of altitude on the number of individuals with tail autotomy ($X^2_{2, 1240} = 33.5$, $P < 0.001$). The post hoc tests reported significant differences between the high-elevation site and the middle- ($Z = 3.83$, $P < 0.001$) and low-elevation sites ($Z = 5.51$, $P < 0.001$), but not between the middle- and low-elevation sites ($Z = 0.67$, $P < 0.78$) (Fig. 4B). The population at the lowest altitude showed the highest frequency, and the population at the highest altitude showed the lowest frequency (Table 2, Fig. 4B). There was no significant effect of sex ($X^2_1 = 1.87$) or color morphotype ($X^2_5 = 7.28$) and no significant effect of the interactions between site and color morphotype ($X^2_{10} = 9.53$), sex and color morphotype ($X^2_5 = 7.11$), site and sex ($X^2_2 = 5.82$), or site, sex, and color morphotype ($X^2_4 = 8.25$).

Potential Predator Richness

We observed a total of 13 potential predator species at the 3 sites combined: 3 mammals, 7 birds, and 3 snakes (Table 3). The lowest-altitude site presented the greatest richness and the highest-altitude site presented the least.

DISCUSSION

Overall, our results suggest a consistent pattern among the 3 methodologies we employed. We found a decrease in the pressure of predation on *S. grammicus* (lower frequency of attacks on lizard-models and lower frequency of lizard tail autotomy) at higher elevation, as well as fewer potential predators. However, contrary to our predictions, we found no differences for sex or color morphotype.

Consistent with our findings, previous studies have reported a greater probability of survival among lizard species at higher altitudes (from 1122 to 3200 m asl; Ortega-Rubio et al. 1999, Méndez-de la Cruz et al. 2008, Domínguez-Godoy et al. 2020), suggesting that this might be linked to reduced predation pressure (Adolph and Porter 1993, Fox et al. 1994). Such a pattern could be due to a combination of factors. In environments where the ambient temperature is low, lizards are generally less active (Pianka and Pianka 1970, Formanowicz et al. 1990, Lemos-Espinal and Ballinger 1995a), performing fewer social interactions (Domínguez-Godoy et al. personal observations) presumably due to the greater cost of thermoregulation at higher altitudes (Díaz de la Vega-Pérez et al. 2019a). It has also been reported that under suboptimal thermal conditions, lizards may employ behavioral strategies such as maintaining a smaller distance between basking sites and shelters, which facilitates escape in the case of attempted predation (Carrascal et al. 1992). Additionally, at cooler sites like higher altitudes, lizards (including *S. grammicus*) tend to be darker, presumably to increase their heating rates (Stuart-Fox et al. 2017). This darker coloration also results in lower contrast with the substrate, and so reduces detection by visual predators (Reguera et al. 2014, Díaz de la Vega-Pérez et al. personal observations). Taken together, these characteristics could reduce the detectability and ease of capture of lizards by visual predators. At higher altitudes, the abundance and diversity of species are generally low (Lomolino 2001, Grytnes and Vetaas 2002); thus, the lower presence of potential predators at the high-elevation site remains a likely major factor for low predation pressure at La Malinche volcano.

Several studies have reported an effect of sex and color morphotype on the probability of lizards being predated (Husak et al. 2006, Paemelaere et al. 2013, Antczak et al. 2019). However, in the present study we found no relation between sex or color morphotype and the frequency of attacks on models or the frequency of tail autotomy. This suggests that in *S. grammicus*, possible behavioral variations associated with sex (Acharya and McNeil 1998) or color morphotype (Pellitteri-Rosa et al. 2017) do not influence the probability of a lizard being detected by visual predators. Rather, at our study location it seems that at lower altitudes, greater contrast of the dorsal coloration between the lizards and the substrate (Cordes and Mouton 1995), as well as greater activity (Marquet et al. 1989, Lemos-Espinal and Ballinger 1995a), increases the risk of the lizards being detected.

Plasticine lizard models are a good option to test predation pressure, even though they cannot replicate all the signals (particularly behavioral) likely involved in attracting the attention of visual predators (Wall and Shine 2009). Males and females are expected to have different behavior patterns associated with reproductive activities; for example, males are generally bolder during the mating season (Stuart-Fox et al. 2003), while color morphotypes are often associated with different behavioral and ecophysiological traits (Sinervo and Lively 1996, San-Jose et al. 2014). Thus, the effect on predation of some behavioral and physiological attributes associated with sex (Husak et al. 2006) or color morphotype (Zajitschek et al. 2012, Pellitteri-Rosa et al. 2017) cannot be accurately assessed using plasticine models alone. However, models can be a useful addition in combination with other methodologies, as in the present study where the results of attacks on the models supported the results of tail autotomy.

In sum, our results indicate that for our study species, *S. grammicus*, predation pressure decreases as altitude increases. Recently, we have started to investigate the costs that this lizard faces when inhabiting high mountain environments (Díaz de la Vega-Pérez et al. 2019a, Domínguez-Godoy et al. 2020). The present study provides valuable additional information for forming a more complete picture of the behavioral strategies allowing this species to survive in contrasting environments along the gradient of high-mountain ecosystems.

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10. CAPÍTULO 3

Too cool to fight: Is ambient temperature associated with male aggressive behavior in the lizard *Sceloporus grammicus*?

Enviado a Behavioral Ecology

RESUMEN EN ESPAÑOL

El comportamiento agresivo se lleva a cabo en el contexto de una competencia intraespecífica para obtener acceso a parejas reproductivas, alimentos o territorios adecuados. No obstante, las confrontaciones agresivas pueden comprometer el tiempo y los recursos necesarios para otras actividades importantes, además de aumentar la probabilidad de sufrir daños físicos o depredación. El comportamiento agresivo es particularmente costoso para los ectotermos porque puede reducir el tiempo disponible para la termorregulación, que es otra actividad que consume mucho tiempo y es energéticamente costosa pero indispensable para los procesos metabólicos y fisiológicos. En este estudio, analicé el efecto de la baja temperatura ambiental sobre el comportamiento agresivo de una lagartija polimórfica (i.e. diferentes morfos de color gular). Nuestra hipótesis fue que el tiempo asignado a la conducta agresiva en entornos de baja calidad térmica compromete el tiempo dedicado a la adquisición y mantenimiento de una temperatura corporal óptima. Encontramos que las lagartijas de la ubicación de baja calidad térmica (i.e. baja temperatura ambiental) exhibieron un comportamiento menos agresivo que los capturados en ubicaciones de calidad térmica media y alta. Estos resultados sugieren que el comportamiento agresivo en ambientes de baja calidad térmica interfiere con la adquisición y mantenimiento de una temperatura corporal adecuada. Por lo tanto, es probable que los beneficios de la termorregulación superen el costo del comportamiento agresivo en sitios de baja calidad térmica.

ABSTRACT

Aggressive behavior is performed in the context of intraspecific competition for gaining access to mates, food, or suitable territories. However, aggressive confrontations may divert time and energy from other important activities and increase the likelihood of suffering physical injury or predation. Aggressive behavior is particularly costly for ectotherms because it may reduce time available for thermoregulation, which is a time-consuming activity but indispensable for optimizing metabolic and physiological processes. In this study, we analyzed the long-term effect of low environmental temperature on the aggressive behavior of a polymorphic lizard (i.e., different throat color morphs). Our hypothesis was that time allocated to aggressive behavior in low thermal quality environments is diverted from time spent on acquisition and maintenance of an optimal body temperature. Accordingly, we found that lizards from the low thermal quality location (i.e., low environmental temperature) exhibited less aggressive behavior than those captured in middle and high thermal quality locations. Our results suggest that aggressive behavior in low thermal quality environments possibly because it interferes with the acquisition and maintenance of an adequate body temperature. Therefore, it is likely that the benefits of thermoregulation outweigh the cost of aggressive behavior at low thermal quality sites.

Key words: High mountain ecosystems, Polymorphism, Cold environments, Mesquite lizard, Aggression.

INTRODUCTION

Aggressive behavior is defined as a series of offensive behaviors (e.g., physical attacks such as bites, kicks, lunges; behavioral displays such as songs, colorful displays, and threats), directed at one or more conspecifics, that impose a cost in the short (e.g., increased stress and energy) or long term (e.g., survival) to the aggressor (Grether et al. 2013; Whiting and Miles 2019). Mostly, these behaviors are displayed in the context of the competition for high-quality territories (Duque-Wilckens et al. 2019), reproductive mates (Baxter et al. 2015), or nutritional resources (Hodge et al. 2009). However, similar behaviors that occur in contexts such as predation, cannibalism, or forced copulation are not considered aggressive displays because the aim of such interactions is not to obtain a resource (Grether et al. 2013). Despite the obvious benefits (e.g., high-quality resources and mates) aggressive confrontations may bring (see: Georgiev et al. 2013), there are also potential costs to the contestants. Besides the increased risk of physical injury or predation, an important cost may be a reduction in the time and energy available to invest into other vital activities (Marler and More 1989; Hsu et al. 2006; Georgiev et al. 2013).

Reptiles are ectotherms and therefore depend on the ambient temperature to regulate their body temperature, which must be maintained within a narrow range to carry out necessary physiological and behavioral processes (Avery et al. 1982; Huey 1982; Adolph and Porter 1993; Meek 1995). Extreme thermal environments, whether too cold or too hot, increase the cost of thermoregulation (Huey and Slatkin 1976), resulting in reptiles under such suboptimal thermal conditions needing to allocate more time to thermoregulatory activities to maintain their body temperature within a sustainable range (Huey 1974). According to the cost-benefit model proposed by Huey and Slatkin (1976), the cost of thermoregulation is determined by the thermal quality of the environment (d_e = the degree of discrepancy between the environmental temperatures available and the body temperatures that animals prefer, Hertz et al. 1993). Therefore, thermal quality decreases as the environmental temperature deviates from the lizard's preferred body temperature (i.e., higher values of d_e). As time spent on aggressive behavior in low thermal quality environments cannot be allocated to thermoregulation, those behaviors may directly interfere with the regulation of body temperature (DeWitt 1967; Engbretson and Livezey 1972; Rusch and Angilletta 2017). Therefore, a low rate of aggressive behaviors would be expected under suboptimal thermal environments.

In lizards, males exhibit inter-individual variation in aggressive behaviors associated with morphological traits such as body (Huyghe et al. 2012) or head size (Huyghe et al. 2005), and color morphotype (Sinervo and Lively 1996, San-José et al. 2014). Color morphotype is defined as the coexistence of two or more distinct color morphs within the same reproductive population (sensu Huxley; see Gray and McKinnon 2007). Such co-occurring morphs often differ in body size and mass, immunocompetence, and/or survival as well as behavior and reproductive alternative mating strategies (McKinnon and Pierotti 2010), which adds flexibility for populations to expand their distribution range and to colonize new environments (Forsman et al. 2008). According to Sinervo and Lively (1996), the coexistence of different morphotypes is possible via a rock-paper-scissors dynamic, which maintains the polymorphism over time through negative frequency dependent selection (Sinervo and Lively 1996; San-José et al. 2014). Interestingly, differential fitness outputs of each color morphotype, driven by local selection pressures can lead to geographic variation in the proportion of color morphotypes among populations (McLean and Stuart-Fox 2014).

The mesquite lizard (*Sceloporus grammicus*, Wiegmann 1828) belongs to the Phrynosomatidae family, and is a small, sexually dimorphic lizard (mean snout-vent length ± SD, males: 63 ± 8.9 mm; females: 56 ± 6.5 mm; Díaz de la Vega-Pérez et al. 2019) with viviparous reproduction (Jiménez-Cruz et al. 2005; Pérez-Mendoza et al. 2013). *S. grammicus* is considered the lizard with the widest distribution in Mexico (Sites et al. 1992; Lemos-Espinal and Ballinger 1995a). It inhabits trees and rocks in a wide variety of habitats, from deserts to forests (e.g., pine, oak) between ~100 and 3900 m (Lemos-Espinal et al. 1998), to mountainous ecosystems between 3900 and 4400 m (Sites 1982; Lemos-Espinal and Ballinger 1995a; Marshall et al. 2006). The *S. grammicus* species complex exhibits throat color polymorphisms, probably based on genetic variation, as reported for *Uta stansburiana* (Sinervo and Zamudio 2001). Within a single population, males may exhibit gray, yellow, or orange throat color morphs, and in absence of the gray morph in the population, males may exhibit blue, yellow, or orange throat color morphs (Bastiaans et al. 2013). As in other phrynosomatid lizards (Corl et al 2010a; Taylor and Lattanzio 2016), in this lizard, there are differences in the level of aggressiveness displayed by males of different color morph (Bastiaans et al. 2013). In populations without the blue throat color morph, the yellow males are the most aggressive

(Bastiaans et al. 2013; Fuentes-Dávila 2018), and those with the highest levels of circulating testosterone (Fuentes-Dávila 2018). This hormone has been positively related to aggressive behavior in different lizard species (Fuentes-Dávila 2018; Marler and Moore 1988; Sinervo et al. 2000), but also with lower survival probability (Marler and Moore 1988;1989). Therefore, the proportion of yellow-throated males would be expected to be the lowest in cold, low thermal quality sites but it has not been evaluated to date.

The main aim of the present study was to evaluate whether (i) the aggressive behavior of the lizard *S. grammicus* is associated with the environmental temperature along an elevational gradient, and (ii) there is an association between aggressiveness and throat color morph at the within population level. Our hypothesis was that time allocated to aggressive behavior in low thermal quality environments (i.e., here in too cold environments) is diverted from time spent on acquisition and maintenance of an optimal body temperature. We therefore expected that individuals that inhabit sites with low thermal quality would display lower levels of aggressive behavior (aggressiveness index and duration of lateral compression, see below) and higher amounts of nonaggressive behaviors (common use of a basking site and substrate licking, see below). We also predicted that, consistent with previous studies, individuals exhibiting the yellow throat color morph would be the most aggressive individuals within each population and consequently, the less frequent in the environment of low thermal quality.

MATERIAL AND METHODS

SAMPLING SITE

The study was conducted from July 2017 to December 2018 in La Malinche National Park, an inactive volcano of 4420 m altitude, in the central Mexican states of Tlaxcala and Puebla. We established three sampling sites based on their thermal characteristics. The low thermal quality site (d_e = 19.81) was located at 4150 m (Lat: 19.2386, Lon: -98.0347; Datum WGS 84), near the peak of the volcano. This site was characterized by an average (± SD) annual air temperature of 6.02 ± 4.7 °C and rocky alpine grassland with scattered shrubs of *Juniperus monticola* (Figure 1A). The mid thermal quality site (d_e = 11.04) was located at 3100 m (Lat: 19.2452, Lon: -98.0012), around La Malinche Scientific Station. This site was mainly covered by coniferous trees (*Pinus montezumae* and *Abies religiosa*), interspersed with clearings of abundant bunchgrass (Figure 1B), and with an average (± SD) air temperature of 9.31 ± 5.5 °C. The high thermal quality site ($d_e = 8.7$) was located at 2600 m (Lat: 19.2274, Lon: -97.9125) at a deserted ranch surrounded by maize fields, shrubs, and herbaceous plants, with an average (± SD) air temperature of 13.20 ± 6.69 °C (Figure 1C; Villers et al. 2006; Domínguez-Godoy et al. 2020).

Figure 1. Study sites at La Malinche National Park. (A) Low thermal quality site. (B) Mid thermal quality site. (C) High thermal quality site.

CAPTURE AND HUSBANDRY

We visited each study site 10 times with a 60-day interval between each day of visit. We captured male lizards by hand or using a lasso. We recorded coordinates of each site of capture using a hand-held GPS unit (Garmin ©, Oregon 360). We identified male lizards by the presence of blue ventral patches and enlarged post-cloacal scales. Females and juveniles were released after identifying their throat color morph.

Male lizards were transported in cloth bags to the facilities of the La Malinche Scientific Station. We recorded the snout-vent length (SVL) to the nearest 1 mm using a transparent ruler in order to assure we only used sexually mature individuals in this study (minimum size at adulthood: low thermal quality site: > 39 mm; mid thermal quality site: > 39 mm, and high thermal quality site: > 44 mm; see Lemos-Espinal and Ballinger 1995b; Jiménez-Cruz et al. 2005). To allow acclimatization before performing behavioral tests, each male was individually housed for 48 hours, in an acrylic terrarium (22 x 14 x 14 cm) with sterile peat moss as substrate, while preventing visual contact between individuals. Daily, each male received two larvae of *Tenebrio molitor* and water, as well as natural sunlight to maintain activity. At the end of the behavioral tests, we marked each lizard with an individual combination of skin marks using a surgical cauterizer (Bovie Change-A-Tip © Del 1) to identify them during potential recapture events (Ekner et al. 2011; Domínguez-Godoy et al. 2020). After cauterization, we applied cicatrizing powder (Kwik Stop © Styptic Powder) to prevent infection. Lizards were captured and manipulated with permission of the Secretaría de Medio Ambiente y Recursos Naturales (permit numbers SGPA/DGVS/15396/15 and SGPA/DGVS/007736/18). After behavioral tests, all lizards were released alive and in good condition at their place of capture. We followed all applicable institutional and national guidelines in Mexco for the care and use of animals in behavioral research. This research complies with the current laws of Mexico and the Animal Behavior Guidelines for experimentation with animals.

THROAT COLOR MORPHS

At all the sites, males had six possible throat color morphotypes: three pure morphs: yellow, orange, and gray, as well as three mixed morphs: yellow with orange, yellow with gray, and orange with gray (Figure 2). A morphotype was determined as pure (yellow, orange, or gray) when the color of the throat scales extended from the center to the margins of the throat (Figure S1). Mixed morphotypes were defined as individuals where the main color of the throat scales was interspersed with scales of a different color (Figure S1). To estimate the proportions of the throat color morphs, we included the data from individuals (males and females) captured from March 2015 to December 2018 at each sampling site.

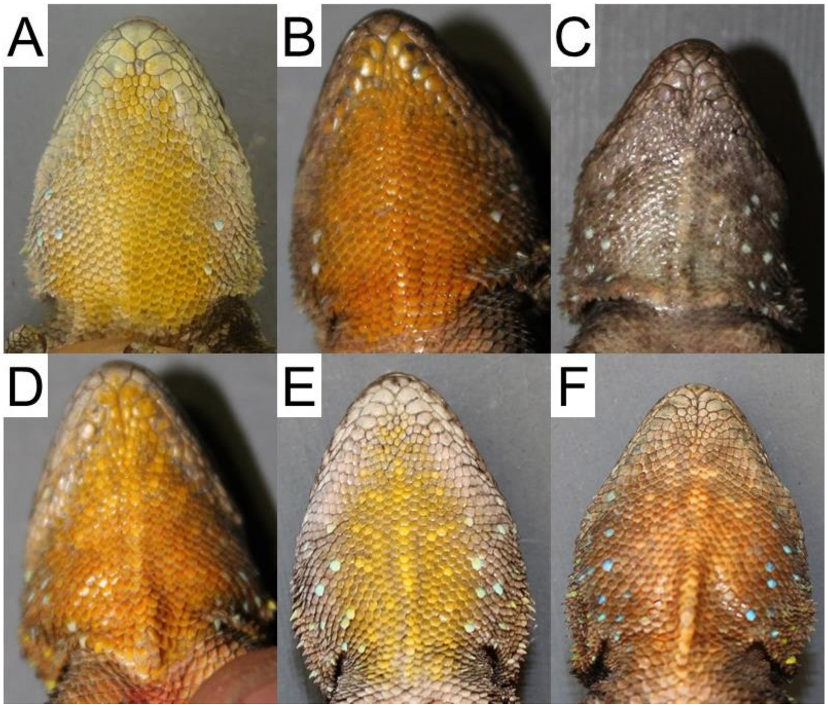

Figure 2. Representative examples of male throat color morphs present in La Malinche National Park: (A) Pure yellow. (B) Pure orange. (C) Pure gray. (D) Yellow-orange. (E) Yellow-gray. (F) Orange-gray.

AGGRESSIVE BEHAVIOR TEST

For the behavioral tests we used a glass arena (60 x 30 x 30 cm) with substrate of sterile peat moss. To promote competition between males we added a natural rock as a basking site (approx 15 x 9 x 7 cm) in the center of the arena, since it has been observed that the limited thermal resources generate competition (Calsbeek and Sinervo 2002; Rusch and Angilletta 2017). Before and during the test, we heated the basking site with an opaque bulb (Osram ©, Concentra BR-30, 75 W) suspended 45 cm above the rock. The temperature of the rock was determined using an infrared thermometer (Fluke ©, FLUKE-561) at the beginning and at the end of the test. The initial temperature of the rock was 24 °C (average substrate temperature in the field), and the final temperature never exceeded 33 °C (non-aversive temperature, and close to the temperature experimentally selected by these lizards; Díaz de la Vega-Pérez et al. 2019). Additionally, we placed a white light lamp (Osram ©, TWIST/865, 60 W) 45 cm above the rock to maintain the activity of the animals during the test. At the end of the test, we replaced the substrate and washed the rock with water and bleach (Clorox ©), to minimize possible chemical cues (Carazo et al. 2008).

We restricted the formation of pairs of males to those from the same site, with the constrain that the two males in a pair could not differ by more than 2 mm in size (SVL). We also excluded males with incomplete tails, as both factors can influence the outcome of confrontations (López and Martín 2001; Sacchi et al. 2009). To avoid the "dear enemy effect" (Carazo et al. 2008), we selected males that had been collected at a minimum distance of 40 m from each other at the capture site (see Bastiaans et al. 2013). We carried out 175 confrontations (low thermal quality site = 59; mid thermal quality site = 40; high thermal quality site = 76; Table S1), with each pair of males tested only once to avoid the effect of previous experience (Hsu et al. 2006). In total, 22 focal males (low thermal quality site = 6; mid thermal quality site = 6; high thermal quality site = 10) were used in more than one contest, but never matched with the same male and never in the same capture visit.

Before starting the test, we provided each male with natural sunlight. We measured body temperature of the contestants with an infrared thermometer (Fluke ©, FLUKE-561), until it gradually reached ~30.7 °C, the preferred body temperature (Díaz-de la Vega-Pérez et al. 2019). Then, we introduced the two males simultaneously into the test arena for 25 min. Behavior trials were recorded with a video camera (Panasonic © HC-V130) to record aggressive interactions (see Table 1) and use of the basking site.

VIDEO RECORD AND RELIABILITY

We analyzed all videos using Solomon Coder software (Version: beta17: 03: 22, Peter 2015), which allows recording of the frequency and/or duration of each of the selected behaviors. All videos were used to record the behavior of the focal male. If necessary, the frame-by-frame function was used to distinguish between individuals. All interactions were analyzed by a single person without knowledge of the origin of the individuals or of their throat color.

To assess intra-observer reliability, the same observer reanalyzed a random subset of four videos for each site (once for each male in the arena). Additionally, to assess inter-observer reliability, a second observer analyzed a different random subset of four videos from each site. With this information we calculated the percentage of agreement within and between observers, using the formula [(# agreements) / (# agreements + # disagreements)] * 100, and found 92.6% of intra-observer agreement and 82.4% of inter-observer agreement.

DESCRIPTION OF BEHAVIORS ANALYZED

AGGRESSIVE BEHAVIORS AND BEHAVIORAL SCORING

To assess individual levels of aggressive behavior we scored seven behaviors (For a detailed description see Table 1) documented as part of the behavioral repertoire during aggressive encounters in lizards (Carpenter and Ferguson, 1977; Carpenter, 1978; Brandt 2003; Weiss and Moore, 2004; Bastiaans et al. 2013; Myers and Paulissen, 2017), including in *S. grammicus* (Bastiaans et al. 2013). Because *S. grammicus* uses visual and chemical signals to communicate (Carpenter, 1978; Bastiaans et al. 2014; Johnson et al. 2019), as well as physical contact between the opponents (Bastiaans et al. 2013; Fuentes-Dávila 2018; Johnson et al. 2019), we included lick the opponent behavior (the lizard's tongue protrudes from its mouth and contacts its opponent) as an indirect sign of aggressive behavior that is related to chemical communication (Bastiaans et al. 2013; Fleishman and Font 2019; Johnson et al. 2019).

Subsequently, we categorized the behaviors based on their intensity (Weiss and Moore 2004), where the contact behaviors (lunge and bite) had the highest score. Thus, each behavior received a value from one to seven, according to its intensity (Table 1). To estimate the global aggressive behavior displayed by each focal subject, we calculated an aggressiveness index using the assigned score of each behavior multiplied by the frequency with which that behavior was displayed. Finally, the sum of these values was used as an index of the aggressiveness of each individual lizard (modified from Baird et al. 1997; López and Martín 2001; Weiss and Moore 2004; Sacchi et al. 2009). As the duration of threatening postures, such as lateral compression of the body, have been suggested to be an indirect measure of endurance capacity during aggressive encounters (Brandt 2003), we also recorded the total time of lateral compressions as a complementary measure.

NON-AGGRESSIVE BEHAVIORS

In contrast to the measures of aggressive behavior, we recorded the time the two lizards simultaneously shared the resource for which they presumably competed (use of the basking site). For this, we recorded the duration of all occasions when the two individuals were perched simultaneously on the rock.

We also recorded substrate licking (the lizard's tongue protrudes from its mouth and contacts the substrate; Table 1). This is related to the chemical recognition of conspecifics (Mason and Parker 2010; Vicente and Halloy 2016) and helps to discriminate between familiar and unfamiliar individuals and potentially to reduce costs associated with the defense and acquisition of resources by avoiding confrontations (López and Martín 2002).

Table 1. Aggressive behaviors, definitions, and scores. Behaviors scoring 1 is the lowest intensity behavior and 7 the highest.

Aggressive behavior	Description	Aggressive score
Tail vibration	The tip of the tail vibrates rapidly while holding onto the substrate.	1
Lick opponent	The lizard approaches the opponent and licks its body.	2
Lateral compression	The lizard adopts a rigid posture, with all four limbs extended and the tail raised. At the same time, it flattens its body in the sagittal plane, which increases the exposure area of the throat and ventral patches. This behavior can occur alone or in combination with push-ups, tail vibrations, lunges or bites, but was recorded individually.	3
Push-Up	This behavior initially starts from lateral compression, subsequently, the lizard begins to move its body up and down, while keeping the tail down. This movement is repeated quickly and multiple bouts. We recorded each of these bouts as one event. Sometimes this behavior is accompanied by a few steps towards the opponent.	4

Tail wave	This behavior initially starts from lateral compression. Subsequently, the lizard moves its body up and down, from the head to the tail, these sequence ends with the tail hitting the ground. Unlike the push-up, this movement does not repeat itself quickly, and it is possible to identify individual events.	5
Lunge	This behavior initially starts from lateral compression. Subsequently, the lizard wobbles his body, from side to side, before laterally throwing his body against the opponent.	6
Bite	The lizard opens his mouth and lunges head-on at his opponent. Sometimes he manages to cling momentarily to his adversary	7

STATISTICAL ANALYSES

AGGRESSIVE BEHAVIOR

We used the focal individual's aggressiveness index as response variable, and the male on the right side of the arena at the beginning of the test was identified as the focal individual in all encounters. To determine the effect of the thermal quality site on aggressive behavior, and to explore if males with the yellow throat morph were the most aggressive at each site, we used a generalized linear mixed model (GLMM) that included site (i.e., high, mid and low thermal quality) and the focal male color morph (i.e., yellow, orange, gray, yellow with orange, yellow with gray and orange with gray) as fixed factors. Additionally, we included the SVL as a covariate and the identity of the individual as a random factor (to control for the fact that some lizards were recaptured). The final model was obtained by successively removing non-significant terms ($P > 0.05$).

To test if the duration of the threat posture during the aggressive behavior test differed depending on the thermal quality of the capture site, we used a GLMM that included the duration of lateral compression as response variable, and the thermal quality site as a fixed factor. Additionally, we included lizards' identity as a random factor.

NON-AGGRESSIVE BEHAVIOR

We used a GLMM to determine if the common use of the basking site differed among the lizards of the three thermal quality sites. We used the duration of the common use of the basking site as a response variable, with site as predictor and identity as a random variable.

Finally, to evaluate if substrate licking behavior differed between the lizards coming from different thermal quality sites, we fitted a GLMM including the frequency of substrate licking as a response variable, thermal quality site as fixed factor, and identity as a random factor.

The GLMMs were performed using the package *glmmTMB* declaring a negative binomial distribution of errors. Post-hoc tests were performed with the package *emmeans*. The fit of models was visually explored and statistically evaluated using a simulation-based approach with the package *DHARMa*. All statistical tests were conducted using R version 4.0.2 (R Core Team 2020).

RESULTS

THROAT COLOR MORPH FREQUENCIES

The frequency of the morphotypes caught differed among the three thermal quality sites ($X^2_2 = 208.17$, $P < 0.001$). The yellow throat males were the most frequent at the high and low thermal quality sites, while at the middle site, the combined morph yellow- gray was the most abundant. At all three sites, the least abundant color morphotype was the combined orange-gray (Table S2; Figure 3).

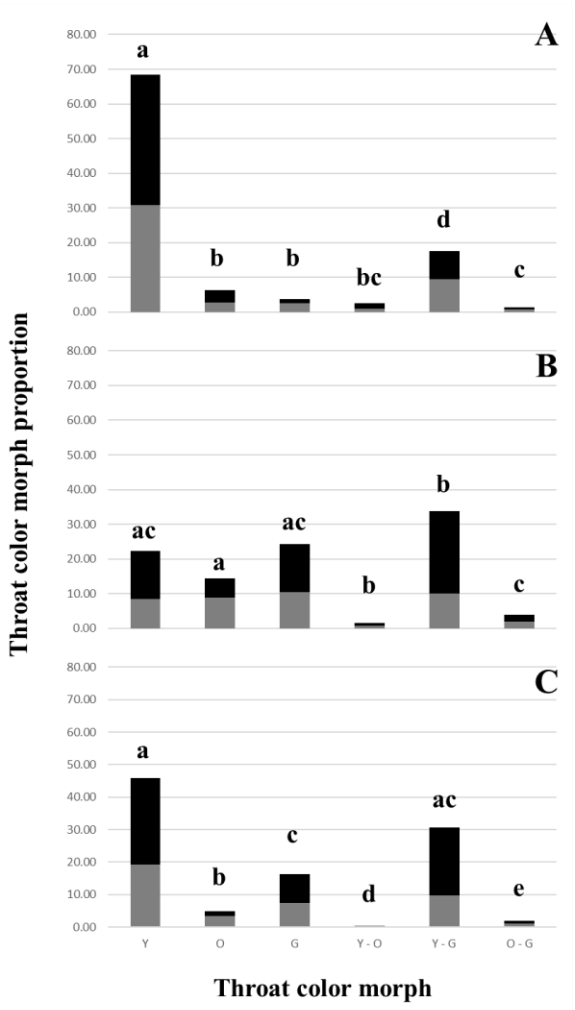

Figure 3. Proportions of each male (gray bars) and female (blak bars) throat color morphs registered from 2015 to 2018 in la Malinche National Park. (A) Low thermal quality site. (B) Mid thermal quality site. (C) High thermal quality site.

AGGRESSIVENESS INDEX

Aggressiveness varied among sites with different thermal quality ($X^2_2 = 24.56$, $P < 0.001$). The post-hoc tests showed that the aggressiveness index was significantly lower at the low thermal quality site compared to the other two sites (low – mid thermal quality site: $t_{170} = -3.697$, $P < 0.001$; low – high thermal quality site: $t_{170} = -4.674$, $P < 0.001$), but that there was no difference between the mid and high thermal quality sites ($t_{170} = -0.282$, $P = 0.957$; Figure 4A). We did not find an effect of the throat color morph ($X^2_5 = 5.54$, $P = 0.35$), or the interaction between throat color morph and site ($X^2_{10} = 10.48$, $P = 0.39$) on the aggressive behavior. Neither did body size influenced aggressiveness ($X^2_1 = 0.71$, $P = 0.78$).

DURATION OF THE THREAT POSTURE

The thermal quality of the site was related to the duration of lateral compressions performed during male-male encounters ($X^2_2 = 31.40$, $P < 0.001$). The post-hoc tests showed that the duration of lateral compression was shorter in lizards from the low thermal quality site compared to the other two sites (low – mid thermal quality site: $t_{171} = -3.746$, $P < 0.001$; low – high thermal quality site: $t_{171} = -5.451$, $P < 0.001$) However, there were no differences between the lizards from the high and mid thermal quality sites ($t_{171} = -0.916$, $P = 0.631$; Figure 4B).

BASKING SITE USE

The duration of common basking site use was associated with the thermal quality of the sites ($X^2_2 = 8.60$, $P = 0.013$). The post-hoc test showed that common basking site use was shorter in lizards from the high thermal quality site compared to individuals from the other two sites (low – high thermal quality site: $t_{170} = 2.435$, $P = 0.041$; mid – high thermal quality site: $t_{170} = 2.452$, $P < 0.040$). However, there were no differences between lizards from the mid and low thermal quality sites ($t_{170} = -0.275$, $P = 0.959$; Figure 4C).

EXPLORATORY BEHAVIOR

The frequency of substrate licking performed by focal males during encounters was not influenced by the capture site ($X^2_2 = 0.19$, $P = 0.906$).

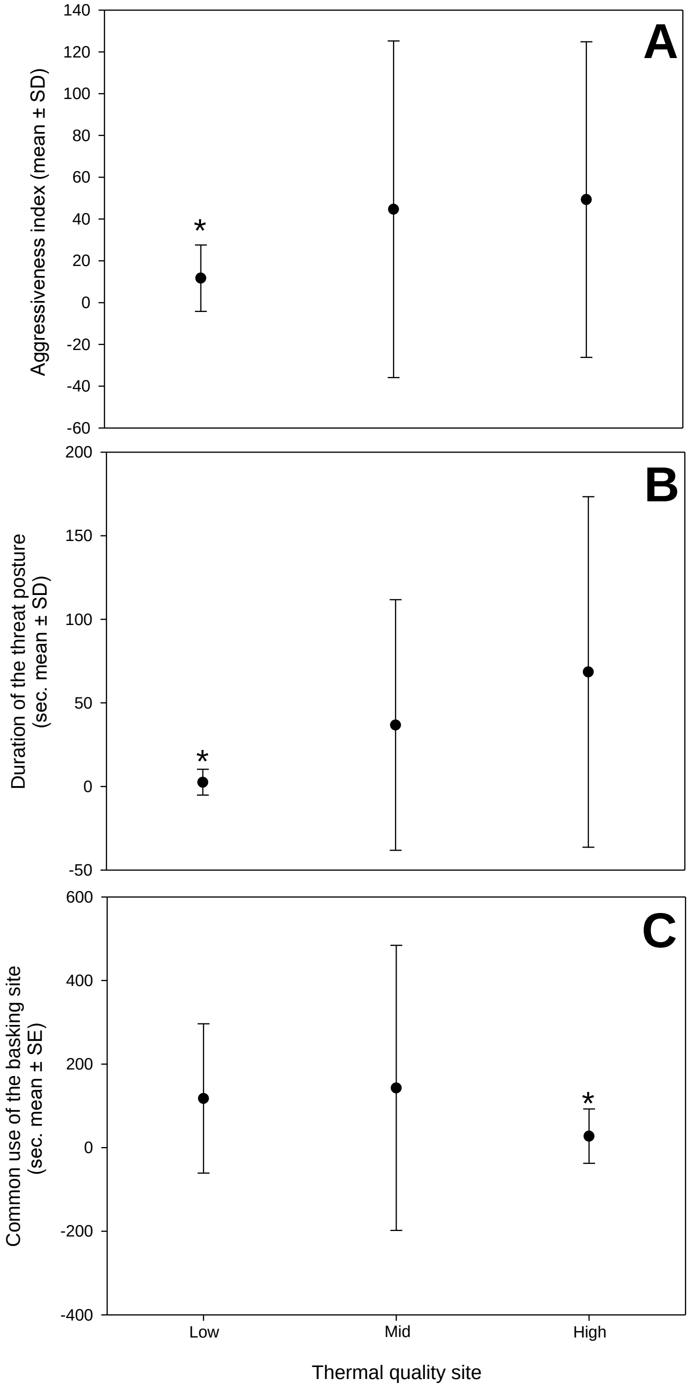

Figure 4. Association between thermal quality site and: (A) aggressive behavior (Mean ± SD), (B) duration of the threat posture (lateral compression; mean ± SD), and (C) common use of the basking site (mean ± SD). Asterisk denote the site that showed statistical differences in the behavior form the other two, see methods for statistical details.

DISCUSSION

Here we evaluated whether aggressive behavior interferes with thermoregulation, and therefore where, and therefore, whether individuals from low quality thermal environments would exhibit less aggressive behavior in controlled trials. As predicted, we found an association between the thermal quality of the site and the aggressive index displayed by males, with individuals from the low thermal quality site being the least aggressive ones. Interestingly, we did not observe an effect of the throat color morph on the aggressiveness index at the within population level.

Our results suggest that aggressive behavior in low thermal quality environments interferes with the acquisition and maintenance of an adequate body temperature. As has been pointed out in several studies, that the aim of aggressive interactions is to take possession of food, territories, or mates during competition with conspecifics (Hodge et al. 2009; Baxter et al. 2015; Duque-Wilckens et al. 2019). However, time, energy loss and the risk of injury or predation during the contest may outweigh the benefits to be gained by fighting, depending on the environmental context (Halliwell et al. 2017). Additionally, the short duration of lateral compression displays by lizards from the low thermal quality site may indicate a high physiological cost of aggressive behavior in thermically restrictive environments. According to Brandt (2003), this posture interferes with aerobic metabolism due to thoracic compression. Then the high levels of aggression may reduce fitness (Knell 2009), and non-aggressive behaviors may be favored (Davis-Rabosky et al. 2012) under low thermal quality ambient conditions. Therefore, it is likely that the benefits of thermoregulation at low thermal quality sites outweigh the cost of aggressive behavior (Díaz de la Vega-Pérez et al. 2019) because the higher metabolic expenditure (Plasman et al. 2020).

Contrary to our expectations (and previous findings), we did not find an association of color morphotype with aggressive behavior. Previous studies have found that yellow throat color morphs have a higher aggressiveness index (Bastiaans et al. 2013). Although these results may be due, in part, to the low numbers of some morphotypes in the confrontations we performed yet note that the most common morph in this study, yellow, was the one with higher reported aggressiveness index in previous studies (Bastiaans et al. 2013; Fuentes-Dávila 2018). At the low thermal quality site, ~80 % of the focal males (Table S1) and ~70 % of all individuals captured (males, females, and juveniles; Table S2) were of the yellow morph. In addition to exhibiting a lower aggressiveness index, individuals from the low thermal quality site showed longer periods of common use of the basking site. Therefore, the high frequency of this throat color morph at the low thermal quality site could suggest a change in the frequency of the population morphotypes (Corl et al. 2010b), a greater flexibility in the aggressive behavior associated with the throat color morphs, or also, possibly be indicative of other attributes associated with this morph, such as greater parasite or disease resistance (McKinnon and Pierotti 2010), that increase the fitness of this morphotype in extreme high mountain environments.

Low thermal quality environments increase thermoregulation costs (Huey and Slatkin 1976) in actively thermoregulating lizards (Blouin-Demers and Nadeau 2005) such as *S. grammicus* (Diaz de la Vega-Pérez et al. 2019). Also, we know that the performance of the physiological functions is influenced by temperature (Avery et al. 1982; Huey 1982; Adolph and Porter 1993; Meek 1995). In addition to being energetically expensive, aggressive behavior can be physiologically restricted by body temperature itself, which limits the muscular activity of the lizards (Herrel et al. 2007). However, previous studies suggest that the mesquite lizard has different morphological (e.g., smaller size and dark dorsal coloration, Barrios-Montiel 2019; González-Morales et al. 2020), physiological (e.g., higher metabolic rate and changes in hematic parameters, González-Morales et al. 2017; Barrios-Montiel 2019; Plasman et al. 2020), and behavioral strategies (e.g., decreased locomotor activity, Lemos-Espinal and Ballinger 1995a) that, together with low predation pressure (Domínguez-Godoy et al. *in press*), allow it to cope with the extreme temperature conditions that prevail in high mountain environments and increasing the probability of survival (Domínguez-Godoy et al. 2020). Then, the reduction in aggressive behavior at the lower thermal quality site, could be a behavioral adaptation to a low temperature environment. If so, it could have repercussions for this species' mating strategies and account for the loss of sexual dimorphism in size (Corl et al. 2010b; Diaz de la Vega-Pérez et al. 2019).

The low aggressiveness index and high frequency of the yellow throat color morph of the lizards at the low thermal quality site could indicate a change in population dynamics (McLean and Stuart-Fox 2014). Because aggressive behavior may be particularly important in male-male competition for access to females, more aggressive males may increase their reproductive success (Lewis et al. 2000) Differences in the ability to monopolize resources can establish alternative mating strategies (Emlen and Oring 1977). According to the alternative mating strategy proposed by Sinervo and Lively in 1996, in polymorphic systems (e.g., *U. stansburiana, Urosaurus ornatus, Zootoca vivipara, S. grammicus*), the coexistence of different morphotypes is achieved through a negative frequency-dependent selection. However, if the fitness of one of the strategies, or morphotypes, overcomes the others, it can lead to the elimination of one or more of the morphs in the population (Zamudio and Sinervo 2003) and promote speciation through the divergence of populations (McLean and Stuart-Fox 2014), as observed in *U. stansburiana* (Corl et al. 2010b). Our study reveals the importance of thermal quality on the performance of aggressive behavior as well as the possible implications in the population dynamics of *S. grammicus*. In addition, it raises new questions to know if there is a definitive change in the frequency of the morphotypes in *S. grammicus*, as well as if it brings adaptive advantages to the yellow throat morph.

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SUPPLEMENTARY MATERIAL

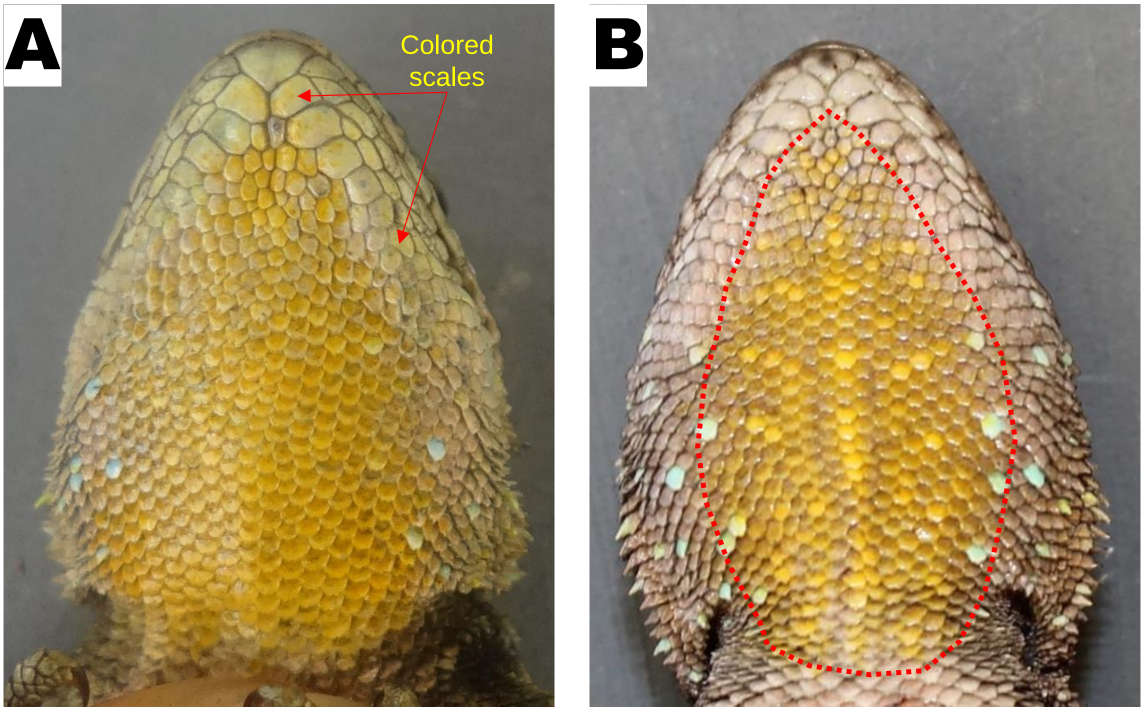

Figure S1. Comparison between A) pure, and B) combined throat color morphs in *S. grammicus* from la Malinche National Park. Dashed red line delimits the throat colored scales.

Table S1. Number of confrontations between different combinations of male (focal and opponent) throat color morphs. (A) Low, (B) mid, and (C) high thermal quality sites.

A

		Opponent throat color morph					
		Y	O	W	Y-O	Y-W	O-W
Focal throat color morph	Y	43	1	0	0	2	0
	O	2	0	0	1	0	1
	G	1	0	0	0	0	0
	Y-O	1	0	0	0	0	0
	Y-G	4	0	0	0	2	0
	O-G	0	0	0	0	0	1

B

		Opponent throat color morph					
		Y	O	W	Y-O	Y-W	O-W
Focal throat color morph	Y	1	3	0	0	0	1
	O	3	3	0	0	6	1
	G	2	4	2	0	1	0
	Y-O	0	1	0	0	0	0
	Y-G	2	5	0	0	1	1
	O-G	1	1	1	0	0	0

C

		Opponent throat color morph					
		Y	O	W	Y-O	Y-W	O-W
Focal throat color morph	Y	16	0	1	0	6	1
	O	4	1	0	0	1	0
	G	6	0	1	2	1	0
	Y-O	4	1	1	0	0	0
	Y-G	13	1	0	1	9	0
	O-G	3	0	1	0	2	0

Table S2. Proportion of male and female throat color morphs observed between 2015-2018 at three different elevations.

	2600 m		**3100 m**		**4150 m**	
Throat color	**Males %**	**Females %**	**Males %**	**Females %**	**Males %**	**Females %**
Yellow	46.32 (107)	45.42 (149)	20.79 (21)	23.17 (35)	65.12 (155)	71.32 (189)
Yellow-Orange	1.29 (3)		01.98 (2)	1.32 (2)	2.1 (5)	3.01 (8)
Yellow-Gray	23.8 (55)	35.36 (116)	24.75 (25)	39.73 (60)	19.74 (47)	15.47 (41)
Orange	8.22 (19)	2.43 (8)	21.78 (22)	9.27 (14)	5.88 (14)	6.79 (18)
Orange-Gray	2.59 (6)	1.52 (5)	4.95 (5)	3.31 (5)	1.68 (4)	1.13 (3)
Gray	17.74 (41)	15.24 (50)	25.74 (26)	23.17 (35)	5.46 (13)	2.26 (6)

11. DISCUSIÓN GENERAL

La temperatura ambiental es determinante para los ectotermos, ya que de ella depende su temperatura corporal y, en consecuencia, el correcto funcionamiento de sus procesos metabólicos (Avery et al. 1982; Adolph y Porter, 1993). A medida que la temperatura ambiental difiere de los requerimientos térmicos de los organismos ectotermos (i.e. menor calidad térmica), incrementan los costos de la termorregulación (DeWitt 1967; Huey y Slatkin 1976). Por lo tanto, se espera que en los sitios de baja calidad térmica las horas de actividad disponibles para realizar sus funciones biológicas se reduzcan (Huey y Slatkin 1976), lo que puede reducir su probabilidad de supervivencia (Downes 2001) y, en periodos prolongados, causar la extirpación o la extinción de algunas especies (Sinervo et al. 2010). Sorpresivamente, en esta investigación, no sólo encontré que la calidad térmica es un factor que influye en la supervivencia de *S. grammicus*, también encontré que existe una relación inversa entre la probabilidad de supervivencia y la calidad térmica. En el sitio más elevado y frío, la probabilidad de supervivencia fue mayor que en los sitios más bajos. La variación en la calidad térmica resulta en diferentes costos de termorregulación para las lagartijas del Mesquite que habitan a lo largo de nuestro sitio de estudio y, en consecuencia, encontré cambios en las presiones de depredación y en la conducta agresiva de los machos. Los resultados de esta investigación sugieren que: 1) no todas las especies son igualmente afectadas por las restricciones térmicas del ambiente y 2) las temperaturas ambientales, altas y bajas, no imponen los mismos costos energéticos.

Comparado con estudios previos (Ortega-Rubio et al. 1999; Zuñiga-Vega et al. 2008), estos resultados coinciden en que la probabilidad de supervivencia es mayor en sitios más elevados. Sin embargo, esta es la primera vez que se utiliza el índice de calidad térmica del ambiente como una variable de interés para explicar estas variaciones (Capítulo 1). Sabemos que el descenso en la calidad térmica de los tres sitios se debe principalmente a que la temperatura ambiental se encuentra por debajo de la temperatura media seleccionada por esta especie (Díaz de la Vega-Pérez et al. 2019), ya que en pocas ocasiones supera la temperatura crítica máxima. Asimismo, sabemos que en el sitio más elevado cerca del 50% de las temperaturas operativas, registradas durante las horas de actividad, se encuentran por debajo de la temperatura crítica mínima (Capítulo 1). Si bien, el contrastante entre la calidad térmica y la supervivencia está parcialmente sustentado por la disminución en las presiones de depredación a mayor elevación (Capítulo 2), es posible que también se deba a una combinación de factores, como las adaptaciones morfológicas, fisiológicas, y conductuales que se han documentado previamente. Por ejemplo, se sabe que las lagartijas que se encuentran en el sitio más elevado tienen una menor talla corporal y mayor pigmentación dorsal que aumenta su tasa de calentamiento corporal (González-Morales et al. 2020), además de poseer una mayor tasa metabólica en reposo (Plasman et al. 2020). Asimismo, algunas investigaciones sugieren que pasar tiempo dentro de refugios térmicos es una estrategia eficiente en ambientes térmicamente estresantes (Andersson et al. 2010; Martín y López 2010), que puede favorecer la supervivencia (Martín et al. 2003; Amo et al. 2007), a través de una menor exposición a depredadores (Pianka y Pianka 1970; Formanowicz et al. 1990), y un menor gasto metabólico (Steffen y Appel 2012). En conjunto, estas características pueden ayudarles a reducir los costos de la termorregulación y promover la supervivencia en condiciones extremas de temperatura.

Las lagartijas que habitan sitios con temperaturas ambientales subóptimas disminuyen su actividad durante los periodos restrictivos del día (Vidal et al. 2010), como se ha observado en *S. grammicus* (Lemos-Espinal y Ballinger 1995). Por otra parte, las lagartijas más activas, que se encuentran en sitios térmicamente más favorables, incurren en un mayor riesgo de depredación debido a que incrementan su detectabilidad ante los depredadores (Pianka y Pianka 1970; Carter et al. 2010). De manera interesante, los mismos factores que favorecen la tasa de calentamiento (i.e. mayor pigmentación dorsal y menor talla corporal) pueden ayudar a *S. grammicus* a pasar desapercibida por los depredadores, como se ha sugerido en otros estudios (Reguera et al. 2014). Adicionalmente, la baja presencia de depredadores potenciales en sistemas de alta montaña, como nuestros sitios de estudio, (Adolph y Porter 1993; Fox et al. 1994; Capítulo 2), puede ayudar indirectamente a contrarrestar los efectos adversos de las bajas temperaturas ya que pueden dedicar menos tiempo a estrategias antidepredatorias. De este modo, las lagartijas que se encuentran en los sitios más elevados y fríos pueden invertir más tiempo en conductas de termorregulación (Lemos-Espinal y Ballinger 1995), incluso incrementar su probabilidad de supervivencia (Capítulo 1).

Encontré una asociación entre la calidad térmica y la conducta agresiva en machos de *S. grammicus*. No sólo observé una disminución en la frecuencia y la intensidad de las conductas agresivas realizadas por los machos del sitio con menor calidad térmica (4150 msnm), también un incremento en la duración de la conducta no agresiva (i.e. uso compartido de la percha). Se ha observado que los individuos termorregulan con menor precisión durante las confrontaciones agresivas (Rusch y Angilletta 2017), por lo que algunos investigadores han sugerido que existe un compromiso con la termorregulación (Engbretson y Livezey 1972). Por lo tanto, es probable que los ambientes térmicamente restrictivos favorezcan a los individuos menos agresivos (Knell 2009). Inexplicablemente, no encontré un efecto del morfotipo gular de los machos sobre la conducta agresiva, como se había reportado anteriormente en esta (Bastiaans et al. 2013; Fuentes-Dávila 2018) y en otras especies relacionadas (Sinervo y Zamudio 2001; Corl et al. 2010; Taylor y Lattanzio 2016). Sin embargo, la abundante presencia del morfotipo amarillo (presuntamente el más agresivo, Bastiaans et al. 2013; Fuentes-Dávila 2018) sugiere que las estrategias conductuales asociadas a los morfotipos no son estáticas, o la presencia de otros posibles atributos asociados a la coloración gular (McKinnon y Pierotti 2010).

En conjunto, estos resultados sugieren que la calidad térmica es un factor ecológico clave para estudiar la ecología de los reptiles, ya que, a diferencia de la temperatura ambiental, nos permite interpretar los resultados en términos de los costos de la termorregulación, con base en los requerimientos térmicos de las especies. Además, muestran que las lagartijas que habitan sitios térmicamente desfavorables cuentan con una serie de adaptaciones morfológicas, fisiológicas y conductuales que favorecen la termorregulación y la ganancia de calor para mantener sus procesos fisiológicos. Asimismo, los resultados sugieren que los costos generados por la disminución en la calidad térmica difieren con relación a la temperatura que restringe la actividad. Por ejemplo, nuestros resultados indican que, la supervivencia incrementa en ambientes fríos, mientras que reportes previos sugieren que el incremento en la temperatura tiene efectos deletéreos para los reptiles (Sinervo et al. 2010; Zhang et al. 2018). Por lo tanto, las futuras investigaciones deberán centrarse en estudiar los efectos causados por la disminución en la calidad térmica bajo diferentes escenarios, por ejemplo: en especies con distribuciones restringidas, especies ovíparas o en ambientes con restricciones causada por el incremento de la temperatura ambiental, para ayudarnos a entender los posibles efectos y repercusiones ante el cambio climático global. En conclusión, a través de la calidad térmica, podemos estudiar la influencia del ambiente térmico sobre la conducta y las dinámicas poblacionales.

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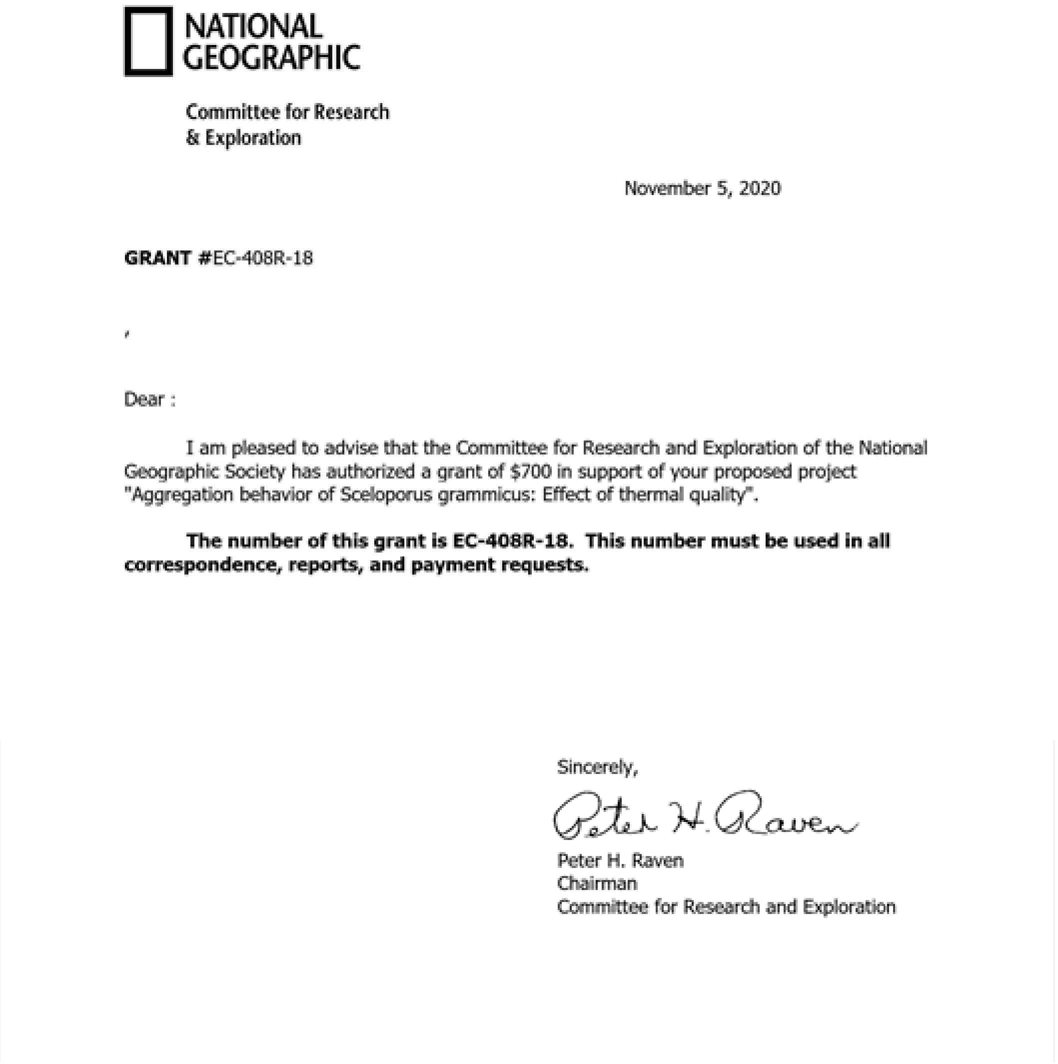
12. FINANCIAMIENTO OBTENIDO Y PRODUCTOS ADICIONALES PUBLICADOS DURANTE EL DOCTORADO

FINANCIAMIENTO

1) National geographic (EC-408R-18)



NATIONAL
GEOGRAPHIC

Committee for Research
& Exploration

November 5, 2020

GRANT #EC-408R-18

,

Dear :

I am pleased to advise that the Committee for Research and Exploration of the National Geographic Society has authorized a grant of $700 in support of your proposed project "Aggregation behavior of Sceloporus grammicus: Effect of thermal quality".

The number of this grant is EC-408R-18. This number must be used in all correspondence, reports, and payment requests.

Sincerely,

Peter H. Raven

Peter H. Raven
Chairman
Committee for Research and Exploration

2) Western North America Naturalist (WNAN-S-20-00026)

Dear Dr. Aníbal H. Díaz de la Vega,

Thank you for your grant proposal to the *Western North American Naturalist*. We received an overwhelming response of over 60 proposals, and we read and reviewed each one. We then rated the proposals a one, two, or three, with one being the highest rating. These ratings were based on many different aspects of the proposal, including how compelling the natural history research proposed was and whether the research could be funded without the *WNAN* grant.

We are pleased to inform you that you have been selected as one of five grant recipients to receive $2,000 to fund your proposed research. Your proposal included a compelling explanation of why your research should be funded, and it focused on the natural history aspect of your research. We will send you another email soon with information about how we will transfer the funds. One year after you receive the funds, please send us an accounting of how you used the funds. Remember that funds cannot be used for institutional overhead.

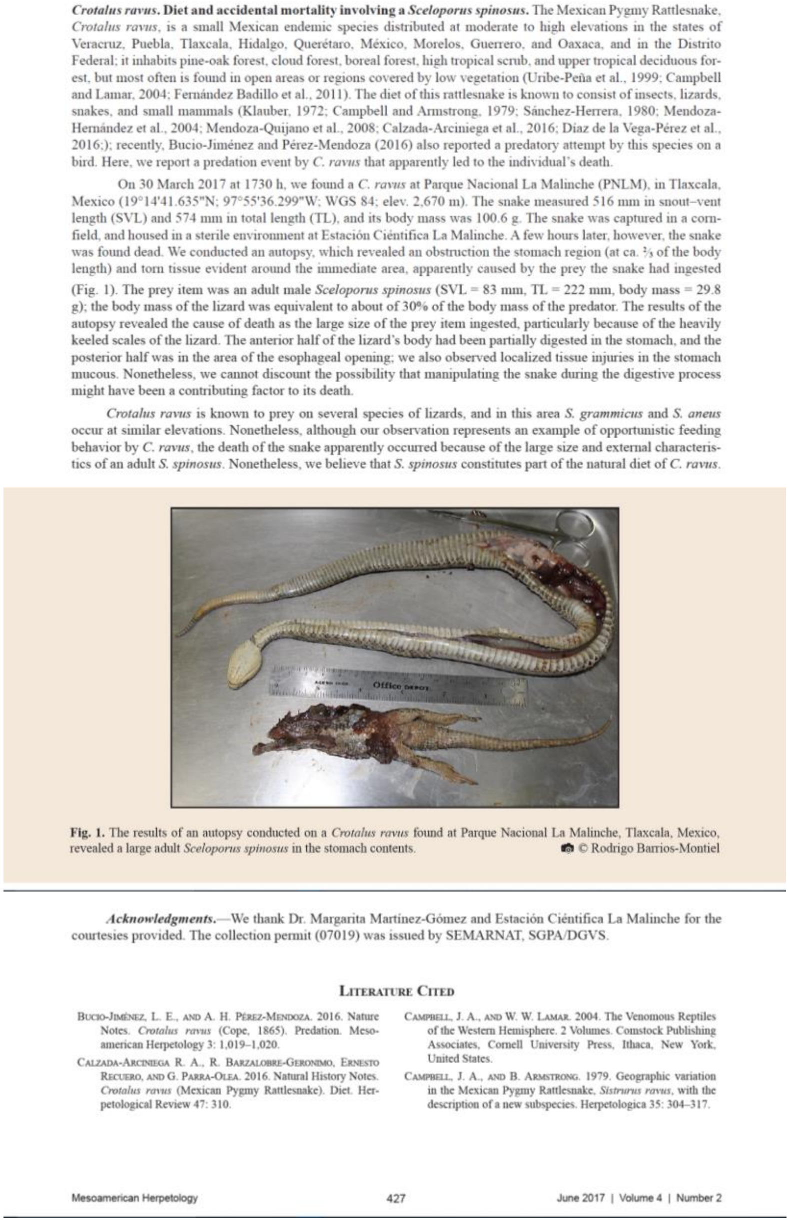
Based on your grant proposal, we except you to submit your finished manuscript to the W*estern North American Naturalist* by July 2019. This manuscript will be sent out for peer review like all other manuscripts we receive. Should your manuscript be accepted, it will be slated for publication in the next issue with space available. As an added benefit of receiving the grant, we will not bill you for page charges.

Thank you again for your exceptional grant proposal. We look forward to working with you throughout your research and the possible publication of your manuscript.

Best regards,
Mark C. Belk, *WNAN* editor-in-chief
Janene Auger, *WNAN* managing editor

Notas científicas

Domínguez-Godoy, M.A., Barrios-Montiel, R., Bautista, A., y Díaz de la vega-Pérez, A.H. 2017. *Crotalus ravus*. Diet and accidental mortality involving a *Sceloporus spinosus*. Mesoamerican Herpetology 4:426-428.



***Crotalus ravus*. Diet and accidental mortality involving a *Sceloporus spinosus*.** The Mexican Pygmy Rattlesnake, *Crotalus ravus*, is a small Mexican endemic species distributed at moderate to high elevations in the states of Veracruz, Puebla, Tlaxcala, Hidalgo, Querétaro, México, Morelos, Guerrero, and Oaxaca, and in the Distrito Federal; it inhabits pine-oak forest, cloud forest, boreal forest, high tropical scrub, and upper tropical deciduous forest, but most often is found in open areas or regions covered by low vegetation (Uribe-Peña et al., 1999; Campbell and Lamar, 2004; Fernández Badillo et al., 2011). The diet of this rattlesnake is known to consist of insects, lizards, snakes, and small mammals (Klauber, 1972; Campbell and Armstrong, 1979; Sánchez-Herrera, 1980; Mendoza-Hernández et al., 2004; Mendoza-Quijano et al., 2008; Calzada-Arciniega et al., 2016; Díaz de la Vega-Pérez et al., 2016;); recently, Bucio-Jiménez and Pérez-Mendoza (2016) also reported a predatory attempt by this species on a bird. Here, we report a predation event by *C. ravus* that apparently led to the individual's death.

On 30 March 2017 at 1730 h, we found a *C. ravus* at Parque Nacional La Malinche (PNLM), in Tlaxcala, Mexico (19°14'41.635"N; 97°55'36.299"W; WGS 84; elev. 2,670 m). The snake measured 516 mm in snout–vent length (SVL) and 574 mm in total length (TL), and its body mass was 100.6 g. The snake was captured in a cornfield, and housed in a sterile environment at Estación Cientifica La Malinche. A few hours later, however, the snake was found dead. We conducted an autopsy, which revealed an obstruction the stomach region (at ca. ⅔ of the body length) and torn tissue evident around the immediate area, apparently caused by the prey the snake had ingested (Fig. 1). The prey item was an adult male *Sceloporus spinosus* (SVL = 83 mm, TL = 222 mm, body mass = 29.8 g); the body mass of the lizard was equivalent to about of 30% of the body mass of the predator. The results of the autopsy revealed the cause of death as the large size of the prey item ingested, particularly because of the heavily keeled scales of the lizard. The anterior half of the lizard's body had been partially digested in the stomach, and the posterior half was in the area of the esophageal opening; we also observed localized tissue injuries in the stomach mucous. Nonetheless, we cannot discount the possibility that manipulating the snake during the digestive process might have been a contributing factor to its death.

Crotalus ravus is known to prey on several species of lizards, and in this area *S. grammicus* and *S. aneus* occur at similar elevations. Nonetheless, although our observation represents an example of opportunistic feeding behavior by *C. ravus*, the death of the snake apparently occurred because of the large size and external characteristics of an adult *S. spinosus*. Nonetheless, we believe that *S. spinosus* constitutes part of the natural diet of *C. ravus*.

Fig. 1. The results of an autopsy conducted on a *Crotalus ravus* found at Parque Nacional La Malinche, Tlaxcala, Mexico, revealed a large adult *Sceloporus spinosus* in the stomach contents.

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Acknowledgments.—We thank Dr. Margarita Martínez-Gómez and Estación Cientifica La Malinche for the courtesies provided. The collection permit (07019) was issued by SEMARNAT, SGPA/DGVS.

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NOTA CIENTÍFICA

DEPREDACIÓN DE LAGARTIJAS POR ***LANIUS LUDOVICIANUS*** (ALCAUDÓN AMERICANO) EN EL PARQUE NACIONAL LA MALINCHE, MÉXICO.

PREDATION OF LIZARDS BY ***LANIUS LUDOVICIANUS*** (LOGGERHEAD SHRIKE) IN LA MALINCHE NATIONAL PARK, MEXICO.

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Abstract.– Here we document predation events of the Loggerhead Shrike (*Lanius ludovicianus*) on two species of lizards in La Malinche National Park.

Keywords.– Impalement behavior, *Sceloporus aeneus*, *Plestiodon brevirostris*.

Resumen.– En esta nota documentamos eventos de depredación del alcaudón americano (*Lanius ludovicianus*) sobre dos especies de lagartijas en el Parque Nacional la Malinche.

Palabras clave.– Conducta de empalamiento, *Sceloporus aeneus*, *Plestiodon brevirostris*.

El alcaudón americano (*Lanius ludovicianus*) es un ave con distribución amplia que se encuentra desde el sur de Canadá hasta el noroeste de Oaxaca (Miller, 1931; Vázquez et al., 2009). Se alimenta de insectos, anfibios, reptiles (Martín & López, 1990; Yosef & Grubb, 1993; Young et al., 2004; Cogalniceanu, 2015), aves y pequeños mamíferos (Bent, 1964; Yosef, 1996; Cogalniceanu et al., 2015). Esta ave es conocida debido a que presenta la conducta de empalamiento de sus presas, ya a que no tiene garras con la fuerza necesaria para despedazar a sus presas, por lo tanto, desarrolló un comportamiento de empalamiento para facilitar la ingesta (Cade, 1995; Cogalniceanu, 2015).

Se ha sugerido que esta conducta tiene diferentes funciones, una de ellas es una estrategia de cortejo de los machos, para exponer a sus presas en estacas naturales o artificiales como “regalos nupciales” para las hembras (Sarkozi & Brooks, 2003), ya que a través de estas señales, las hembras pueden evaluar la calidad de los machos y su capacidad para proveer alimento (Lefranc & Worfolk, 1997; Yosef, 2008). Otras funciones son las la de almacenar el alimento, defender un territorio y la competencia reproductiva (Smith, 1972; Cogalniceanu et al., 2015; Lara-Resendiz et al., 2019).

El 26 de junio de 2018 encontramos 12 lagartijas empaladas colocadas en estacas naturales en distintas perchas. Estas presas estaban distribuidas a lo largo de un camino de terracería entre los límites de los municipios de San Juan Ixtenco y Ziltlaltépec de Trinidad Sánchez Santos (19.227744°N, 97.91145°W; WGS 84, 2600 m s.n.m.) dentro del Parque Nacional La Malinche, Tlaxcala, México. Registramos un transecto lineal de 76 x 15 m a lo largo del camino rodeado de cultivos de maíz y pastizales inducidos. En total registramos 55 posibles sitos de percha de *L. ludovicianus*, de los cuales, únicamente siete presentaron lagartijas empaladas en estacas. La coloración de los parches ventrales y la presencia/ausencia de escamas postcloacales, nos permitieron identificar 11 lagartijas adultas de la especie *Sceloporus aeneus* (seis machos y cinco hembras), así como una cría de *Plestiodon brevirostris* (Fig. 1). Los sitios seleccionados por *L. ludovicianus* para empalar a las presas fueron arbustos del género *Salvia* y magueyes pulqueros (*Agave salmiana*), de una altura de 80 a 120 cm en los arbustos y de 140 a 180 cm en los magueyes aproximadamente.

Aunque hemos observado otras especies de lagartijas (*Aspidoscelis costata*, *Barisia imbricata*, *Prynosoma orbiculare*, *Sceloporus grammicus* y *S. spinosus*) en esta elevación dentro

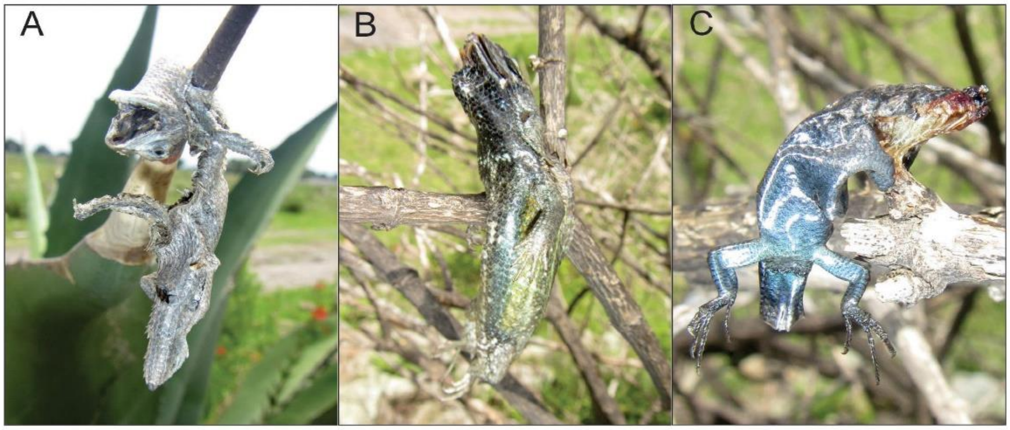

Figure 1. (A) *Sceloporus aeneus* in the spine of *Agave salmiana*, (B) Male of *S. aeneus* in a *Salvia* bush, (C) Young Plestiodon brevirostris in a *Salvia* bush in La Malinche National Park, Tlaxcala, Mexico. Photos: Anibal H. Díaz de la Vega-Pérez.

Figura 1. (A) *Sceloporus aeneus* en espina de maguey pulquero, (B) *S. aeneus* macho en arbusto de *Salvia*, (C) Cría de *Plestiodon brevirostris* en arbusto de *Salvia* en el Parque Nacional La Malinche, Tlaxcala, México. Fotos: Aníbal H. Díaz de la Vega-Pérez.

del Parque Nacional La Malinche que podrían ser incluidas en la dieta del alcaudón americano, únicamente *S. aeneus* y *P. brevirostris* fueron registradas como presas durante este muestreo. Nuestras observaciones sugieren que *S. aeneus* es potencialmente una de las principales presas que *L. ludovicianus* incluye en su dieta, debido a que es muy abundante en esta elevación. Las zonas abiertas cercanas a los cultivos y pastizales inducidos podrían promover que el alcaudón americano forrajee activamente en estos sitios en el Parque Nacional La Malinche.

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Artículo

Romero-Báez, Ó., Santos-Bibiano, R., Domínguez-Godoy, M.A., Miles, D. B., y Muñoz-Nolasco, F.J. 2020. Thermal ecophysiology of a native and an invasive gecko species in a tropical dry forest of Mexico. Journal of Thermal Biology. 102607. https://doi.org/10.1016/j.jtherbio.2020.102607

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Thermal ecophysiology of a native and an invasive gecko species in a tropical dry forest of Mexico

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