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FACULTAD DE CIENCIAS BIOLÓGICAS

“Compromisos de la termorregulación conductual en hábitats
perturbados de un ecosistema cálido”

T E S I S

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RESUMEN GENERAL

Las extinciones de animales asociadas al calentamiento del hábitat se asocian con el aumento de tiempo en conductas termorreguladoras, como refugiarse a la sombra, a costa del tiempo disponible para otras actividades. Para entender los *trade-off* de las conductas termorreguladoras debemos considerar tres cuestiones. Primero, dilucidar los costos asociados de las conductas termorreguladoras: costos de energía, tiempo y seguridad. Por ejemplo, destinar menos energía a procesos fisiológicos, destinar menos tiempo a otras actividades esenciales y aumentar el riesgo de depredación, respectivamente. Segundo, debemos considerar el contexto de los animales como su época reproductiva y la pérdida del hábitat. Tercero, debemos plantear la aplicación de este conocimiento a la conservación biológica. Por lo tanto, el objetivo general fue profundizar en el efecto del calentamiento del hábitat, asociado a la pérdida de cubierta vegetal, sobre los costos de las conductas termorreguladoras en reptiles terrestres no aviares. Planteamos tres objetivos particulares. Primero, revisar de manera sistematizada los artículos científicos sobre los tres tipos de costos de las conductas termorreguladoras de reptiles terrestres considerando los ambientes cálidos o frescos de los sitios de estudio. Encontramos que los costos de seguridad fueron estudiados con más frecuencia que los de energía en ambientes frescos y latitudes templadas, solo registramos un estudio de latitudes tropicales, y casi no había estudios para serpientes y tortugas. El segundo objetivo particular fue poner a prueba la existencia de un *trade-off* entre conductas territoriales y termorreguladoras de una lagartija territorial, *Sceloporus ochoterenae*. Registramos el primer *trade-off* entre conductas territoriales y termorreguladoras en

un animal terrestre. Descubrimos como el *trade-off* era afectado por la cubierta vegetal, temperatura microclimática y presencia de un intruso conespecífico. El tercer objetivo particular fue poner a prueba la efectividad de un área protegida para conservar la cubierta vegetal y regular sus temperaturas microclimáticas asociadas, así como el efecto de ambas sobre la termorregulación de lagartijas simuladas de *Sceloporus horridus*. Encontramos que la cubierta vegetal fue mayor dentro del área protegida que en los alrededores más perturbados, y fue mayor 20 años después de su declaración, lo cual se vio reflejado en menores temperaturas microclimáticas del hábitat, así como menores temperaturas corporales y tasas metabólicas basales de las lagartijas simuladas. Esta tesis reúne, genera y aplica conocimiento sobre los costos de las conductas termorreguladoras de reptiles terrestres para colaborar con el entendimiento de los efectos indirectos del calentamiento del hábitat sobre los reptiles terrestres.

INTRODUCCIÓN GENERAL

El calentamiento del hábitat es una realidad en múltiples partes del mundo debido a la pérdida de la cubierta vegetal y el calentamiento climático (Franco et al. 2006). Los reptiles terrestres no aviares (*de aquí en adelante* reptiles terrestres) mitigan el calentamiento del hábitat mediante conductas termorreguladoras para mantener su homeostasis (Kearney et al. 2009) y el rendimiento de sus procesos fisiológicos (Tuff et al. 2016). Las conductas termorreguladoras implican diversos costos, por ejemplo, tiempo invertido en mantenerse caliente o fresco a costa del tiempo invertido en otras actividades (Angilletta 2009). Los costos de las conductas termorreguladoras para mitigar el calentamiento del hábitat se asocian a extinciones de múltiples especies de lagartijas (Sinervo et al. 2010) y aves (Riddell et al. 2019). En consecuencia, debemos entender los costos de las conductas termorreguladoras e identificar sus vacíos de conocimiento. Debemos aportar conocimiento a los costos de conductas termorreguladoras poco explorados que afecten la sobrevivencia y/o reproducción. Debemos plantear acciones de mitigación que disminuyan los costos de las conductas termorreguladoras derivadas del calentamiento del hábitat. Esta tesis aporta a estas tres metas.

El bosque tropical estacionalmente seco (BTES) pierde su cubierta estacionalmente o por actividades humanas lo que afecta su temperatura. Los BTES son uno de los ecosistemas más amenazados del mundo (*revisado en* Portillo-Quintero y Sánchez-Azofeifa 2010). Sólo el 29% de la superficie original del BTES de México permanecía como bosque primario en 2004 (*revisado en* Portillo-Quintero y Sánchez-Azofeifa 2010). La pérdida de la cubierta vegetal de forma natural o antropogénica provoca el calentamiento del hábitat. Por un lado, los cambios

estacionales de temperatura y precipitación en los BTES conducen a que la mayoría de los árboles tiren sus hojas en la estación seca (*revisado en Portillo-Quintero y Sánchez-Azofeifa 2010*). La defoliación intervino en el calentamiento medio del aire de 3.8°C en dos BTES de Chamela, México (*Siliceo-Cantero et al. 2016*). Por otro lado, la disminución del 44% de la cubierta vegetal por la deforestación aumentó la temperatura media del suelo en 3.4°C en el BTES de Chamela, México (*Suazo-Ortuño et al. 2008*). La deforestación puede intensificar los efectos de la estación seca sobre la temperatura y humedad del hábitat. Por ejemplo, la temperatura media del aire fue 4°C más alta en pastizales antropogénicos que en polígonos conservados en el BTES de Guanacaste, Costa Rica durante la estación seca (*Klemens et al. 2011*).

El cambio en los microclimas del hábitat puede afectar la temperatura corporal de los reptiles terrestres, lo cual incide sobre su desempeño térmico. Por ejemplo, de manera estacional, la temperatura corporal media de iguanas *Ctenosaura oaxacana* fue 2.3°C más alta durante la estación seca que en la lluviosa en el BTES de Montecillo Santa Cruz, Oaxaca, México (*Valenzuela-Ceballos et al. 2015*). El calentamiento corporal de reptiles terrestres incide sobre su curva desempeño térmico. La curva de desempeño térmico es la representación gráfica de la medición de alguna actividad física o proceso fisiológico del organismo como función de su temperatura corporal (*Aparicio-Ramirez et al. 2021*). El desempeño aumenta lentamente desde la temperatura crítica mínima del organismo hasta la temperatura voluntaria mínima (VT_{min}), sigue aumentando hasta alcanzar sus valores más altos en el rango de temperaturas óptimas, el desempeño comienza a disminuir cerca de la temperatura voluntaria máxima (VT_{max}), luego de lo cual

disminuye rápidamente hacia la temperatura crítica máxima (Camacho y Rusch 2017).

Cuando la temperatura corporal de los reptiles terrestres supera su VT_{max} , se sobrecalientan. Si los reptiles terrestres no pueden disminuir su temperatura corporal, el sobrecalentamiento sostenido puede afectar sus caracteres de historia de vida o incluso comprometer su probabilidad de sobrevivencia, amenazando en última instancia la persistencia de sus poblaciones (Bestion et al. 2015). Por ejemplo, lagartijas *Zootoca vivipara* experimentaron un ciclo de vida acelerado y una menor sobrevivencia de los adultos en encierros silvestres que eran 2°C más cálidos que la temperatura ambiente de un bosque templado, lo que llevó a predecir su extirpación en 20 años (Bestion et al. 2015).

Los reptiles terrestres en general evitan sobrecalentarse mediante conductas termorreguladoras (Camacho y Rusch 2017). Los reptiles terrestres suelen aumentar su inversión de tiempo en conductas termorreguladoras a medida que aumenta la temperatura del hábitat en ambientes cálidos (Lara-Reséndiz et al. 2015; James y Porter 1979). Por ejemplo, lagartijas *Gambelia sila* aumentaron su porcentaje de tiempo de actividad en madrigueras para refrescarse en praderas con menor densidad de arbustos (Gaudenti et al. 2021). Aves y mamíferos también pueden evitar el sobrecalentamiento mediante conductas termorreguladoras (*revisado en* Cunningham 2021). Por ejemplo, cabras *Capra Ibex* evitaron las altas temperaturas de los valles durante primavera-verano al desplazarse a mayores elevaciones en praderas alpinas (Mason et al. 2017).

Los reptiles terrestres no pueden mantener una inversión indefinida en conductas termorreguladoras debido a sus tres costos asociados. Los tres costos

son la disminución en la disponibilidad energética para otros procesos fisiológicos, llamado costo de energía; disminución en el tiempo de actividad disponible para otras actividades esenciales, llamado costos de tiempo; aumento del riesgo de depredación o de enfrentamientos, llamado costo de seguridad (Huey y Stevenson 1979; Angilletta 2009 p. 111). Por ejemplo, con respecto al costo de energía, la distancia que recorrieron lagartijas *Cordylus oleofseni* (Basson et al. 2017) y *Crotaphytus collaris* (Brewster et al. 2013) para calentarse bajo lámparas alejadas entre sí fue mayor cuando eran encendidas alternadamente que cuando ambas se mantenían encendidas en ambientes frescos de laboratorio. Con respecto al costo de tiempo, lagartijas *Psammotromus algirus* pasaron más tiempo resguardadas en puntos sombreados de bosques templados en 2017 que en 1997 debido al calentamiento atmosférico (Díaz et al. 2022). Con respecto al costo de seguridad, tortugas *Gopherus polyphemus* retardaron su escape al escondite ante la presencia de un depredador potencial cuando el interior de sus escondites era más fresco que el exterior en un bosque de pino (Radzio y O'Connor 2017). Lagartijas *Lacerta monticola* disminuyeron su tiempo dentro del refugio después de un intento de depredación cuando el interior de sus escondites era más fresco que el exterior en un laboratorio (Polo et al. 2005).

Ha habido avances significativos en el estudio de los costos de las conductas termorreguladoras, no obstante, no están claras ciertas cuestiones relevantes. El estudio de los costos de las conductas termorreguladoras se enfocó en costos energéticos de diversas especies de lagartijas (Huey y Webster 1976). Posteriormente se actualizó el conocimiento sobre los costos de energía con lagartijas *Agama atra* en un matorral de proteáceas y diversas especies de insectos

alrededor del mundo (*revisado en* Fey et al. 2019). Se actualizó el conocimiento sobre los costos de tiempo con múltiples especies de aves y mamíferos terrestres de regiones desérticas (*revisado en* Cunningham et al. 2021). No obstante, actualmente no contamos con una revisión que abarque los tres costos de conductas termorreguladoras como fue sugerido (Huey y Stevenson 1979). Los costos de las conductas termorreguladoras varían con respecto al contexto ecológico del reptil terrestre (Angilletta 2009; Garland et al. 2022), pero esto no ha sido considerado en las revisiones relativas a los costos de conductas termorreguladoras (*excepto* Fey et al. 2019). Por lo tanto, necesitamos una revisión que englobe los costos de energía, tiempo y seguridad de las conductas termorreguladoras y que los analice considerando su contexto ecológico. La revisión planteada enriquecería el marco teórico sobre los *trade-off* asociados a las conductas termorreguladoras.

Los reptiles terrestres son modelos adecuados para poner a prueba los potenciales *trade-offs* de las conductas termorreguladoras porque dependen de su hábitat para termorregular. En específico, los reptiles terrestres de ambientes cálidos como el BTES experimentan una estación seca de cuatro a seis meses durante primavera-verano, en la cual disminuye el porcentaje de cubierta vegetal y aumenta la visibilidad del hábitat (*revisado en* Dirzo et al. 2011). Estos cambios estacionales propiciaron temperaturas del aire más altas en un BTES de Chamela, México (Suazo-Ortuño et al. 2008), menor disponibilidad alimenticia para insectívoros en un BTES de Chamela, México (Lister y Aguayo 1992) y mayor visibilidad frente a depredadores en un BTES de Brasil (Ferreira y Faria 2021) en comparación con la estación lluviosa. En consecuencia, reptiles terrestres del BTES

como *Sceloporus melanorhinus* y *S. utiformis* disminuyen su actividad (García et al. 2010) y guecos de *Chlamydosaurus kingii* buscan microhábitats frescos con más frecuencia (Christian y Bedford 1995) durante la estación seca que, durante la lluviosa. El cambio estacional en el uso de hábitat y horario de actividad de los reptiles terrestres del BTES mitiga el agotamiento de sus reservas de agua y energía (Christian y Bedford 1995; García et al. 2010). No obstante, algunos reptiles terrestres del BTES mantienen altas tasas de actividad durante la estación seca. Por ejemplo, lagartijas de *Sceloporus horridus*, *S. spinosus* (Valdéz-González y Ramírez-Bautista 2002) y *S. ochoterenae* (Bustos-Zagal et al. 2011) comienzan a realizar flexiones y cabeceos con intenciones de cortejo y defensa del territorio fuera de sus escondites durante la estación seca del BTES. De tal manera que, la estación seca del BTES favorece conductas termorreguladoras para mantenerse fresco, pero a la vez presenta reptiles terrestres realizando actividades esenciales para su reproducción fuera de sus refugios, lo cual plantea *trade-offs* potenciales entre sus conductas termorreguladoras y conductas reproductivas.

La cubierta vegetal afecta los *trade-off* entre las conductas termorreguladoras y la pérdida de oportunidades para realizar otras actividades esenciales (Kearney 2013; Gaudenti et al. 2021; Lara-Reséndiz et al. 2022). La vegetación intercepta la radiación solar, aumenta la humedad del hábitat y dispone una estructura vertical y horizontal de microhábitats cuyos microclimas pueden ser explotados por los animales para termorregular (Davis et al. 2019; Pincebourde y Woods 2020). En consecuencia, la conservación de la cubierta vegetal puede mantener servicios ecosistémicos como la regulación de la temperatura microclimática. Por ejemplo, el porcentaje de la cubierta vegetal promedio es generalmente mayor dentro de las

áreas protegidas del mundo que en las áreas adyacentes no protegidas (*revisado por* Laurance et al. 2012 y Geldmann et al. 2013b), incluyendo ecosistemas áridos como la sabana (Wasiolka y Blaum 2011) y el desierto (Al-Sayegh et al. 2020). Entonces, las áreas protegidas deberían mantener microclimas más frescos al proteger la cubierta vegetal y, por tanto, disminuir el riesgo de sobrecalentamiento de los reptiles terrestres en comparación con las áreas no protegidas. Sólo conocemos un estudio empírico que puso a prueba esta idea, el cual no encontró un patrón claro (Al-Sayegh et al. 2020). Las temperaturas corporales medias diarias de lagartijas *Uromastix aegyptia* fueron similares en las áreas protegidas y no protegidas adyacentes de un desierto, a pesar de que la cubierta vegetal promedio fue mayor en las áreas protegidas que en las no protegidas (Al-Sayegh et al. 2020). Para entender mejor si y cómo las áreas protegidas mitigan el sobrecalentamiento de los reptiles, necesitamos estudios que comparen el efecto de las áreas protegidas sobre la cubierta vegetal, y a su vez sobre el microclima experimentado por los reptiles terrestres considerando sus conductas termorreguladoras.

El objetivo general de la tesis fue profundizar en el efecto del calentamiento del hábitat debido a la pérdida de cubierta vegetal sobre los costos de las conductas termorreguladoras en reptiles terrestres. Para ello se plantearon los siguientes tres objetivos particulares. Primero, revisar la literatura sobre los tres tipos de costos de las conductas termorreguladoras de reptiles terrestres considerando la temperatura ambiental de los sitios de estudio como componente del contexto ecológico. Para ello comparamos la frecuencia de estudios entre los tres costos de conductas termorreguladoras, después realizamos esta comparación entre ambientes cálidos y frescos, comparamos la frecuencia de estudios entre zonas latitudinales, grupos

taxonómicos y aproximaciones metodológicas. El segundo objetivo particular consistió en tres fases. Primero, poner a prueba la existencia de un *trade-off* entre conductas territoriales y termorreguladoras de una lagartija territorial, *Sceloporus ochoterenae*, del BTES en Morelos, México. Segundo, determinar la conducta limitante del *trade-off*. Tercero, determinar el efecto de la cubierta vegetal, temperatura microclimática, y presencia de un intruso conespecífico sobre el *trade-off*. Para esto registramos el tiempo que diferentes machos realizaban flexiones, como indicadores de conductas territoriales, y se refugiaban a la sombra, como indicadores de conductas termorreguladoras, en territorios con distinta cubierta vegetal y, por ende, con distinta temperatura microclimática. El tercer objetivo particular fue poner a prueba la efectividad de un área protegida de BTES para conservar la cubierta vegetal y regular las temperaturas microclimáticas disponibles para la termorregulación de lagartijas simuladas de *Sceloporus horridus*, una especie de lagartija generalista del BTES en Morelos, México. Para esto comparamos la cubierta vegetal y temperatura microclimática asociada, así como variables de la ecología térmica de lagartijas simuladas de *S. horridus* a su escala espacial y considerando sus conductas termorreguladoras entre el interior y alrededores de la Reserva de la Biósfera Sierra de Huautla, así como durante su declaración y 20 años después. Esta tesis aporta al estudio de los *trade-off* de las conductas termorreguladoras de reptiles terrestres de ambientes cálidos, así como la aplicación de este conocimiento a la evaluación de implementaciones de conservación biológica, como áreas protegidas.

CAPÍTULO 1. Costos de la termorregulación conductual en reptiles terrestres: revisión sistematizada.

Abstract

Los reptiles terrestres no aviares amortiguan el efecto de la temperatura ambiental sobre su temperatura corporal mediante conductas termorreguladoras. Las conductas termorreguladoras plantean tres costos asociados. Primero, destinar menos energía a procesos fisiológicos, costo de energía. Segundo, destinar menos tiempo a otras actividades esenciales, costo de tiempo. Tercero, aumentar el riesgo de depredación, costo de seguridad. Estos tres costos plantean *trade-offs* que funcionan como uno de los mecanismos por los cuales el calentamiento climático está causando extinciones. Actualmente no contamos con una revisión que aborde en conjunto los tres tipos de costos de las conductas termorreguladoras, que considere el contexto ecológico, ni que se enfoque en reptiles terrestres. En consecuencia, nosotros revisamos de manera sistematizada los artículos científicos sobre los costos de energía, tiempo y seguridad de las conductas termorreguladoras de reptiles terrestres desde 1900 hasta 2019. Consideramos 28 artículos científicos y los categorizamos según el tipo de costo de la termorregulación, si el estudio se realizó en un ambiente cálido o fresco, zona latitudinal del sitio de estudio, grupo taxonómico estudiado y aproximación metodológica. Encontramos que los tres tipos de costos se estudiaron con una frecuencia similar. Los tipos de costos fueron estudiados con una frecuencia similar en ambientes cálidos. Los costos de seguridad fueron estudiados con más frecuencia que los de energía en ambientes frescos y en latitudes templadas. Solo registramos un estudio para latitudes

tropicales. Las tortugas y serpientes se estudiaron en menor frecuencia que las lagartijas. Los estudios se concentraron en experimentos de campo o laboratorio. Las marcadas diferencias de la biología térmica entre reptiles terrestres de latitudes tropicales y templadas dificultan extender a los de latitudes tropicales las predicciones de los de latitudes templadas sobre sus costos de conductas termorreguladoras. Sugerimos que los costos de tiempo por ocupar refugios frescos podrían aumentar conforme aumente la temperatura del hábitat en ambientes cálidos. Sugerimos que los costos de seguridad por competir por refugios frescos podrían aumentar conforme aumente el calentamiento del hábitat en ambientes cálidos.

Palabras clave: conducta termorreguladora, *trade-off*, reptil, latitud tropical, calentamiento climático.

Introducción

La termorregulación se refiere a la capacidad de los reptiles terrestres no aviares (*de aquí en adelante* reptiles terrestres) para mantener su temperatura corporal dentro de sus temperaturas preferidas por medio de ajustes fisiológicos y conductuales (*revisado en* Huey 1982). Los reptiles terrestres termorregulan con mayor precisión cuanto menos diverge su temperatura corporal de su intervalo de temperaturas preferidas (Hertz et al. 1993). Los reptiles terrestres que termorregulan con precisión pueden mantener un desempeño óptimo de los caracteres termosensibles asociados a su adecuación; por ejemplo, locomoción, percepción, metabolismo y reproducción (*revisado en* Huey 1982; Bels y Russell 2019).

La inversión de los reptiles terrestres en conductas termorreguladoras conllevan costos de energía, tiempo y seguridad que plantean *trade-offs*. La energía y tiempo invertidos por el reptil terrestre en termorregular para obtener sus beneficios supone tres costos (Angilletta 2009). Primero, la disminución en la disponibilidad de energía para otros procesos fisiológicos genera un costo de energía. Segundo, la disminución en la disponibilidad de tiempo de actividad para otras actividades esenciales genera un costo de tiempo. Tercero, el aumento en la frecuencia de interacciones ecológicas negativas como la depredación o competencia generan un costo de seguridad (Angilletta 2009).

El contexto del reptil terrestre puede repercutir en los costos de energía, tiempo y seguridad asociados a sus conductas termorreguladoras. La intensidad de los costos y *trade-offs* del reptil terrestre dependen de los recursos y condiciones de su ambiente, así como de su estado fisiológico, es decir, de su contexto ecológico (*sensu* Garland et al. 2022). Los tres costos asociados a las conductas termorreguladoras de reptiles terrestres podrían variar entre ambientes frescos y cálidos. Por un lado, los reptiles terrestres de latitudes templadas necesitan calentarse ya que sus ambientes frescos suelen presentar temperaturas ambientales menores a sus temperaturas preferidas (*revisado en* Deutsch et al. 2008; Kearney et al. 2009; Sunday et al. 2014). Por otro lado, los reptiles terrestres de latitudes tropicales necesitan refrescarse ya que sus ambientes cálidos suelen presentar temperaturas ambientales iguales o mayores a sus temperaturas preferidas (*revisado en* Deutsch et al. 2008; Kearney et al. 2009; Sunday et al. 2014).

Con respecto al costo de energía, lagartijas de *Cordylus oelofseni* (Basson et al. 2017) y *Crotaphytus collaris* (Brewster et al. 2013) se desplazaron continuamente para mantenerse en parches insolados que cambiaban de lugar en un laboratorio con el fin de calentarse en ambientes frescos. De manera similar, lagartijas de *Acanthodactylus longipes* se desplazaron mayores distancias en dunas vegetadas más deforestadas con el fin de refrescarse bajo arbustos en ambientes cálidos (Attum y Eason 2006).

Con respecto al costo de tiempo, lagartijas de *Iberolacerta cyreni* pasaron hasta el 80% de su tiempo de actividad exponiéndose en puntos insolados para calentarse en ambientes frescos de laboratorio (Aguado y Braña 2014). Mientras, lagartijas de *Psammodromus algirus* pasaron hasta el 90% de su tiempo de actividad en sitios sombreados para refrescarse durante los meses más cálidos del año en un bosque templado (Díaz et al. 2022).

Con respecto a la pérdida de seguridad, la exposición de lagartijas de *Agama planiceps* en puntos insolados para calentarse las expuso ante sus depredadores en ambientes frescos de una savana (Carter et al. 2010). Lagartijas de *Lacerta monticola* acortaron su duración dentro de escondites frescos para minimizar el enfriamiento de sus cuerpos luego de un intento de depredación en laboratorio (Polo et al. 2005). Por otro lado, la conducta termorreguladora de usar refugios para refrescarse en ambientes cálidos podría disminuir la visibilidad del reptil ante depredadores, escapando así del *trade-off* termorregulación-depredación.

Los costos de conductas termorreguladoras cuentan con múltiples avances significativos, no obstante, existen cuestiones relevantes que aún no son abordadas. En 1974 se planteó que las conductas termorreguladoras de lagartijas

Anolis cristatellus implicaban costos de energía por buscar sitios soleados en un bosque tropical lluvioso (Huey 1974). Posteriormente, se actualizaron algunas nociones sobre los costos de energía de las conductas termorreguladoras con lagartijas *Carlia spp.* en un bosque seco de *Melaleuca* (Vickers et al. 2011) y con lagartijas *Agama atra* en un matorral de proteáceas (Fey et al. 2019). Después se actualizaron algunas nociones sobre los costos de tiempo de las conductas termorreguladoras con múltiples especies de aves y mamíferos terrestres de ambientes cálidos (Cunningham et al. 2021). A pesar de los avances mencionados, importantes cuestiones sobre los costos de conductas termorreguladoras de reptiles terrestres quedan por resolver desde la ecología y la biología de la conservación. Por ejemplo, no se han integrado en un solo estudio los costos de energía, tiempo y seguridad de las conductas termorreguladoras como fue propuesto inicialmente (Huey y Webster 1976). No se ha considerado explícitamente el efecto del contexto ecológico sobre dichos costos, con excepción de (Fey et al. 2019). No se ha considerado una revisión sobre el tema enfocándose en reptiles terrestres, grupo vulnerable en temas de conservación biológica de vertebrados terrestres (*revisado en* Roll et al. 2017).

Los costos de las conductas termorreguladoras pueden estar aumentando en frecuencia, lo que agudiza el problema sobre su falta de conocimiento. La frecuencia de las conductas termorreguladoras va en aumento debido al incremento en las temperaturas microclimáticas provocadas por la pérdida del hábitat y el calentamiento climático (Ortega et al. 2016; Díaz et al. 2022). En consecuencia, los costos de las conductas termorreguladoras también pueden estar aumentando en frecuencia e intensidad (*revisado en* Cunningham et al. 2021). Por ejemplo, cabras

Capra ibex están pasando menos tiempo forrajeando en los valles de matorrales alpinos, los cuales son más productivos pero también más calientes, con el fin de mantenerse más tiempo refrescándose en laderas frescas (Mason et al. 2017).

Tanto la falta de conocimiento como el aumento en la frecuencia de costos de conductas termorreguladoras hacen necesaria la síntesis del conocimiento al respecto considerando el contexto ecológico de reptiles terrestres. Nosotros realizamos una revisión sistematizada de literatura científica sobre los costos de energía, tiempo y seguridad de las conductas termorreguladoras de reptiles terrestres para abordar las siguientes preguntas ¿alguno de los tres tipos de costos cuenta con menos estudios que los otros?, ¿La frecuencia de estudio de los tipos de costos varía entre ambientes frescos y cálidos?, ¿Los estudios al respecto están distribuidos aleatoriamente entre regiones geográficas, grupos taxonómicos y aproximaciones metodológicas?

Consideramos como modelo de estudio a los reptiles terrestres por dos razones. Primero, los reptiles terrestres son especialmente sensibles a la oferta térmica disponible, la cual explotan para termorregular (Hertz et al. 1993). Segundo, los reptiles terrestres están subrepresentados en las áreas protegidas a pesar de componer un tercio de la riqueza de los vertebrados terrestres (*revisado en* Roll et al. 2017).

Métodos

La presente revisión sistematizada (*sensu* Grant y Booth 2009) consistió en 5 fases sucesivas explicadas a continuación: búsqueda, filtrado, categorización, análisis y resultados y discusión.

Búsqueda de los registros. Buscamos artículos científicos revisados por pares, no literatura gris, en los que se hubieran estudiado los costos de conductas termorreguladoras realizadas por reptiles terrestres. Los términos de búsqueda incluyeron varios términos de tres temas: reptiles terrestres, termorregulación conductual y costos de conductas termorreguladoras. Buscamos los términos en el título, abstract y palabras clave de los artículos mediante el motor de búsqueda de Web of Science. Consideramos registros desde 1900 hasta marzo de 2019, periodo que comprendía la base de datos de Web of Science. Buscamos los registros que incluían los términos del primer tema, posteriormente refinamos la búsqueda con los términos del segundo tema y, finalmente, refinamos la búsqueda con los términos del tercer tema. Entonces, nuestra oración de búsqueda inicial fue la siguiente: TS=(tigmotherm\$ OR heliotherm\$ OR stenotherm* OR euritherm\$ OR poikilotherm\$ OR "cold blood" OR reptile\$ OR lizard\$ OR toad\$ OR snake\$ OR Sceloporus OR Phrynosomatidae OR skink\$ OR anolis OR gecko\$ OR viper\$ OR boa). Después, refinamos la búsqueda inicial con la siguiente oración: "behavioral thermoregulation" OR "thermoregulatory behavior" OR "behaviorally regulate body temperature" OR "thermal regulation" OR "regulation of body temperature" OR "therm* quality" OR "therm* precision" OR "therm* efficiency" OR "therm* safety" OR thermoregulation OR thermoregulatory OR CTmax OR CTmin. Finalmente, refinamos la búsqueda con la siguiente oración: tradeoff\$ OR "trade-off\$" OR "cost-benefit\$" OR "cost benefit\$" OR "net\$benefit" OR compromise OR optimality OR optimal OR cost\$ OR benefit\$ OR maxim*.

Filtrado de los registros. Encontramos un total de 609 registros. Leímos los títulos, abstracts y, de ser necesario, las introducciones y métodos de los registros

encontrados. Cuatro de los registros estaban repetidos. En 329 registros no se abordaban reptiles terrestres, sino mamíferos, aves, anfibios, artrópodos o reptiles acuáticos. 276 registros sí abordaban reptiles terrestres. En 211 registros no se abordaban conductas termorreguladoras, sino por ejemplo, señales de comunicación, respuesta inmunitaria o conductas de hidrorregulación. 65 registros sí abordaban conductas termorreguladoras. En 47 registros no se abordaban costos de las conductas termorreguladoras, sino por ejemplo, estudios sobre termofisiología, ecología térmica o modelos de riesgo de extinción. 18 registros sí abordaban costos explícitos de las conductas termorreguladoras, por ejemplo, más energía invertida en el desplazamiento para termorregular a costa de la energía invertida en otros procesos fisiológicos, más tiempo invertido en termorregular a costa del tiempo invertido en otras actividades, más frecuencia o intensidad de interacciones ecológicas negativas como depredación o competencia por realizar conductas termorreguladoras.

Descartamos la mayoría de los registros, lo cual puede tener tres explicaciones no excluyentes. Primero, los artículos que incluyen términos de los tres temas considerados son poco numerosos, a pesar de que los mismos términos cuentan con numerosos artículos por separado. Segundo, nos aseguramos de que los artículos que incluían los términos de los tres temas no solo los mencionaran, sino que realmente investigaran costos de conductas termorreguladoras realizadas por reptiles terrestres. Tercero, es una práctica común eliminar más del 95% de los registros encontrados durante el proceso de filtrado en revisiones sobre temas biológicos (*por ejemplo*, Mantyka-pringle et al. 2012; Geldmann et al. 2013a; Winter et al. 2016; Fuller et al. 2020; Mesa-Sierra et al. 2022).

Posterior al filtro de los registros, leímos las referencias de los 18 artículos resultantes, pero solo exploramos el abstract, introducción y método de aquellas referencias cuyo título fuera cercano a nuestro tema de estudio. Incluimos los artículos de las referencias que aprobaron el proceso de filtrado, es decir, en los que se estudiaron costos de conductas termorreguladoras realizadas por reptiles terrestres. Mediante este proceso agregamos 22 registros más. Removimos tres registros de que no abordaban costos de las conductas termorreguladoras de manera explícita, sino en términos del índice de precisión térmica. Dicho índice no es una expresión de la energía o tiempo invertidos en la termorregulación o del cambio en la frecuencia de interacciones ecológicas, sino que es la desviación absoluta de la temperatura corporal del organismo con respecto a su intervalo de temperaturas seleccionadas (Hertz et al. 1993). Removimos nueve artículos que exploraban circunstancias en las que se secundaban las conductas termorreguladoras en pos de realizar otras conductas más relevantes en esas circunstancias, por ejemplo, poca disponibilidad hídrica, época de apareamiento, dificultad física para desplazarse o presencia de depredadores. Estos nueve registros escapaban al ámbito del presente estudio, no obstante, discutimos su relevancia para estudios posteriores. Finalmente, nuestro tamaño muestral fue de 28 artículos, 18 de la búsqueda inicial y 10 de la búsqueda en las referencias (tabla 1.1).

Categorización de los artículos seleccionados. Identificamos cinco categorías de cada artículo seleccionado con base en la lectura de su introducción, métodos y resultados. Las cinco categorías son las siguientes: tipo de costo de las conductas termorreguladoras, sitios de estudio en un ambiente cálido o fresco, zona latitudinal,

grupo taxonómico y aproximación metodológica. Identificamos si la inversión en conductas termorreguladoras suponía el uso de energía y/o suponía la falta de energía para procesos fisiológicos (costo de energía), el uso de tiempo y/o la falta de tiempo para otras actividades (costo de tiempo), o el aumento en la frecuencia de interacciones ecológicas negativas como el riesgo de depredación (costo de seguridad). Identificamos si el estudio se había realizado con temperaturas diurnas en desiertos o en escenario simulados en los que se elevó la temperatura del hábitat, de ser así, demarcamos que el sitio de estudio ocurrió en ambientes cálidos. Identificamos la zona latitudinal, tropical (0–23.5°) o templada (23.5–66°). Dividimos la zona templada en subtropical (23.5–35°) o templada (35–66°) dada la marcada temperatura y humedad de la zona subtropical dentro de latitudes templadas. Identificamos el grupo taxonómico del modelo de estudio hasta el nivel de especie; además, agrupamos a los modelos de estudio en lagartijas, serpientes o tortugas dado que son agrupaciones empleadas para abordar la conservación biológica de reptiles terrestres (*revisado en* Roll et al. 2017). Investigamos la historia de vida de las especies de los registros seleccionados con el fin de conocer si la frecuencia de estudios sobre conductas termorreguladoras variaba con respecto a los caracteres de historia de vida. Los caracteres de historia de vida fueron longitud hocico cloaca promedio de las hembras (llamado talla), masa de nidada promedio, tamaño de nidada promedio, frecuencia reproductiva promedio y modo reproductivo. Identificamos la aproximación metodológica del estudio en campo, encierro, laboratorio, simulación o mixto, este último cuando el estudio abordaba más de una aproximación metodológica.

Análisis estadísticos. Para saber si había diferencias significativas en el número de artículos entre los grupos de las distintas categorías, comparamos la frecuencia observada entre grupos contra una frecuencia equitativa entre grupos mediante la prueba exacta de bondad de ajuste, también llamada prueba binomial (BT). La prueba binomial nos permite hacer comparaciones cuando una o más de las celdas cuentan con menos de 10 observaciones. No realizamos la prueba de bondad de ajuste de X^2 porque requería un mayor tamaño de muestra a pesar de ser más conocida. Realizamos seis comparaciones independientes, a saber, comparamos el número de artículos (i) que abordaron costos de energía, tiempo o seguridad; (ii) que abordaron costos de energía, tiempo o seguridad tanto en ambientes cálidos como en frescos; (iii) que se abordaron en zonas latitudinales tropicales, subtropicales o templadas; (iv) que abordaron costos de energía, tiempo o seguridad en cada una de las tres zonas latitudinales consideradas; (v) que se abordaron con lagartijas, serpientes o tortugas terrestres; (vi) y que se abordaron mediante una de las cinco aproximaciones metodológicas consideradas. Realizamos pruebas de Kruskal-Wallis para saber si los tres tipos de conductas termorreguladoras de reptiles terrestres diferían con respecto a los caracteres de historia de vida considerados: talla de las hembras, masa de nidada, tamaño de nidada y frecuencia reproductiva. Realizamos una prueba exacta de Fisher para saber si el número de artículos sobre costos de conductas termorreguladoras era distinto entre modos reproductivos. Realizamos todas las pruebas estadísticas y gráficas en R (R Core Team 2020).

Tabla 1.1. Estudios considerados en la revisión sistematizada. Mencionamos el tipo de costo evaluado en el estudio, breve descripción del estudio, si el sitio de estudio ocurrió en un ambiente cálido, latitud y aproximación metodológica del estudio y cita de cada uno de los 28 estudios considerados en la revisión sistematizada.

| Costo | Descripción | Cálido | Latitud | Aproximación | Cita |
|---------|--|--------|---------|--------------|-----------------------------|
| Energía | Crecimiento (mm día-1) vs. desplazamiento para calentarse cuando dos lámparas distanciadas están siempre prendidas o se prenden alternadamente | No | 34.800 | Laboratorio | Brewster et al. 2013 |
| Energía | Distancia (m) recorrida para termorregular entre un hábitat con mayor y menor heterogeneidad térmica | Sí | 31.846 | Encierro | Rusch et al. 2018 |
| Energía | Distancia (cm) recorrida para refrescarse entre un hábitat con mayor y menor cubierta vegetal | Sí | 31.083 | Campo | Attum y Eason 2006 |
| Energía | Energía (J) de desplazamiento para calentarse entre dos lámparas distanciadas y siempre prendidas o prendidas alternadamente | No | -34.349 | Mixto | Basson et al. 2017 |
| Energía | Distancia (cm) recorrida para termorregular entre una lagartija de menor y mayor talla corporal | No | NA | Simulación | Alford y Lutterschmidt 2012 |
| Energía | Energía (J) de desplazamiento para refrescarse entre un ambiente menos y más cálido | Sí | NA | Simulación | Sears y Angilletta 2015 |

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|--------|--|----|---------|-------------|---------------------------|
| Tiempo | Número de grillos ingeridos vs. excavar más profundo para refrescarse entre un ambiente menos y más cálido | Sí | -31.333 | Laboratorio | Beltrán et al. 2021 |
| Tiempo | Porcentaje de tiempo de actividad resguardado bajo el suelo para refrescarse entre un hábitat con mayor y menor cubierta vegetal | Sí | 35.191 | Campo | Gaudenti et al. 2021 |
| Tiempo | Duración (s) de forrajeo en un lugar fresco vs. perchando en un lugar cálido entre un ambiente menos y más fresco | No | NA | Laboratorio | Balasko y Cabanac 1998 |
| Tiempo | Tiempo (h) de restricción de actividad por refugiarse para refrescarse entre un sitio menos y más caliente | Sí | 26.871 | Mixto | Lara-Reséndiz et al. 2015 |
| Tiempo | Porcentaje del tiempo de actividad en exploración vs. en termorregulación cuando las hembras están no o sí grávidas | No | NA | Encierro | Lorioux et al. 2013 |
| Tiempo | Duración (s) de periodos de percha para calentarse entre un hábitat con mayor y menor radiación solar | No | 51.455 | Laboratorio | Avery et al. 1982 |
| Tiempo | Porcentaje de avistamientos perchando para calentarse entre un hábitat menos y más fresco | No | 49.883 | Mixto | Gvoždík 2002 |
| Tiempo | Porcentaje del tiempo de actividad en fisuras de rocas para refrescarse entre las horas diurnas más frescas y cálidas | Sí | 29.250 | Campo | Grant 1990 |

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|-----------|--|----|---------|-------------|-------------------------------|
| Tiempo | Porcentaje de avistamientos perchando para calentarse entre un hábitat menos y más fresco | No | 40.813 | Campo | Aguado y Braña 2014 |
| Seguridad | Probabilidad de supervivencia entre dos porcentajes de tiempo de actividad perchando, 0–7% y 8–14% | No | 30.167 | Campo | Sperry y Weatherhead 2009 |
| Seguridad | Porcentaje de lagartijas en parches insolados para calentarse sobre porcentaje de modelos nulos en parches insolados entre un sitio menos y más fresco | No | 40.517 | Mixto | Díaz 1997 |
| Seguridad | Tiempo (s) de emergencia del refugio para calentarse luego de un ataque simulado entre un refugio menos y más fresco | No | 40.813 | Campo | Martín y López 2003 |
| Seguridad | Tiempo (s) de emergencia del refugio para calentarse luego de un ataque simulado entre un refugio menos y más fresco | No | 40.75 | Laboratorio | Polo et al. 2005 |
| Seguridad | Índice de agresión para apropiarse del parche cálido proviniendo de un ambiente menos o más fresco | No | -33.711 | Laboratorio | Kondo y Downes 2007 |
| Seguridad | Tiempo (s) de emergencia del refugio para calentarse luego de un ataque simulado entre individuos inoculados con una solución salina o lipopolisacáridos | No | 43.317 | Laboratorio | Iglesias-Carrasco et al. 2016 |

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|-----------|--|----|---------|-------------|------------------------|
| Seguridad | Tiempo (s) de emergencia del refugio para calentarse luego de un ataque simulado entre un refugio menos y más fresco | No | -16.800 | Mixto | Andersson et al. 2010 |
| Seguridad | Tiempo (s) de emergencia del refugio para calentarse luego de un ataque simulado entre un refugio menos y más fresco | No | 40.813 | Campo | Martín y López 1999 |
| Seguridad | Tiempo (s) de emergencia del refugio para calentarse luego de un ataque simulado entre un refugio menos y más fresco | No | 40.813 | Laboratorio | Amo et al. 2007 |
| Seguridad | Proporción de lagartijas que huyen al escondite luego de un ataque simulado entre un refugio con igual o menor temperatura que el exterior | No | 31.996 | Campo | Cooper y Wilson 2008 |
| Seguridad | Tiempo (min) fuera del escondite subterráneo para calentarse después de un ataque simulado entre un escondite menos y más fresco | No | 30.750 | Campo | Radzio y O'Connor 2017 |
| Seguridad | Número de serpientes adultas en un refugio fresco sin olor a depredador o en un uno cálido con olor a depredador | No | -34.893 | Laboratorio | Webb et al. 2009 |
| Seguridad | Porcentaje de avistamientos de hembras grávidas entre un hábitat menos y más descubierto para calentarse | No | 42.536 | Campo | Foster et al. 2009 |

Resultados y discusión

Tipos de costos. La distribución de estudios fue similar entre los tipos de costos. No hubo diferencias significativas en el número de estudios que abordaron el costo de energía (n=6), tiempo (n=9) o seguridad (n=13) (fig. 1.1).

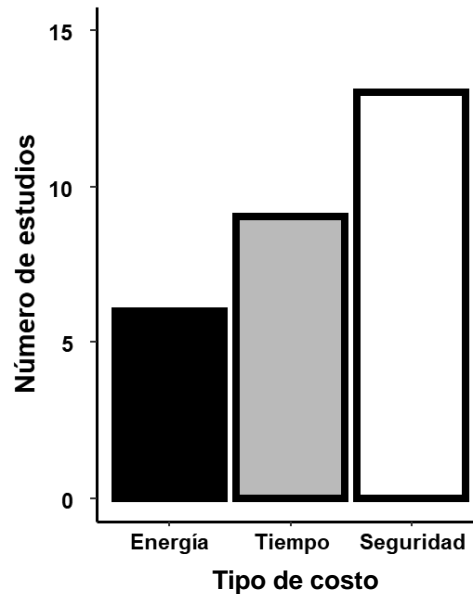


Figura 1.1. Frecuencia de los estudios que abordaron costos de energía, tiempo, o seguridad derivados de conductas termorreguladoras.

Tipos de costos entre ambientes cálidos y frescos. Algunos estudios se llevaron a cabo en ambientes cálidos como desiertos y otros en ambientes frescos como bosques templados, lo cual demarca la biología térmica de los reptiles terrestres (ver *introducción*). Consideramos dicha diferencia como parte del contexto ecológico de los reptiles terrestres. Los tipos de costos fueron estudiados con una frecuencia distinta entre ambientes cálidos y frescos. En ambientes cálidos, el costo de perder seguridad (n=0) fue estudiado con una frecuencia similar que el

de perder tiempo (n=4), y el costo de perder energía (n=3) se estudió con una frecuencia intermedia al de los otros dos costos. En ambientes frescos, el costo de perder seguridad (n=13) fue estudiado con mayor frecuencia que el de perder energía (n=3; BT, $p=0.0213$), y el costo de perder tiempo (n=5) se estudió con una frecuencia intermedia al de los otros dos costos (fig. 1.2).

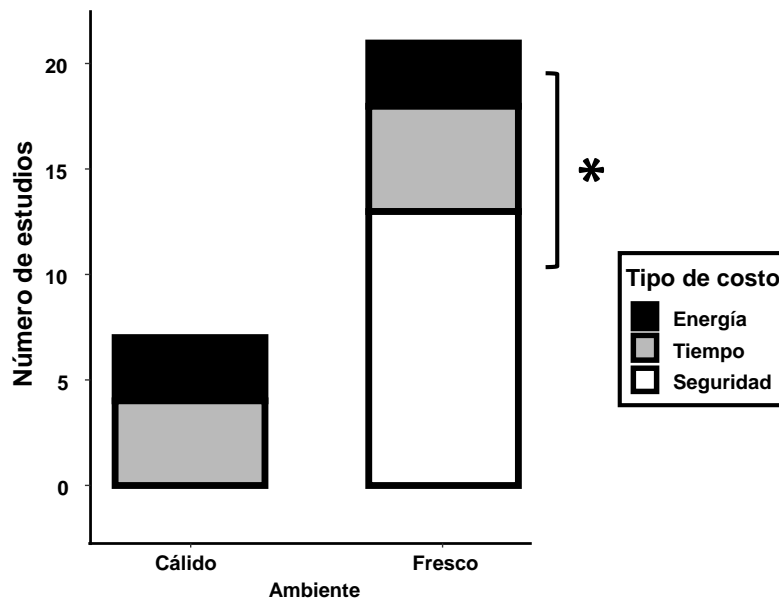


Figura 1.2. Frecuencia de los estudios que abordaron costos de energía, tiempo o seguridad derivados de conductas termorreguladoras entre ambientes cálidos y frescos. El corchete indica la comparación entre dos grupos y el asterisco la diferencia significativa <0.05 .

El número de estudios entre los tres tipos de costos de conductas termorreguladoras en ambientes cálidos fue similar. La falta de diferencias significativas puede deberse a una falta de poder estadístico relacionado al reducido

tamaño muestral de los registros de ambientes cálidos (n=7) en comparación con el de ambientes frescos (n=21).

El costo de energía de conductas termorreguladoras en reptiles terrestres podría variar entre ambientes cálidos y frescos. El costo de energía en ambientes cálidos ocurrió debido a la distribución de la cubierta vegetal o parches sombreados en los tres estudios considerados al respecto. Por ejemplo, lagartijas *Acanthodactylus longipes* se desplazaron una mayor distancia para refugiarse debajo de arbustos conforme los parches de vegetación eran menos frecuentes y más alejados entre sí en dunas de arena (Attum y Eason 2006). Lagartijas *Sceloporus jarrovi* recorrieron mayores distancias para alternar entre parches sombreados e insolados conforme se agregaban los parches sombreados en simulaciones (Sears y Angilletta 2015) o en un matorral xérico (Rusch et al. 2018). En cambio, el costo de energía en ambientes frescos ocurrió debido a la distribución de las fuentes de calor en los tres artículos considerados al respecto (Alford y Lutterschmidt 2012; Brewster et al. 2013; Basson et al. 2017). Por ejemplo, lagartijas *Cordylus oleofseni*, *Crotaphytus collaris* y lagartijas simuladas se desplazaron más para calentarse cuando los investigadores alejaban las fuentes de calor de ellas (Alford y Lutterschmidt 2012) o cuando alternaban las fuentes de calor entre dos lugares alejados entre sí en condiciones de laboratorio (Brewster et al. 2013; Basson et al. 2017).

Los costos de tiempo de conductas termorreguladoras podría diferir entre reptiles terrestres de ambientes cálidos y frescos. El costo de tiempo en ambientes cálidos ocurrió por durar más tiempo en parches sombreados para evitar altas

temperaturas o bajas humedades en los tres artículos considerados al respecto (Grant 1990; Lara-Reséndiz et al. 2015; Gaudenti et al. 2021). Por ejemplo, lagartijas *Sceloporus merriami* duraron más tiempo en fisuras de rocas para refrescarse en las horas más calientes en un matorral desértico (Grant 1990). Lagartijas *Saiphos equalis* duraron más tiempo excavando para alcanzar sitios de anidación más frescos en detrimento del tiempo dedicado al forrajeo en un laboratorio (Beltrán et al. 2021). Por otro lado, el costo de tiempo en ambientes frescos ocurrió por mantenerse ocupando parches cálidos en detrimento del tiempo invertido en realizar otras actividades en lugares más frescos (Avery et al. 1982; Balasko y Cabanac 1998; Gvoždík 2002; Lorigoux et al. 2013; Aguado y Braña 2014). Por ejemplo, iguanas *Iguana iguana* duraron más tiempo perchando en parches calientes sin alimento en detrimento del tiempo forrajeando en parches frescos con alimento en condiciones de laboratorio (Balasko y Cabanac 1998). Serpientes *Vipera aspis* grávidas duraron menos tiempo explorando su territorio por durar más tiempo termorregulando en comparación con serpientes no grávidas en un laboratorio (Lorigoux et al. 2013).

El efecto del calentamiento climático sobre los costos de tiempo de conductas termorreguladoras puede diferir entre reptiles terrestres de ambientes cálidos y frescos. Modelos mecanísticos de distribución de especies frente al calentamiento climático han predicho que los reptiles terrestres tropicales reducirán sus horas de actividad a favor de conductas termorreguladoras para refrescarse (Kearney et al. 2009; Kearney 2013). Por otro lado, los reptiles terrestres de latitudes templadas aumentarán sus horas de actividad porque podrán acceder a sus temperaturas preferidas por más tiempo (Huey et al. 2010). Este fenómeno también podría ocurrir

entre estaciones. Por ejemplo, el tiempo de actividad de lagartijas *Mesalina bahaeldini* en matorrales disminuirá en el verano y aumentará en el invierno debido al calentamiento climático (Stark et al. 2023). La evidencia presentada arriba concuerda con los cuatro artículos de nuestra revisión sistematizada que indican que los reptiles terrestres de ambientes cálidos aumentan su inversión de tiempo para refrescarse conforme se calienta su hábitat (Grant 1990; Lara-Reséndiz et al. 2015; Beltrán et al. 2021; Gaudenti et al. 2021). Así mismo, la evidencia presentada arriba concuerda con los cinco artículos de nuestra revisión sistematizada que indican que los reptiles terrestres de ambientes frescos aumentan su inversión de tiempo para calentarse conforme se enfría su hábitat (Avery et al. 1982; Balasko y Cabanac 1998; Gvoždík 2002; Lorient et al. 2013; Aguado y Braña 2014).

El costo de perder seguridad en ambientes frescos puede ocurrir cuando los reptiles terrestres se exponen en parches abiertos, compiten por acceder a parches calientes o evitan regresar a sus escondites. Por ejemplo, lagartijas *Psammmodromus algirus* en un bosque de encino (Díaz 1997) y serpientes hembra grávidas de *Sistrurus catenatus* en un bosque mixto (Foster et al. 2009) se expusieron con más frecuencia en puntos abiertos y soleados en ambientes más frescos. Lagartijas simuladas (Sperry y Weatherhead 2009) o moldes de lagartijas en un BTES (Ferreira y Faria 2021) que estaban expuestas en puntos abiertos fueron atacadas con mayor frecuencia que en puntos cubiertos.

El costo de perder seguridad en ambientes frescos puede ocurrir cuando el interior de los escondites es más fresco que el exterior de acuerdo con los 11 artículos al respecto de la revisión sistematizada. La temperatura corporal de los reptiles terrestres puede disminuir lo suficiente como para disminuir el rendimiento

térmico de sus procesos fisiológicos si ocupan escondites cuyo interior es más frío que el exterior (Martin y Lopez 1999c). En consecuencia, tortugas *Gopherus polyphemus* retardaron su escape al escondite ante la presencia de un depredador potencial en un bosque de pino (Radzio y O'Connor 2017) o lagartijas *Sceloporus virgatus* retardaron su escape ante el ataque de un depredador potencial en una ribera de río (Cooper y Wilson 2008). Múltiples especies de reptiles terrestres disminuyeron su tiempo dentro del escondite luego del ataque de un depredador conforme el interior de su escondite era más fresco que el exterior (Martín y López 1999a; Polo et al. 2005; Andersson et al. 2010; Iglesias-Carrasco et al. 2016). Esto es más evidente en reptiles juveniles de *Lacerta monticola* en comparación con adultos en praderas (Martín y López 2003a) y en hembras grávidas de *Iberolacerta cyreni* en comparación con no grávidas en praderas (Amo et al. 2007).

El costo de perder seguridad en ambientes frescos puede ocurrir mediante competencia intra e interespecífica por parches calientes según los 2 artículos al respecto de nuestra revisión sistematizada. Por ejemplo, Guecos nocturnos de *Oedura lesueurii* presentaron una mayor frecuencia e intensidad de agresiones al competir por puntos cálidos cuando habían experimentado ambientes más frescos durante el día en un laboratorio (Kondo y Downes 2007). Solo registramos un estudio que consideraba el horario nocturno y, por ende, un reptil terrestre de hábitos nocturnos (Kondo y Downes 2007). Serpientes de *Hoplocephalus bungaroides* ocuparon sitios calientes a pesar de estar ocupados por sus depredadores y ser depredados ocasionalmente (Webb et al. 2009).

La pérdida de seguridad no fue estudiada en ambientes cálidos en nuestra revisión sistematizada. Los reptiles terrestres suelen escapar a sus escondites

cuando perciben a un depredador o son atacados por este (*revisado en Samia et al. 2016*). Los reptiles terrestres también usan los escondites para evitar sobrepasar sus óptimos térmicos en ambientes cálidos (*modelado en Kearney et al. 2009; Sunday et al. 2014*) porque suelen ser más frescos que su exterior (*revisado en Martín 2001*). Creemos entonces que las conductas antidepredatorias usualmente coinciden con las conductas termorreguladoras en ambientes cálidos, por lo cual, no registramos algún costo de seguridad de conductas termorreguladoras en ambientes cálidos. No obstante, el costo de seguridad podría aumentar en ambientes cálidos si aumenta la competencia por refugios frescos para mitigar los efectos letales y subletales del sobrecalentamiento conforme se intensifique el calentamiento climático.

La frecuencia de estudios entre los costos de conductas termorreguladoras de reptiles terrestres difirió en ambientes frescos, pero no en ambientes cálidos. La falta de comparaciones significativas en ambientes cálidos puede deberse a la falta de poder estadístico, evidente ante la disparidad en el tamaño muestral de estudios entre ambientes frescos ($n=21$) y cálidos ($n=7$).

Distribución geográfica de los sitios de estudio. La distribución de los 24 artículos que informaron el sitio de colecta fue heterogénea entre zonas latitudinales. Específicamente, hubo menos estudios en latitudes tropicales ($n=1$) que en subtropicales ($n=13$; BT, $p=0.0018$) y templadas ($n=10$; BT, $p=0.0117$), y similar número de estudios en latitudes subtropicales y templadas (fig. 1.3). Los costos de conductas termorreguladoras fueron estudiados con una frecuencia similar en latitudes subtropicales. En cambio, el costo de seguridad fue estudiado

con más frecuencia (n=7) que el costo de energía (n=0) en latitudes templadas (BT, p=0.0156; Fig. 1.3).

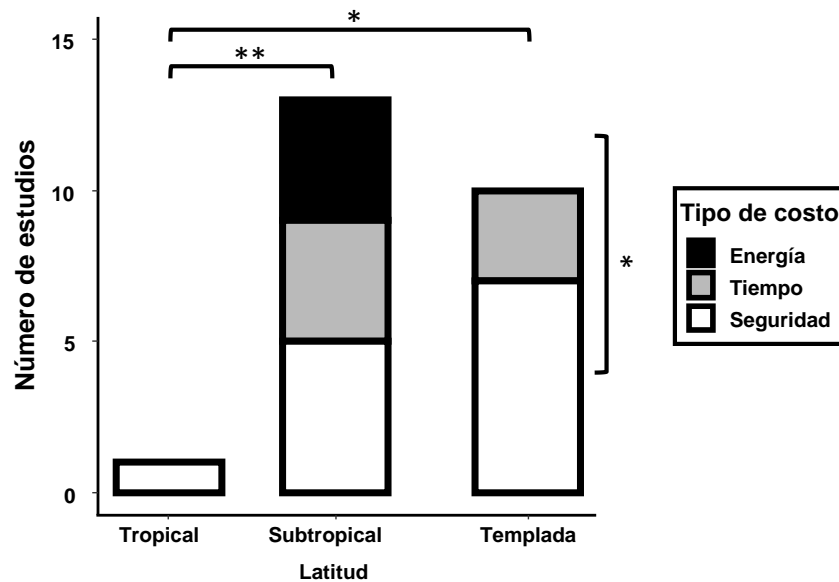


Figura 1.3. Frecuencia de los estudios realizados en latitudes tropicales, subtropicales o templadas (columnas), y dentro de cada zona latitudinal, la frecuencia de estudios que abordaron costos de energía, tiempo o seguridad (la gama de grises). Los corchetes indican comparaciones con diferencias significativas donde un asterisco denota diferencias significativas <0.05 y dos asteriscos <0.01. Los corchetes horizontales indican la diferencia significativa entre zonas latitudinales, mientras que el corchete vertical indica la diferencia significativa entre la frecuencia de estudios que abordaron costos de seguridad y de energía en latitudes templadas.

La mayor frecuencia de estudios en latitudes templadas se repite en otros estudios aunque la riqueza de especies sea mayor en latitudes tropicales.

Encontramos que la frecuencia de estudios sobre costos de conductas termorreguladoras de reptiles terrestres era menor en latitudes tropicales que en templadas. Este sesgo geográfico también ocurre en el estudio del efecto del calentamiento climático sobre los reptiles terrestres (*revisado en Winter et al. 2016*). Las latitudes tropicales y longitudes asiáticas cuentan con menos estudios sobre el efecto del calentamiento climático sobre los reptiles terrestres en comparación con latitudes templadas del hemisferio norte y longitudes americanas y europeas (*revisado en Winter et al. 2016*). Así mismo, el número de estudios sobre la densidad poblacional de reptiles terrestres es mayor en latitudes templadas que en tropicales (*revisado en Santini et al. 2018*). El desequilibrio en el número de artículos sobre reptiles terrestres entre latitudes tropicales y templadas es particularmente notable porque la riqueza de especies de reptiles terrestres es más alta en latitudes tropicales que en templadas (*revisado en Roll et al. 2017*).

La biología térmica de los reptiles terrestres de latitudes templadas y tropicales es distinta por lo que hay que elaborar predicciones pertinentes para cada grupo. Los reptiles terrestres de latitudes templadas y tropicales evolucionaron diferentes adaptaciones térmicas debido al clima más fresco y variable de las latitudes templadas y al clima más cálido y constante de las latitudes tropicales (Huey et al. 2009). Los reptiles terrestres de latitudes templadas cuentan con mayor margen de seguridad térmica, rango de tolerancia térmica (*revisado en Sunday et al. 2014*), capacidad de aclimatación térmica (*revisado en Tewksbury et al. 2008*), así como menor sensibilidad fisiológica a la variación térmica del hábitat (*revisado en Deutsch et al. 2008; Sunday et al. 2014*) y tasa metabólica (*revisado en Dillon et al., 2010*) que los reptiles terrestres de latitudes tropicales. Dichas diferencias

dificultan extender a los reptiles terrestres tropicales las predicciones de los reptiles terrestres de latitudes templadas sobre sus costos de conductas termorreguladoras.

Los reptiles terrestres de latitudes templadas presentaron costos de energía con menos frecuencia que costos de seguridad. Las latitudes templadas tienen ambientes frescos con mayor frecuencia que latitudes tropicales (revisado en Sunday et al. 2014). En consecuencia, los reptiles terrestres de latitudes templadas buscan calentarse con mayor frecuencia que los de latitudes tropicales (revisado en Kearney et al. 2009), por ejemplo, en sitios descubiertos. La exposición de los reptiles terrestres en sitios descubiertos aumenta su visibilidad frente a los depredadores. Por ejemplo, modelos de plastilina de lagartijas fueron atacadas con más frecuencia en sitios descubiertos que en cubiertos de dunas de arena vegetadas (Daly et al. 2008). Perchas cálidas con bajo riesgo de depredación podrían disminuir los costos de seguridad de las conductas termorreguladoras en latitudes templadas, por ejemplo, montículos de piedras (Díaz et al. 2006). Estos refugios también serían relevantes en ambientes frescos donde los costos de seguridad también fueron más frecuentes que los costos de energía.

Grupos taxonómicos. Los costos de conductas termorreguladoras se estudiaron con mayor frecuencia en lagartijas (n=22) que en serpientes (n=4; BT, $p=0.0001$) y tortugas (n=1; BT, $p<0.0001$), y con igual frecuencia entre serpientes y tortugas (fig. 1.4). Pocos estudios fueron realizados con integrantes de las familias Testudinidae (n=1) para tortugas y Colubridae (n=1), Elapidae (n=1) y Viperidae (n=2) para serpientes. Los estudios en lagartijas de las familias Iguanidae (n=4) y Lacertidae (n=11) representaron el 55% de los 27 estudios que consideraron

taxones específicos. Los géneros más estudiados de ambas familias fueron *Sceloporus* (n=4) e *Iberolacerta* (n=5), respectivamente. El resto de los géneros solo fueron estudiados en un estudio cada uno. *Carlia rubrigularis* fue la especie del artículo realizado en latitudes tropicales (Andersson et al. 2010). Uno de los estudios fue una simulación de una lagartija sin características de un género o especie en particular.

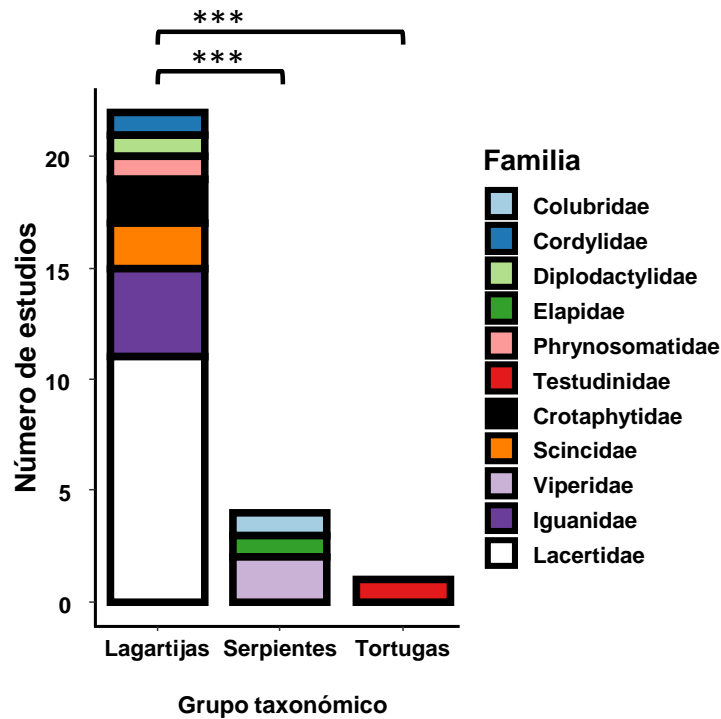


Figura 1.4. Número de estudios realizados con familias de lagartijas, serpientes o tortugas. Los corchetes indican comparaciones con diferencias significativas donde tres asteriscos denotan diferencias significativas <math><0.001</math>.

Las lagartijas pudieron representar más de la mitad de los registros porque son animales conspicuos, abundantes, fáciles de observar y, algunas de sus especies, fáciles de capturar. Nuestros resultados concuerdan con estudios previos.

Por ejemplo, las lagartijas resultaron con una mayor riqueza de especies proyectada que las serpientes, y éstas que las tortugas a nivel global (*revisado en* Biber et al. 2023). Las familias Lacertidae y Viperidae fueron estudiadas con mayor frecuencia acerca del efecto del calentamiento climático sobre la distribución y diversidad de lagartijas y serpientes, respectivamente (*revisado en* Biber et al. 2023).

Las lagartijas proveen importantes servicios ecosistémicos, pero son poco consideradas en proyectos de conservación biológica. Lagartijas, serpientes y tortugas prestan múltiples servicios ecosistémicos, en particular, las lagartijas son importantes controladores biológicos de invertebrados, dispersores de semillas y fuentes de proteínas para sus depredadores (*revisado en* Valencia-Aguilar et al. 2013; Cortés-Gomez et al. 2015). Los servicios ecosistémicos que proveen los reptiles terrestres pueden vulnerarse si son afectados negativamente por las actividades antropogénicas, como el calentamiento del hábitat (Valencia-Esquivel et al. 2023). Las lagartijas son vulnerables a las actividades antropogénicas ya que están menos representadas en las áreas protegidas. Por ejemplo, la distribución espacial de la riqueza de lagartijas se correlaciona menos que en serpientes con la distribución espacial de la riqueza de aves y mamíferos. Las aves y mamíferos son grupos generalmente utilizados para seleccionar áreas prioritarias para la conservación biológica (*revisado en* Roll et al. 2017). Las lagartijas presentaron más estudios sobre los costos de sus conductas termorreguladoras que serpientes y tortugas lo cual nos permite colaborar con la biología de la conservación para mitigar la vulnerabilidad al calentamiento de los reptiles terrestres, especialmente de las lagartijas, y con ello coadyuvar en la prevalencia de sus servicios ecosistémicos.

La talla de hembras adultas, masa de nidada, tamaño de nidada o frecuencia reproductiva de las especies de reptiles terrestres consideradas fueron similares entre los distintos tipos de costos de conductas termorreguladoras. Además, los costos de conductas termorreguladoras se estudiaron con una frecuencia similar entre reptiles terrestres con distinto modo reproductivo.

Aproximación metodológica. Los estudios realizados en simulaciones (n=2) y encierros (n=2) fueron menos frecuentes que los realizados en campo (n=10; BT, $p=0.0386$; Fig. 1.5).

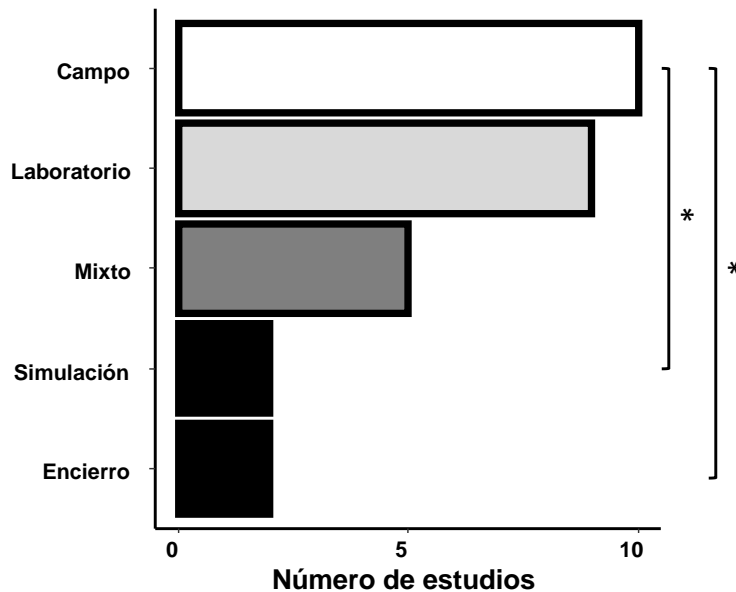


Figura 1.5. Número de estudios por aproximación metodológica. Los corchetes indican comparaciones con diferencias significativas y el asterisco denota diferencias significativas <0.05 .

Hay al menos 28 artículos sobre costos de termorregulación en reptiles terrestres, sin embargo, solo 5 de esos artículos integraron distintas aproximaciones metodológicas, por ejemplo, simulaciones y experimentos. Las simulaciones que describen fenómenos biológicos brindan predicciones valiosas para la biología de la conservación (Brook et al. 2000). Cuando las predicciones se ponen a prueba, nos permiten conocer los alcances y la capacidad de nuestro conocimiento para explicar y predecir el efecto de las actividades humanas en los sistemas biológicos. Por lo tanto, necesitamos más estudios que muestren las predicciones simuladas sobre el funcionamiento de un sistema biológico y enseguida que lo pongan a prueba. Por ejemplo, la termorregulación de lagartijas simuladas y reales de *Cordylus oleofseni* se comparó entre escenarios de baja y alta calidad térmica (Basson et al. 2017). La simulación mostró que las lagartijas reducían su distancia recorrida para ahorrar energía cuando la calidad térmica era baja, mientras que no tenían necesidad de gastar energía termorregulando cuando la calidad térmica era alta (Basson et al. 2017). Sin embargo, el experimento en laboratorio mostró que las lagartijas reales se movían más que las lagartijas simuladas. Las lagartijas se movían más cuando la calidad térmica era baja para mantener el rendimiento térmico de sus procesos biológicos, pero también cuando la calidad térmica era alta para explorar su entorno (Basson et al. 2017).

Limitaciones e investigación futura

En la presente revisión sistematizada agrupamos, analizamos y discutimos la evidencia sobre los costos de las conductas termorreguladoras en reptiles terrestres. Consideramos el contexto ecológico de los reptiles terrestres,

específicamente el régimen de la temperatura ambiental. El calentamiento climático es una extensión lógica de la temperatura ambiental que nos faltó abordar con mayor profundidad dentro del contexto ecológico. El calentamiento climático afecta a los animales terrestres a través de efectos indirectos principalmente (Cahill et al. 2013); por ejemplo, el cambio en las interacciones ecológicas, la disponibilidad de alimento (Cahill et al. 2013), así como los *trade-off* de energía (Fey et al. 2019), tiempo (Cunningham et al. 2021) y, probablemente, de seguridad asociados a conductas termorreguladoras.

Los costos de las conductas termorreguladoras podrían aumentar en frecuencia e intensidad debido al calentamiento climático. El calentamiento climático ha aumentado la frecuencia de conductas termorreguladoras durante los últimos 20 años en al menos dos especies de lagartijas, *Iberolacerta cyreni* en un bosque de pino (Ortega et al. 2016) y *Psammodromus algirus* en un bosque de encino (Díaz et al. 2022). Los *trade-off* asociados a los costos de conductas termorreguladoras deben ser considerados ya que pueden intervenir en la sobrevivencia de las aves a corto plazo (*revisado en* Riddell et al. 2019), así como en la evolución de historias de vida y viabilidad de poblaciones de reptiles terrestres a largo plazo (Buckley et al. 2015; Muñoz y Bodensteiner 2019). Futuros trabajos podrían enfocarse en los efectos de la intensificación de los costos de las conductas termorreguladoras de reptiles terrestres con motivo del calentamiento climático.

Las conductas termorreguladoras y sus costos asociados dependen del contexto del reptil terrestre. La inversión en conductas termorreguladoras difiere de acuerdo con múltiples caracteres propios de los reptiles terrestres como su talla (Gregory y Tuttle 2016), sus reservas de energía (Brewster et al. 2013) y agua

(Ladyman y Bradshaw 2003), su modo reproductivo (Wang et al. 2017), su etapa ontogénica (Xu y Ji 2006) y gravidez (Crane y Greene 2008), su especialización térmica (Lourdais et al. 2013) y su estrategia de historia de vida (Adolph y Porter 1993). La inversión en conductas termorreguladoras también difiere con respecto a múltiples factores externos a los reptiles terrestres como el tipo de vegetación (Theisinger et al. 2017), cubierta vegetal (Tuff et al. 2016) y estacionalidad (Christian y Bedford 1995), la calidad térmica del hábitat (Basson et al. 2017) y su distribución (Sears y Angilletta 2015), la densidad (Polo et al. 2005) y letalidad (Martín y López 1999b) de los depredadores, la presencia de competidores (Kondo y Downes 2007) y patógenos (Scholnick et al. 2010). Nosotros ahondamos en un factor extrínseco de los costos de las conductas termorreguladoras de reptiles terrestres. No obstante, no es posible ahondar en todos los caracteres intrínsecos y factores extrínsecos que pueden afectar los costos de las conductas termorreguladoras de reptiles terrestres ya que, como la presente revisión sistematizada, requieren de un estudio particular para profundizar en el tema apropiadamente.

En la presente revisión sistematizada no abordamos las circunstancias que restringen la inversión de los reptiles terrestres en conductas termorreguladoras en pos de ahorrar energía o aumentar su seguridad. Por ejemplo, lagartijas *Tropidurus torquatus* (Leirião et al. 2019) y *Zootoca vivípara* (Herczeg et al. 2008) invirtieron menos energía en desplazarse para termorregular conforme disminuía la temperatura operativa de su hábitat en un ambiente fresco de laboratorio. Lagartijas *Anolis carolinensis* disminuyeron sus temperaturas corporales por debajo de sus

temperaturas preferidas ante la disminución de la disponibilidad alimenticia en un laboratorio (Brown y Griffin 2005). Lagartijas *Podarcis muralis* (Amo et al. 2004) en laboratorio y lagartijas simuladas (Mitchell y Angilletta 2009) evitaron los parches calientes de mayor calidad térmica cuando percibían pistas de depredadores en ambientes frescos. Las restricciones de las conductas termorreguladoras emergen del supuesto de que mantener dichas conductas supone un mayor riesgo para la sobrevivencia que restringirlas. Futuros trabajos podrían abarcar y ahondar en la diversidad de contextos que restringen las conductas termorreguladoras.

El estudio de las conductas termorreguladoras y sus costos asociados puede aplicarse para investigaciones futuras como aumentar la eficacia en la distribución en acciones de conservación biológica. Se ha planteado elaborar paisajes de calor (*sensu* Cunningham et al. 2021) o más propiamente mapas de sobrecalentamiento. Los mapas de sobrecalentamiento deberían mostrar la distribución de las conductas termorreguladoras y sus costos asociados. Podríamos prever los sitios y periodos donde se concentren los costos de las conductas termorreguladoras, que a su vez nos permitiría plantear la distribución de obras que mitiguen los efectos subletales del calentamiento del hábitat. Las obras podrían variar en escala, desde montículos de rocas y cercas vivas hasta áreas protegidas y corredores biológicos, así como adecuarse al origen del calentamiento del hábitat, a saber, el calentamiento climático y/o la pérdida del hábitat.

Conclusiones. Nuestra revisión sistematizada tuvo cinco resultados principales, discutidos en sus respectivos apartados. Primero, la frecuencia de estudios entre los tres tipos de costos fue similar. Segundo, la frecuencia de estudios entre los tres tipos de costos fue similar en ambientes cálidos. Por otro

lado, el costo de seguridad fue estudiado con mayor frecuencia que el de energía en ambientes frescos, y el costo de tiempo fue intermedio a ambos. Tercero, los costos de conductas termorreguladoras fueron estudiados con menor frecuencia en latitudes tropicales que en latitudes subtropicales y templadas. Esto indica la peligrosa falta de información sobre los costos de las conductas termorreguladoras en reptiles terrestres tropicales. Cuarto, los costos de conductas termorreguladoras fueron estudiados con menor frecuencia en tortugas y serpientes que en lagartijas. Quinto, los estudios realizados en simulaciones y encierros fueron menos frecuentes que los realizados en campo, mientras que los estudios mixtos y realizados en laboratorio fueron intermedios al resto.

Previo a esta revisión sistematizada se consideraba que el estudio de los costos de las conductas termorreguladoras estaba dominado por costos de energía (Herczeg et al. 2006; Angilletta 2009; Vickers et al. 2011; Fey et al. 2019). En consecuencia, se predecía que la estrategia de los individuos de reptiles terrestres entre termorregular o termoconformar en ambientes frescos dependía del costo energético para mantener la temperatura corporal dentro de su intervalo de temperaturas preferidas. No obstante, la presente revisión sistematizada muestra que los costos de conductas termorreguladoras están dominados por costos de seguridad, más que costos energéticos, en ambientes frescos y latitudes templadas. Nosotros actualizamos el estudio de los tres costos de conductas termorreguladoras considerando otros costos no-energéticos y el contexto ecológico de los reptiles.

CAPÍTULO 2. Temporal *trade-off* between territorial and thermoregulatory behaviors of a generalist lizard in a dry forest.

Manuscrito enviado el 10 de mayo de 2023 a la revista *Oecologia*, evidencia en el anexo 1.

Abstract

Avoiding dangerously hot body temperatures is important for survival, but animals may perform reproductive behaviors at the expense of behaviors used to cool down (or vice-versa), resulting in a thermoregulation-reproduction *trade-off*. Although this *trade-off* has been demonstrated in semi-aquatic animals, it has not been studied in terrestrial ectotherms. This is an important research gap given the importance of survival-reproduction *trade-offs* in evolutionary ecology and the pace of habitat warming due to vegetation loss and global climate change. We explored this *trade-off* in territorial males of the lizard *Sceloporus ochoterenae*, which mates during the hot-dry season in seasonally dry tropical forest. We first confirmed the existence of a temporal *trade-off* between performing push-ups (a territorial behavioral display) versus sheltering in the shade (thermoregulatory behavior), then used confirmatory path analysis to explore how it is affected by vegetation cover, microclimate temperature, and the presence of a conspecific intruder. We found that territories with less vegetation cover had higher microclimate temperatures, where focal males spent more time performing push-ups at the expense of sheltering in the shade. Focal males also spent more time performing push-ups the longer an intruder was present, who was also affected by the environmental variables. Territorial males spent more time in sunny spots when performing push-ups despite the potential for overheating, perhaps because the display is more effective when performed in the

open. The potential effects of continued habitat warming on this *trade-off* vary widely, including intensifying it, driving lizards to change their daily activity rhythms, and chronic overheating.

Keywords:

Vegetation loss, microclimate temperature, overheating, *Sceloporus*, territoriality.

Introduction

Life history theory addresses the strategies used by organisms to allocate resources among self-maintenance, growth, and reproduction. These three components compete for a limited amount of energy, nutrients, and time, giving rise to *trade-offs* among them (Braendle et al. 2011). For example, resources invested in reproduction cannot be used for self-maintenance, leading to the *trade-off* between reproduction and self-maintenance (Stearns 1989). Investing more in reproduction than self-maintenance at a given time consumes energy reserves, decreases opportunities for other activities, and may jeopardize the individual's safety, which together may reduce the likelihood of their continued survival and/or ability to invest in potential future reproductive attempts, i.e., the *trade-off* between current and future reproduction (Braendle et al. 2011).

The *trade-off* between current and future reproduction has been explored considering longevity and fecundity in warm habitats. According to optimization models (Thunell et al. 2022) and experiments (Bestion et al. 2015), an increase in reproductive effort at the expense of a lower growth rate is favored in warm habitats, resulting in a demography characterized by smaller, younger adults with lower longevity but higher fertility (*the hotter is smaller* hypothesis, Kingsolver and Huey

2008). At the same time, growth rate trades off with longevity (Lee et al. 2013). Reproductive effort generates reproductive costs, which in turn, can compromise survival so much as to truncate residual reproductive value prematurely. For example, reproductive behaviors during mating and gestation may increase the visibility of animals to their predators (Lorioux et al. 2013) or increase exposure to the lethal or sub-lethal effects of overheating (Darnell et al. 2020). Consequently, iteroparous animals may invest in behavioral adjustments that favor survival, such as antipredatory or thermoregulatory behaviors, while decreasing their investment in reproductive behaviors.

In sexually reproducing animals, finding and securing access to mates requires a series of behaviors that can incur energy, time, and safety costs. In many animals (e.g., *Austruca mjoeberg*, Darnell et al. 2020; *Pseudemoia entrecasteauxii*, Stapley 2006), territorial males attract attention and communicate their quality to potential mates and conspecific intruders through territorial behaviors such as static and mobile visual signals. Mobile visual signals cost energy (Zhu et al. 2020) and time (Allen and Levinton 2014); therefore, males should maximize the efficiency of their signals (Fleishman and Font 2019), for example by displaying in sites that maximize their visibility.

Males of several lizard species tend to occupy and display in open, sunny spots during their mating season (Martín and López 1999; Meek and Avery 2008; Carter et al. 2010). This may increase the visibility of their mobile visual signals (Bian et al. 2019). However, open, sunny sites also increase the risk of predation (Cooper and Vitt 2002), and in hot and dry ecosystems, sun exposure increases the lethal and sub-lethal effects of overheating (i.e., that the individual's body temperatures

exceed its behavioral thermal tolerance range; Allen and Levinton 2014). Ectotherms can avoid overheating by performing thermoregulatory behaviors, such as shuttling to cooler microhabitats (Kearney 2013; Díaz et al. 2022). However, sheltering in shady microhabitats reduces the opportunities to carry out activities in sunny microhabitats (e.g., behavioral displays; reviewed in Cunningham et al. 2021). This is expected to result in a temporal *trade-off* between territorial and thermoregulatory behaviors for males that tend to occupy and display in open, sunny spots during their mating season in hot ecosystems. The existence of this *trade-off* has been demonstrated in intertidal crabs (Darnell et al. 2020) and sea lions (Bohórquez-Herrera et al. 2014) during their mating season, but not, to our knowledge, in any terrestrial vertebrate inhabiting hot, dry environments.

The hot and dry conditions during the dry season in seasonally dry tropical forests (SDTF) present a challenging context for thermoregulation and therefore offer an ideal context in which to test the temporal *trade-off* between territorial and thermoregulatory behaviors. The SDTF has two seasons marked by large differences in the amount of precipitation, with most trees losing their leaves in the dry season to conserve water (Siliceo-cantero et al. 2016). This seasonal defoliation increases the amount of solar radiation that reaches the ground, increasing in turn both the visibility (Ferreira and Faria 2021) and the ambient temperature of the habitat (Valenzuela-Ceballos et al. 2015). In addition, the abundance of arthropods decreases during the dry season (Lister and Aguayo 1992), thus reducing food availability for insectivorous animals. Despite these conditions, multiple diurnal lizard species inhabiting SDTF court and defend their territory during the dry season (Valdéz-González and Ramírez-Bautista 2002;

Bustos-Zagal et al. 2011; Granados-González et al. 2015). In addition to natural seasonal defoliation, SDTF is one of the most anthropized ecosystems on Earth due to deforestation and its transformation into agricultural fields and grazing land (Mesa-Sierra et al. 2022). These anthropogenic disturbances create a landscape with variable vegetation cover where different individuals, depending on the location of their home ranges, experience different environmental conditions during the same dry season.

Sceloporus ochoterenae is a disturbance-tolerant insectivorous lizard that inhabits SDTF, including open sites (Saldaña-de la Riva 1987). It defends territories during the dry season (Bustos-Zagal et al. 2011), which makes it an appropriate model to test the *trade-off* between territorial and thermoregulatory behaviors. Similar to many species of lizards (Martins 1993), including sympatric species of the same genus (Bussjaeger 1971), males of *S. ochoterenae* perform mobile visual signals, including push-ups, during their reproductive season in order to court and defend their territory. Its reproductive season occurs from the end of the dry season (May) to the middle of the rainy season (July; Bustos-Zagal et al. 2011). During the dry season, SDTF lizard species are less active (Lister and Aguayo 1992; García et al. 2010), seek cooler microhabitats more frequently, and thus have lower metabolic rates (Christian et al. 1996, 2003) than during the rainy season, allowing them to conserve water and energy. For example, *S. ochoterenae* shelters in shady spots or crevices to decrease its body temperature during its active hours.

Since deforestation increases both temperature (Valenzuela-Ceballos et al. 2015) and visibility in the habitat (Ferreira and Faria 2021), ectotherms are at greater risk of overheating and predation in more deforested sites. Thus, ectotherms are

expected to perform thermoregulatory and antipredatory behaviors more frequently in more deforested territories at the expense of other fundamental behaviors such as territorial defense, for example, occupying shady spots and performing push-ups less frequently. Nonetheless, in order to ensure reproduction, resident male ectotherms (e.g., *Uca pugilator*, *Eumeces laticeps*) in open sites tend to court females even at the risk of overheating (Allen and Levinton 2014) and deter intruders even in the face of potential predators (Cooper 1999) during their mating season. Thus, under the hypothesis of a temporal *trade-off* between territoriality and thermoregulation, we expected that when using shady spots to thermoregulate, *S. ochoterena* loses opportunities to defend its territory, and that this *trade-off* is more intense the lower the vegetation cover (and thus the higher the ambient temperature) in its territory.

In this study, we explore the interactions between vegetation cover, microclimate temperature, and the presence of conspecific intruders with the possible *trade-off* between the time that territorial males of *S. ochoterena* spent performing push-ups (as a proxy for territorial behaviors) and spent sheltering in the shade (as a proxy for thermoregulatory behaviors) during their mating season in the dry season of a SDTF. To do this, we carried out a field study in which we recorded the time spent by different males doing push-ups and sheltering in shady spots in territories that varied in vegetation cover and microclimate temperature. Using these data, we first tested the assumption that males are more likely to perform push-ups when they are in sunny spots compared to when they are in shady spots (*sensu* Bian et al. (2019); based on the hypothesis that displaying in the open increases the effectiveness of their territorial signals, as described in Bian et al. 2019; Fleishman

and Font 2019). Second, we evaluated the existence of a negative relationship between the time males spent doing push-ups and their time spent in shady spots, which would support the existence of a temporal *trade-off* between the two behaviors (*sensu* Garland et al. 2022). Third, we used confirmatory path analysis to explore the relationships among vegetation cover, microclimate temperature, and the presence of conspecific intruders and their effects on the dynamics of the territoriality-thermoregulation *trade-off*, and to determine which of the two behaviors was limiting the *trade-off*.

In the confirmatory path analysis, we evaluated three alternative general hypotheses of the effects of the predictors on the time focal males performed push-ups and sheltered in shady spots (Fig. 1). The first hypothesis proposed that in territories with less vegetation cover, the microclimate temperature increases, which increases the risk of overheating, so males prioritize sheltering in shady spots at the expense of time performing push-ups (Fig. 1 A–C). The second hypothesis proposes that in territories with less vegetation cover, the microclimate temperature increases, which increases the visibility and body temperature of focal males, such that males spend more time doing push-ups at the expense of time sheltering in shady spots (Fig. 1 D–F). The third hypothesis proposes that the effect of the vegetation cover on the *trade-off* is not due to its effect on thermoregulation, but rather on antipredatory behaviors; in territories with less vegetation cover, focal males are more visible to potential predators, so males prioritize sheltering in the shade as an antipredatory (rather than thermoregulatory) behavior, at the expense of time spent performing push-ups (Fig. 1 G–I). Within each of these general hypotheses, we considered three variations, resulting in nine total models (Fig. 1). In the first variation

of each general model, the behaviors of focal males vary with respect to vegetation cover and/or microclimate temperature only (A, D, G); in the second, with respect to the above factors plus an increase in push-ups by focal males with increasing time present of a conspecific intruder (B, E, H); and in the third, in addition to the above factors, the vegetation cover and/or microclimate temperature affected the presence of intruder males in the same way as the focal male (C, F, I; Fig. 1). In addition to exploring the ecology and selection regime of this species, a better understanding of the dynamics and limiting factors of this *trade-off* will provide information that could have important implications in the context of global warming and anthropogenic loss of vegetation cover.

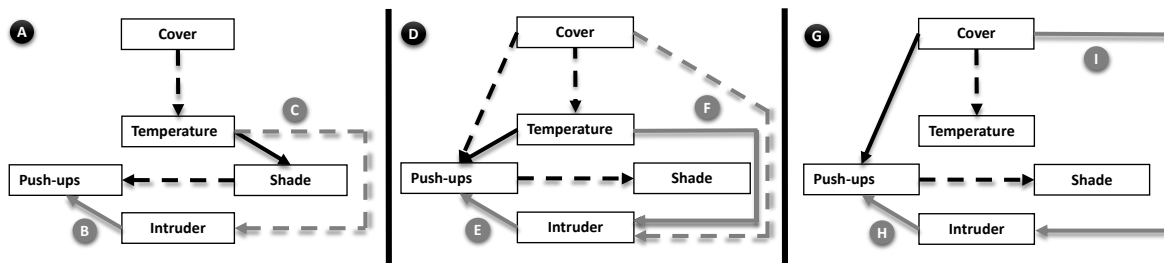


Fig. 2.1 Diagrammatic models illustrating the causal relationships predicted under three alternative general hypotheses about the effect of the vegetation cover in the territory of focal males on the potential *trade-off* between their time spent performing push-ups (Push-ups) and sheltering in shady spots (Shade). The direction of the arrows denotes the direction of causality of the relationships. Solid arrows denote positive relationships and dashed arrows indicate negative relationships. The three general hypotheses are as follows: in territories with lower vegetation cover, focal males either (A) prioritize thermoregulation to minimize their risk of overheating; (D)

prioritize performing push-ups to defend their territories; or (G) prioritize time in the shade to minimize their risk of predation. For each general hypothesis, three alternative models were considered. The first alternative models consider only the relationships between the behaviors of the focal male, the vegetation cover (Cover) and the microclimate temperature (Temperature; black lines; A, D, G). The second, in addition to those relationships, considers that the presence of a conspecific intruder (Intruder) increases the focal male's time performing push-ups (grey lines; B, E, H). The third, in addition to the previous relationships, the intruder is affected by the vegetation cover and/or the microclimate temperature in the same way as the focal male (grey lines; C, F, I). These general hypotheses and alternative models are described in more detail in the Introduction section

Methods

Study site. The study site is centered at coordinates 18°32'47.9"N, 98°56'43.9"W at 1,200 masl, within the ejido of El Limón in the Sierra de Huautla Biosphere Reserve, in south-central Mexico. The average annual temperature is $22.8 \pm 1.87^{\circ}\text{C}$ (average \pm standard deviation), and annual rainfall is 877.3mm (SMN 2000). The dry season occurs between November and May, and the months with the highest mean monthly temperature are April and May ($25.75 \pm 0.07^{\circ}\text{C}$) (SMN 2000). Eighty-eight percent of the annual rainfall occurs from June–October (SMN 2000). The most widespread vegetation type is seasonally dry tropical forest (SDTF; CONANP 2005). In 2005, 56% of the territory of El Limón was occupied by forests in conserved status, 19% in disturbed status, 12% by vegetation in secondary succession, and 13% by constructions and agricultural fields (De Leon-Ibarra 2005). The dominant trees in

this ecosystem are *Acacia cochliacantha*, *A. farnesiana*, *Ipomoea pauciflora*, and *Mimosa benthamii* (Martinez-Garza et al. 2011).

Study species. *Sceloporus ochoterenae* is endemic to the Balsas River Basin in southwestern Mexico, distributed from 520–2,134 masl, in SDTF and temperate forests (Saldaña-de la Riva 1987; Bustos-Zagal et al. 2011). *Sceloporus ochoterenae* is an oviparous (Bustos-Zagal et al. 2011) diurnal species that tolerates dry and warm environments (Saldaña-de la Riva 1987). It occupies the ground, rocks, shrubs, and logs (Saldaña-de la Riva 1987). *Sceloporus ochoterenae* is a thermoregulatory lizard; two different populations maintained an average field body temperature of 34.1°C, which did not differ between sexes or vary as a function of body size (Lemos-Espinal et al. 1997).

Experimental design. The study period was from April–May, which includes the warmest period of the year (SMN 2000) and corresponds to the beginning of reproductive investment in *S. ochoterenae* males (Bustos-Zagal et al. 2011). We walked potential *S. ochoterenae* habitat from 9h–18h, an interval that encompasses the activity hours reported for the species (Saldaña-de la Riva 1987). We alternated the direction and starting point of these walks to avoid confounding the sampling time with the vegetation cover of the territories; after the sampling period, we verified that there was no significant relationship between these variables (Pearson $r = 0.12$, $P = 0.4417$).

During the walks, we searched for males that were performing the territorial push-up display (Fleishman and Font 2019). Upon sighting a displaying male, the observer (IVE) moved more than 8m away from the focal male, covered himself with a camouflage pattern fabric, and waited 5 min for the focal male to habituate. The

observer recorded the activity of the focal male with binoculars using 0/1 recording at 1-minute intervals (Dawkins 2007) over a 30min period (similar to other observational studies in lizards, e.g., Stamps 1977; Anderson and Karasov 1981; Stapley 2006). Using two categories, we estimated the time spent on territorial and thermoregulatory behaviors by counting the number of intervals during which the focal male performed push-ups (=1) and occupied shady spots (=1), respectively. Given that in lizards the presence of a conspecific intruder implies the risk of losing the territory (Díaz-Uriarte 1999, 2001) and can evoke a stronger territorial response than when no intruder is present, we also recorded the number of intervals during which an intruder was visible within a 3m radius of the focal male. Since the reproductive success of male lizards is positively related to the number of females within their territory and to the number of copulations (Lebas 2001; Haenel et al. 2003), we also recorded the number of intervals during which a female was present within a radius of 3m of the focal male and the number of copulations during the entire test. However, at the end of the sampling, we only recorded the presence of females in three tests, and we did not observe copulations during any test. Since the sample size was insufficient to analyze this variable specifically, we eliminated these three tests to avoid the potential confounding effect. If the focal male disappeared from sight, we excluded that interval from the test; if he disappeared for more than 10 continuous intervals, we abandoned that territory and began the search for another male. We could repeat the test in the territories with incomplete tests, restarting the test.

After the observation period ended, we recorded the percent vegetation cover in the territory by taking a vertically oriented hemispherical photograph 50cm above

the ground at the point where we initially sighted the focal male. We processed the hemispherical photographs with the software Gap Light Analyzer (Frazer et al. 1999). The vegetation cover quantified was used as an explanatory variable in the path analysis, as well as to calculate the microclimate temperature (see the following paragraph). After taking the hemispherical photograph, we recorded the geographic coordinates of the territory and marked it with flagging tape placed ~8m from the sight point to avoid repeating the test at that site.

To estimate the thermal conditions in the territory of each focal male, we calculated the microclimate temperature (°C) using the NichemapR `micro_ncep` subroutine (Kearney et al. 2020). We ran this model for the geographic coordinates of each territory; for the model parameters, we input the mating season of the species as the date range of the analysis (01-April-2021 to 31-May-2021), the activity hours of the species (9h–18h) as the hour range, the percentage of vegetation cover quantified from the hemispherical photographs as the percent shade, the leaf area index at 1.5 (used for SDTF during the dry season; Maass et al. 1995), the albedo at 0.24 (Barradas and Adem 1992), and the leaf angle quotient at 0.

Statistical analysis. The sample size was 36 focal males. First, we tested the assumption that males were more likely to perform push-ups when in sunny spots versus when in shady spots. For this, we performed a generalized linear mixed model where the sampling unit was the 1 min interval, the binomial response variable was whether the male performed push-ups or not, and the explanatory variable was whether or not the male was in the shade during that interval. The identity of the focal male was included as a random variable to avoid pseudoreplication. Second, we evaluated the existence of a negative relationship (which supports the existence

of a *trade-off*) between performing push-ups and occupying shady spots. To do this, we used a generalized linear model with a Poisson error distribution and log link function to determine whether the number of intervals during which the focal males performed push-ups was negatively related to the number of intervals spent in shady spots during the test. We included the logarithm of the number of intervals recorded per period as an offset to account for variation in the total test duration due to missing intervals for some individuals.

Third, we used confirmatory path analysis to compare among the nine alternative proposed models of causal relationships among the percentage of vegetation cover, microclimate temperature, time with intruder present, and time during which focal males performed push-ups and sheltered in shady spots (Fig. 1). We assessed the consistency between each causal model and the data using the directional separation method (d-sep; Shipley 2004). This method consists of generating a directional acyclic diagram (DAG) for each model of causal relationships, extracting the conditional independences of the DAG, applying a hypothesis test for each conditional independence, extracting their null probabilities, and generating a combined null probability for each DAG based on Fisher's combined test (Shipley 2013). If the combined null hypothesis is not rejected, it means that the causal relationships posed in the DAG are consistent with the data.

For the hypothesis tests, we performed a Poisson regression whenever the response variable was the number of intervals in each test (including the logarithm of the number of intervals recorded by period as an offset to compensate for differences in the total number of intervals recorded). We used a quasipoisson distribution because there was overdispersion in our data. We performed a simple

linear regression when the response variable was continuous (microclimate temperature). We then defined the most consistent DAG with the data using the combined information criterion (CIC; Gonzalez-Voyer and von Hardenberg 2014). Since the number of parameters of each DAG ($n=8$) exceeded the quotient of the number of tests ($n=36$) divided over 40 (numerical constant), we used the CIC corrected for small sample sizes (CICc; Johnson and Omland 2004). We utilized R to run our statistical tests and figures (R Core Team 2020). The electronic supplementary material is available at (Valencia-Esquivel et al. 2023).

Results

The odds of performing push-ups decreased by 16.2% when males were in shady spots compared to when they were in sunny spots (binomial GLMM; fixed effect, $-1.548 -1.821 \pm 0.325$ [Intercept, logit \pm SE]; random effect [id of focal male], 1.522 ± 1.234 [variance \pm SD]; $z = -5.606$, $P = <0.001$). This confirmed that focal males were more likely to perform push-ups in the sun than in the shade.

We found a negative relationship between the time focal males spent performing push-ups and the time they spent sheltering in shady spots. The proportion of the total test period that focal males performed push-ups decreased by 7% for each additional interval they spent sheltering in the shade (GLM Poisson, $-1.033 -0.074 \pm 0.015$ [intercept, $\log(\beta) \pm$ SE], $t = -4.95$, $P = <0.001$; Fig. 2). It is important to note that this relationship was not an artifact of exclusivity between the two behavioral categories (*sensu* Garland et al. 2022), since push-ups and sheltering in shade spots were not mutually exclusive conditions in the behavioral scoring (i.e.,

a focal male could both perform push-ups and be in the shade during the same interval).

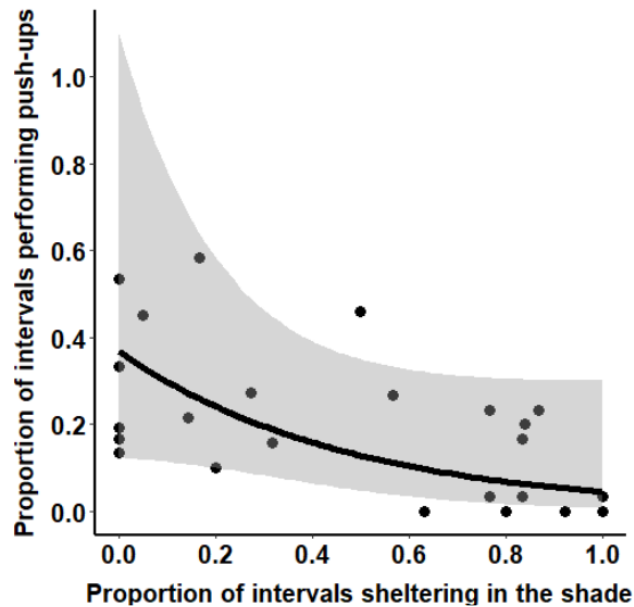


Fig. 2.2 Relationship between the time males spent in shady spots and time spent performing push-ups. The proportion refers to the number of intervals in which the corresponding behavior was observed divided by the total intervals in the observation period for each focal male. The 36 focal males are represented by the points, and the gray shaded area indicates the 95% confidence interval around the trend line from a Poisson regression (black curve; solid line significant at $P < 0.001$)

According to confirmatory path analysis, all DAGs except C had a combined null probability > 0.05 ; that is, they were accepted by the d-sep method. DAG F had the lowest CICc value and, therefore, was the most consistent with the data (Table 1). The other models had substantially less support ($\Delta\text{CICc} > 16$ for the other models; Table 1).

Table 2.1 Results of the d-sep method applied to the nine alternative DAGs. For each DAG, the table contains the result of Fisher’s combined test (Fisher’s C), the degrees of freedom (df), the combined null probability (*P*) corresponding to Fisher’s C, the number of parameters, the value of the information criterion corresponding to Fisher’s C (CICc), and the difference in CICc of each model relative to the most supported model (Δ CICc). Model C (*italics*) had a significant combined null probability, so it was discarded as it was inconsistent with the data, and its CICc and Δ CICc are not reported. The DAG values most consistent with the data (F) are in bold type

| DAG | Fisher’s | | | | Δ CICc | |
|----------|--------------|-----------|-------------|------------|---------------|-------------|
| | C | df | <i>P</i> | Parameters | CICc | |
| A | 43.76 | 14 | 0.97 | 8 | 65.09 | 27.70 |
| B | 32.17 | 12 | 0.88 | 8 | 53.50 | 16.11 |
| <i>C</i> | <i>8.68</i> | <i>10</i> | <i>0.01</i> | <i>9</i> | — | — |
| D | 38.81 | 12 | 0.97 | 8 | 60.14 | 22.75 |
| E | 34.36 | 10 | 0.98 | 8 | 55.69 | 18.30 |
| F | 12.47 | 6 | 0.59 | 9 | 37.39 | 0.00 |
| G | 41.77 | 14 | 0.95 | 8 | 63.10 | 25.71 |
| H | 35.01 | 12 | 0.93 | 8 | 56.35 | 18.96 |
| I | 29.43 | 10 | 0.92 | 9 | 54.35 | 16.96 |

DAG F indicates that the territories with less vegetation cover presented higher microclimate temperatures (linear regression, $12.795 - 0.186 \pm 0.061^\circ\text{C}$ (Intercept, $\beta \pm \text{SE}$); $t = -3.06$, $P = 0.0043$; Fig. 3). Focal males spent more time performing push-ups in territories with less vegetation cover (GLM Poisson, $-0.096 - 0.056 \pm 0.018$ (Intercept, $\log(\beta) \pm \text{SE}$); $t = -3.09$, $P = 0.0040$) and higher microclimate temperature (GLM Poisson, $-12.085 + 0.302 \pm 0.113$ (Intercept, $\log(\beta) \pm \text{SE}$); $t = 2.67$, $P = 0.0117$). Focal males that spent more time performing push-ups spent less time sheltering in shady spots (GLM Poisson, $-0.073 - 0.144 \pm 0.029$ (Intercept, $\log(\beta) \pm \text{SE}$); $t = -4.93$, $P < 0.001$). The time focal males spent performing push-ups increased with increasing time that an intruder was present (GLM Poisson, $-2.214 + 0.317 \pm 0.112$ (Intercept, $\log(\beta) \pm \text{SE}$); $t = 2.84$, $P = 0.0077$). Intruders were affected by the habitat characteristics of the focal territory; there were more intervals during which an intruder was present in the territories with lower vegetation cover (GLM Poisson, $-1.095 - 0.093 \pm 0.039$ (Intercept, $\log(\beta) \pm \text{SE}$); $t = -2.38$, $P = 0.0231$) and higher microclimate temperature (GLM Poisson, $-43.402 + 1.140 \pm 0.245$ (Intercept, $\log(\beta) \pm \text{SE}$); $t = 4.66$, $P < 0.001$; Fig. 3).

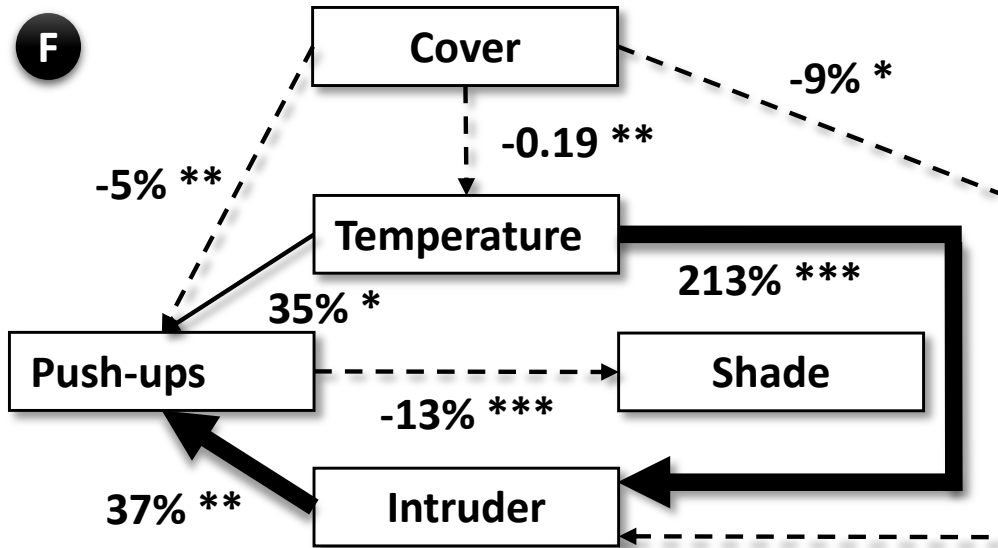


Fig. 2.3 Causal relationships of the F model, the DAG that was most consistent with the data. Boxes represent the percentage of vegetation cover (Cover), microclimate temperature (Temperature), number of intervals with an intruder present (Intruder), and number of intervals during which focal males performed push-ups (Push-ups) and sheltered in shady spots (Shade). The direction of the arrows denotes the direction of the causal relationship, and arrow thickness is proportional to the magnitude of the relationship. Solid lines denote positive relationships and dashed lines negative relationships. The numbers are the percentage change expected in the response variable with a one-unit increase in the predictor (i.e., the coefficient of the Poisson regression transformed to express it on the original scale of the data), except for the Temperature-Cover relationship, which is the coefficient from the simple linear regression. The number of asterisks denotes the level of significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Full numerical results can be found in the Results section

Discussion

In this study we tested the existence of a temporal *trade-off* between territorial and thermoregulatory behaviors in territorial males of *S. ochoterenae* during their mating season in the dry season of a SDTF. We first tested and confirmed the assumption that territorial males of *S. ochoterenae* display territorial behaviors (e.g., push-ups) more frequently in sunny spots than in shady spots. We then evaluated whether there was a negative relationship between these territorial and thermoregulatory behaviors in focal males. We found a clear negative relationship, which is consistent with the existence of a *trade-off*. Finally, we explored the effects of vegetation cover, microclimate temperature, and the presence of an intruder in the territory on the dynamics of the *trade-off* and determined whether territorial or thermoregulatory behavior (or neither) acted as the limiting factor in the *trade-off*. We found that territories with less vegetation cover had higher microclimate temperatures, where focal males spent more time performing push-ups at the expense of the time spent sheltering in shady spots. Focal males spent more time performing push-ups the longer an intruder was present, and intruders were also affected by the characteristics of the territory, spending more time in territories with less vegetation cover and higher microclimate temperatures.

Territoriality-thermoregulation trade-off. Life history theory predicts that lifetime reproductive success is maximized by optimizing the allocation of resources among self-maintenance, growth, and reproduction across all of an animal's different life stages, such that this allocation is shaped by natural selection. We demonstrated the existence of a temporal *trade-off* between territoriality and thermoregulation in a

terrestrial species under hot conditions, where the main thermal pressure is to cool off rather than to warm up. A similar *trade-off* has been described in two semi-aquatic animals (Allen and Levinton 2014; Bohórquez-Herrera et al. 2014). Male intertidal crabs (*Austruca mjoebergi*) endured high temperatures at the surface rather than sheltering underground in order to court potential mates (Darnell et al. 2020), while male sea lions (*Zalophus californianus*) traversed high temperatures on the beach rather than cooling off in the water to ward off intruders from their harem and stop fights between females (Carey 2010; Bohórquez-Herrera et al. 2014).

The causal relationships most consistent with our data, as determined by confirmatory path analysis, showed that territorial males performed push-ups at the expense of sheltering in the shade (Model F). Thus, in our system, the strategy of focal males is apparently to prioritize territorial behaviors during their mating season—because push-ups allow these lizards to defend their territories and to court (Martins 1993; Sheldahl and Martins 2000)—even though this likely increased the risk of overheating or being depredated (Fleishman and Font 2019). This is consistent with the previously mentioned examples of the territoriality-thermoregulation *trade-off* in crabs (Darnell et al. 2020) and sea lions (Carey 2010). However, it should be noted that this was at a specific time of year, phenological stage, and biological context and may not be the case at other times or under other circumstances. Given that reproductive effort cannot be sustained indefinitely, the other two general hypotheses could occur during the pre or post-mating season of focal males, when they should decrease their reproductive effort in order to increase the investment in self-maintenance. We expect that similar territoriality-

thermoregulation *trade-offs* could occur in other ectothermic species inhabiting hot-dry ecosystems.

We expected that males would maximize the efficiency of their signals by performing their push-up displays in open, sunny places where they are most visible (Martín and López 1999; Meek and Avery 2008; Carter et al. 2010), since mobile visual signals are costly in terms of energy (Zhu et al. 2020) and time (Allen and Levinton 2014). Our data supported this prediction, showing that males were more likely to perform push-ups while in sunny spots; there was a 3.4% chance that males would perform push-ups during a given interval in the shade, compared to a 21.3% chance when in the sun. Our results are consistent with two previous studies in which male lizards occupied sunny spots more frequently when engaged in mating activities (Meek and Avery 2008; Howells 2013). In one, territorial male lizards (*Physignathus lesueurii*) occupied sunny spots more frequently than non-territorial males during the mating season (Meek and Avery 2008). In the other, male lizards (*Sceloporus undulatus*) used sites with less vegetation cover than females during the mating season, but with more vegetation cover than females in the post-mating season (Howells 2013). This suggests that occupying sunny locations is specifically linked to male reproductive behaviors.

There is evidence of other temporal *trade-offs* in which lizards prioritize reproduction over self-maintenance, such as in reproductive versus antipredatory behaviors. For example, territorial male *Agama planiceps*, *Eumeces laticeps*, *Psammodromus algirus*, and *Sceloporus virgatus* allow predators to approach to a closer distance before fleeing to shelter when females (Cooper 1999; Martín and López 1999) or intruders are present (Cooper 1999; Cooper and Wilson 2008). In

our study, territorial males prioritized territorial behaviors in sunny spots over avoiding potential overheating during their mating season, especially when an intruder was present. This is similar to intertidal crabs (Darnell et al. 2020) and sea lions (Bohórquez-Herrera et al. 2014). In both the territorial-antipredation and territorial-thermoregulation *trade-offs*, focal males chose not to retreat to shady-cool refuges where they would be unable to protect their territories or attract females. The decreased use of shady and cool refuges by ectotherms to escape from predators or to avoid overheating during their mating season must be considered when accounting for their sensitivity to the heating of their habitats. For example, multiple simulations evaluate the effectiveness of thermoregulatory behaviors of terrestrial ectotherms in avoiding the lethal and sub-lethal effects of overheating (Kearney 2013; Valencia-Esquivel et al. 2023). However, the realism of such simulations could be improved by decreasing the likelihood that simulated terrestrial organisms display thermoregulatory behaviors during their mating season if this happens in the wild as in our case.

Effect of vegetation cover and microclimate temperature on focal males and intruders. Vegetation cover affected the time performing push-ups in two ways. On one hand, there was a direct negative effect of vegetation cover on time performing push-ups (i.e., not mediated by any of the other variables included in our analyses). Focal males spent more time performing push-ups in less covered territories, maybe because open (i.e., unobstructed and illuminated) territories increase the effectiveness of push-ups in lizards (Bian et al. 2019). A similar relationship was found in territorial males of *Anolis* lizards, which performed fewer mobile displays in

sites with lower visibility (i.e., more complex habitats; Johnson et al. 2009). On the other hand, there was an indirect effect of vegetation cover, consisting of a negative effect of vegetation cover on microclimate temperature combined with a positive effect of temperature on time spent deploying push-ups, as we had proposed. More open territories are warmer than less open territories because they receive a higher input of solar radiation (Tuff et al. 2016), and warmer territories allow ectotherms to reach higher body temperatures (Lara-Reséndiz et al. 2022). It is possible that male lizards tolerated the higher temperatures of more open territories because those territories allowed particularly high effectiveness of their displays.

The indirect effect of vegetation cover on the time deploying push-ups, through its direct effect on microclimate temperature, has a thermal limit. Vegetation cover loss increases the mean air temperature of forests (Tuff et al. 2016) and reduces the number and diversity of thermal refuges under the canopy (Scheffers et al. 2014). Under these circumstances, remaining in sunny spots to perform push-ups could increase the focal male's body temperature. If the body temperature surpasses the thermal tolerance range, performance rapidly decreases in the short term, and maintaining body temperatures at or above the behavioral tolerance range in a sustained way can lead to sub-lethal thermogenic effects in the short or medium term. For example, overheating can accelerate the expenditure of energy reserves (Rall et al. 2010) and water loss (Pintor et al. 2016), forcing the ectotherm to increase its foraging rate (Rall et al. 2010) or limiting its activities to cool places (Pintor et al. 2016). However, both of these compensation strategies are likely to be challenging in the dry season of a seasonal tropical ecosystem when vegetation cover and primary productivity are lower (Lister and Aguayo 1992). In temperate and

subtropical latitudes, the viability of ectotherm populations may also be at risk if they consistently experience habitats that are warmer than those in which they evolved (Sinervo et al. 2010; Bestion et al. 2015).

Intruders spent more time in territories with less vegetation cover and higher microclimate temperature. This may be due to two non-exclusive reasons. First, it may suggest that habitat selection in *S. ochoterenae* is under selection pressure, thus the resident male and the intruder seek similar habitats. Second, intruders could more easily detect resident males in more exposed territories. On the other hand, the positive relationship between the time spent by the resident male performing push-ups and the time the intruder spent in the focal territory could be because the focal male performed push-up displays specifically directed at the intruder in order to deter the intruder and/or because the resident male responded with push-ups to push-ups performed by the intruder male (we did not quantify the time the intruders spent performing push-ups).

Effect of habitat warming on the territoriality-thermoregulation trade-off. Our results suggest that territorial males of *S. ochoterenae* are currently prioritizing territorial behaviors over thermoregulatory ones during their early breeding season, but this could change if habitat temperature increases further. Habitat warming caused by habitat loss (Kearney 2013) and climate change (Bestion et al. 2015) impacts the population viability of ectotherms because body temperature affects their life histories (Adolph and Porter 1993; Anderson et al. 2011). If terrestrial habitats continue to warm, reproductive costs may increase to the point that males reduce their reproductive effort or even skip the reproductive event (Cruz-Flores et

al. 2021). For example, when the body temperature of male lizards of *Sceloporus occidentalis* (a congener of our study species) exceeds their preferred temperature, they stop their territorial behaviors against intruders and start thermoregulatory behaviors such as sheltering in shady spots (Engbretson and Livezey 1972). Indeed, this has already been demonstrated in one of the species where the territoriality-thermoregulation *trade-off* has been observed; the probability of aggressive interactions on land between male sea lions (*Z. californianus*) for harem dominance decreases with increasing air temperature beyond 30°C (Bohórquez-Herrera et al. 2014). Thus, if habitats of *S. ochoterenae* continue to warm in the coming decades, it may drive males to prioritize self-maintenance (i.e., future reproduction) over current reproduction.

If the microclimate temperature continues to increase, and if physiological plasticity (MacLean et al. 2019) and thermoregulatory behaviors (Díaz et al. 2022) are insufficient to avoid the risk of overheating in sunny spots, the environment could select in favor to males restrict their push-ups to the cooler diurnal hours or to shady spots. On one hand, animals can avoid the hottest hours of the day by following a bimodal activity pattern (Sears et al. 2011). For example, *Phrynosoma goodei* (Lara-Resendiz et al. 2014) and *Uromastyx aegyptia* (Al-Sayegh et al. 2020) avoid the hottest hours at midday by concentrating their activities in the morning and evening. On the other hand, the lower efficiency of mobile visual signals in shady spots can be compensated by increasing their emission rate (Bian et al. 2019). However, this solution would increase the energy costs of reproduction, which could lead to further competition for energy reserves between reproduction and other activities. In such a case, the temporal *trade-off* between territorial and thermoregulatory behaviors

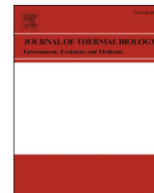
would weaken, but the energetic *trade-off* between territorial behaviors and other activities would intensify.

Conclusions. In this study we must explore whether this temporal *trade-off* occurs in other terrestrial species inhabiting hot environments and predict how this *trade-off* would be affected by warmer temperatures due to habitat loss and climate warming, for example using computational modeling. If males were to prioritize thermoregulatory over territorial behaviors in the face of habitat warming, thermoregulatory behaviors could compete for energy (Fey et al. 2019), time (Cunningham et al. 2021), and safety with other activities. This assessment should be prioritized for terrestrial ectotherms that inhabit warm environments of tropical and subtropical latitudes because they have a narrower thermal performance curve and therefore pay a higher cost for failing to thermoregulate than those that inhabit cool environments of temperate latitudes (Fey et al. 2019).

CAPÍTULO 3. Protection from overheating of simulated *Sceloporus horridus* lizards in a biosphere reserve of seasonally dry tropical forest in central Mexico.

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Protection from overheating of simulated *Sceloporus horridus* lizards in a biosphere reserve of seasonally dry tropical forest in central Mexico

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ABSTRACT

In seasonally dry ecosystems, loss of vegetation cover leads to warmer microclimates that can increase lizards' body temperatures to the point of threatening their performance. Preserving vegetation by establishing protected areas may mitigate these effects. We used remote sensing to test these ideas in the Sierra de Huautla Biosphere Reserve (REBIOSH) and surrounding areas. First, we determined whether vegetation cover was higher in the REBIOSH compared to adjacent unprotected areas to the north (NAA) and south (SAA). Then, we used a mechanistic niche model to test whether simulated *Sceloporus horridus* lizards in the REBIOSH experienced a cooler microclimate, higher thermal safety margin, longer foraging duration, and lower basal metabolic rate compared to adjacent unprotected areas. We compared these variables between 1999, when the reserve was declared, and 2020. We found that vegetation cover increased from 1999 to 2020 in all three areas; it was higher in the REBIOSH than in the more anthropized NAA, and was intermediate in the less anthropized SAA in both years. The microclimate temperature decreased from 1999 to 2020 and was lower in the REBIOSH and SAA than in the NAA. Thermal safety margin increased from 1999 to 2020; it was higher in the REBIOSH than in the NAA and intermediate in the SAA. Foraging duration increased from 1999 to 2020 and was similar among the three polygons. Basal metabolic rate decreased from 1999 to 2020 and was higher in the NAA than in the REBIOSH and SAA. Our results suggest that the REBIOSH provides cooler microclimates that increase the thermal safety margin and lower the metabolic rate of this generalist lizard compared to the NAA, and that the REBIOSH could contribute to increased vegetation cover in its surroundings. Besides, protecting original vegetation cover is an important part of climate change mitigation strategies more generally.

1. Introduction

Seasonally dry tropical forests are one of the most seriously threatened ecosystems worldwide (Portillo-Quintero and Sánchez-Azofeifa 2010). By 2004, an average of 66% of seasonally dry tropical forest area in America had been converted to croplands and livestock pastures, and only 29% of Mexican seasonally dry tropical forest area remained as primary forest (Portillo-Quintero and Sánchez-Azofeifa 2010). The loss of canopy cover leads to intense warming, especially in arid ecosystems. On one hand, natural seasonal changes in seasonally dry tropical forests lead to the majority of trees dropping their leaves in the dry season, resulting in a 28% decrease in canopy cover and a 3.8 °C increase in air temperature in two Mexican seasonally dry tropical forests (Siliceo-Cantero et al., 2016). On the other hand, vegetation loss from human activities also decreases canopy cover. For instance, a 44% decrease in vegetation cover due to anthropogenic disturbance increased the mean

soil temperature by 3.4 °C in patches of a Mexican seasonally dry tropical forest (Suazo-Ortuño et al., 2008). These two effects can combine to further compound the naturally hot and dry conditions during the dry season, resulting, for example in 4 °C higher temperatures in anthropogenic pastures than in primary forests in a Costa Rican seasonally dry tropical forest (Klemens et al., 2011).

The body temperature of terrestrial ectotherms like lizards depends on the thermal characteristics of their habitats. Microclimate changes, including anthropogenic and seasonal changes, can therefore affect lizards' body temperatures. For example, mean temperatures of *Sceloporus aeneus* lizards were higher when the shade availability in their refuges was experimentally decreased in hot environments (Rangel-Patiño et al., 2020). In the case of seasonal changes, mean temperatures of *Ctenosaura oaxacana* iguanas were 2.3 °C higher during the dry season than in the rainy season in a Mexican seasonally dry tropical forest (Valenzuela-Ceballos et al., 2015). High body

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temperatures are relevant because they strongly impact lizards' performance. Performance indicators such as growth rate, running speed, and predation success all strongly and suddenly decrease when body temperatures exceed the species' optimal temperature range (reviewed by Huey 1982). In addition, ectotherm metabolism increases positively with body temperature (de Andrade, 2018; due to increased enzyme kinetics), thereby increasing the intake needed to compensate for such a cost of living (Vucic-Pestic et al., 2011) or decreasing selected body temperatures (Gilbert and Miles 2016). Lizards therefore use thermoregulatory behaviors to sustain the interval of body temperatures that allow them to carry out their activities (interval of voluntary thermal tolerances; Camacho and Rusch 2017). In hot microclimates, lizards usually increase their investment in thermoregulatory behaviors as environment temperatures increase. For instance, in natural contexts, *Carlia* spp. lizards increased their investment in thermoregulatory behaviors during the summer when the habitat was hotter than in the winter (Vickers et al., 2011), and *Sceloporus occidentalis* lizards in an arid woodland restricted their activities to shadier microhabitats and higher perch heights than those in a temperate forest (Asbury and Adolph 2007). However, lizards cannot increase their investment in thermoregulatory behaviors indefinitely, since they incur costs in terms of energy, time, predation risk, and investment in other activities such as foraging or reproductive behaviors (Huey and Slatkin 1976). For example, the conversion of a conserved seasonally dry tropical forest to a pasture decreased the time that the tortoise *Gopherus evgoodei* had the necessary body temperatures to carry out its activities such as foraging (Lara-Reséndiz et al., 2022).

The extremes of the interval of voluntary thermal tolerances are the voluntary thermal minimum (VT_{min}) and voluntary thermal maximum (VT_{max}). When lizards' body temperatures exceed VT_{max} they overheat; in the short term, their performance decreases (reviewed by Camacho and Rusch 2017), which in the long term can translate into decreased survival, and ultimately threaten populations (Bestion et al., 2015). For example, *Zootoca vivipara* lizards experienced an accelerated life cycle and lower adult survival in field enclosures that were 2 °C warmer than the mean ambient temperature, which led to the prediction that the population would be locally extinct within 20 years (Bestion et al., 2015). Given the risks of overheating, it is particularly relevant to determine how close a lizard is to ceasing activity to cool down before exceeding its VT_{max} —in other words, the difference between VT_{max} and body temperature. We refer to this variable as the “thermal safety margin”, similar to how it is defined by Sunday et al. (2014).

Protected areas, by protecting vegetation cover, should maintain cooler microclimates and thus decrease lizards' risk of overheating compared to unprotected areas. There are several examples of higher mean vegetation cover within protected areas than in unprotected adjacent areas (reviewed by Geldmann et al., 2013 and Laurance et al., 2012, and references therein), including arid ecosystems such as semi-arid savanna (Wasiolka and Blaum 2011) and desert (Al-Sayegh et al., 2020). This leads to the straightforward expectation that higher vegetation cover in protected areas in arid ecosystems generate microclimates that are more conducive to lizard thermoregulation. However, we know of only one empirical study testing this idea, which did not find clear support for it (Al-Sayegh et al., 2020). The daily mean body temperatures of *Uromastix aegyptia* lizards were similar among protected and unprotected areas of a desert, even though the mean vegetation cover was higher in the protected than in the unprotected areas (Al-Sayegh et al., 2020). To better understand whether and how protected areas provide protection from overheating for the lizard populations inhabiting them, we need studies that compare the effect of protected areas on vegetation cover, and in turn on the microclimate experienced by lizards, at their spatial scale and considering their thermoregulatory behaviors.

In this study, we tested the hypothesis that the Sierra de Huautla Biosphere Reserve (REBIOSH) has habitats with higher vegetation cover and cooler microclimate that provide *Sceloporus horridus* lizards with

higher thermal safety margin, foraging duration, and lower metabolic rate compared to its surrounding area. The REBIOSH covers 59,031 ha in south-central Mexico and 60.6% of its area is seasonally dry tropical forest. This region has a marked dry season from November to mid-May (Torres et al., 2009). The hottest months of the dry season challenge lizard thermoregulation and have the lowest ecosystem productivity (i. e., prey availability) (Siliceo-Cantero et al., 2016; Singh and Chaturvedi 2018). *Sceloporus horridus* uses a variety of microhabitats, where they forage with a sit-and-wait strategy and where males court and defend territories in high and conspicuous places from March through June (Bussjaeger 1971; Bustos-Zagal et al., 2013; Castro-Franco et al., 2017). The fact that the most demanding period for lizard's thermoregulation (which requires available shade) is also the period during which *S. horridus* males invest in courtship and territory defense (in the open), sets up a potential trade-off between thermoregulatory and reproductive behaviors during the dry season. This is a particularly biologically important context in which to assess whether the REBIOSH provides cooler microclimates for *S. horridus* thermoregulation than its surroundings.

We used data on climate, vegetation cover, behavior, and thermal biology to simulate the microclimate temperature experienced by simulated *S. horridus* lizards and their thermoregulation in the REBIOSH and in the unprotected area bordering the reserve. We carried out the comparisons considering the conditions when the REBIOSH was declared in 1999 and after 20 years of protection (2020). We addressed five distinct, but related questions. Compared to the unprotected surrounding area: 1) Did the area within the REBIOSH have higher vegetation cover?; 2) Was the simulated microclimate cooler within the REBIOSH?; 3) Was the thermal safety margin higher for simulated *S. horridus* lizards within the REBIOSH (i.e., did they maintain body temperatures farther below the species' VT_{max})?; 4) Did the simulated lizards spend more time foraging within the REBIOSH?; 5) Did the simulated lizards have a lower metabolic rate in the REBIOSH? We expected that the REBIOSH would have habitats with higher vegetation cover and cooler microclimate, as well as simulated lizards with higher thermal safety margins, longer foraging duration, and lower metabolic rate than its unprotected surroundings. We expected these differences to be stronger in 2020, after 20 years of protection of the REBIOSH.

2. Materials and methods

2.1. Study area

The study area included the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected area surrounding it, located mostly in the state of Morelos (Fig. 1a, b; southwest corner at coordinates 18.1713N, 99.66340 and northeast corner at 18.7855N, 98.5264W) between the Trans-Mexican Volcanic Belt and the Sierra Madre Occidental biogeographic provinces.

In the study area, the average monthly rainfall during the core months of the rainy season (July–September) is 169.0 mm (SD = 4.3 mm) and the mean temperature of the hottest months of the dry season (March–May) is 25.7 °C (SD = 1.3 °C) (SMN 2010; Fig. S1). The seasonally dry tropical forest of the REBIOSH has an arboreal stratum 4–10 m tall dominated by the families Fabaceae, Poaceae, Asteraceae, and Burseraceae, and by the species *Conzattia multiflora*, *Lysiloma acapulcense*, *Lysiloma divaricatum*, *Bursera* spp., and *Ceiba* spp. (CONANP 2005). There are also small patches of conifer forests and grasslands (CONANP 2005).

Within the REBIOSH, there are 30 small towns, connected by dirt tracks and paved roads, where there is small-scale farming, ranching, and selective timber extraction. To the north of the REBIOSH, the landscape is relatively flat, and in 2015 there were large areas of pastures and croplands, roads and highways, as well as larger towns and cities (CONABIO 2020). To the south, the landscape is mainly mountainous, and in 2015 there were small areas of croplands, human

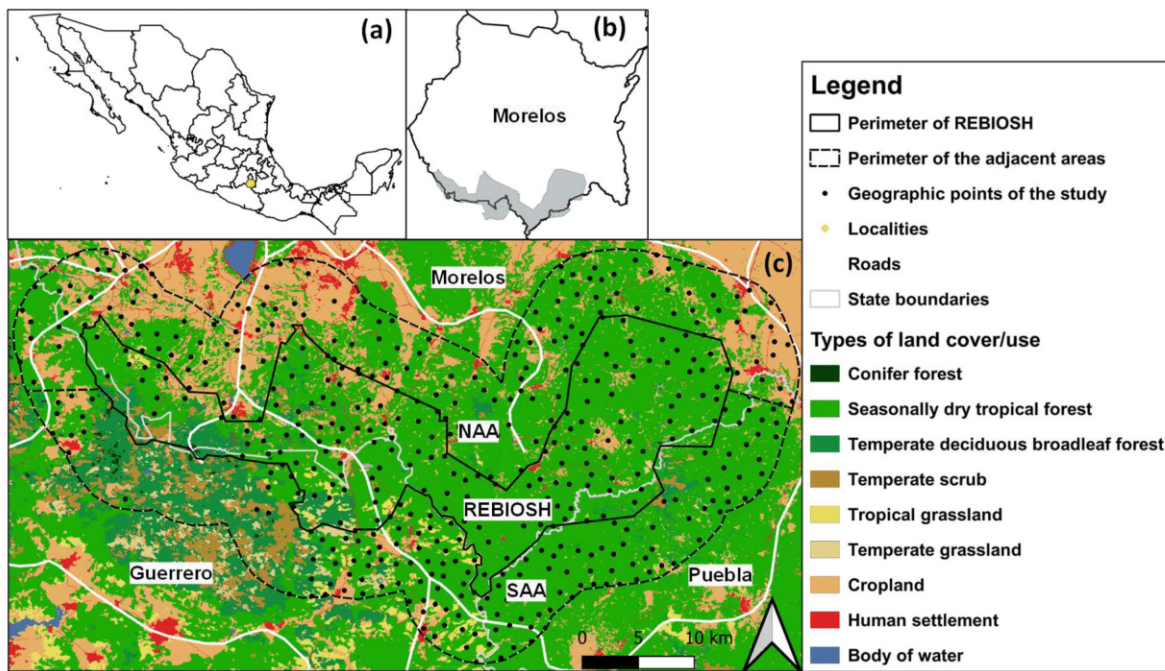


Fig. 1. Maps of the study area. (a) Location of Morelos state in south-central Mexico. (b) Location of the Sierra de Huautla Biosphere Reserve (REBIOSH) in southern Morelos. (c) Map of land use/cover (CONABIO 2020) and sampling points (“simulated home ranges”) within the three study polygons: REBIOSH, north adjacent area (NAA), and south adjacent area (SAA). Note that the 150 sampling points within each polygon were restricted to the altitudinal range shared among the three polygons (759–1470 masl).

settlements, and few paved roads (CONABIO 2020). Even before 1999, the area that was eventually declared as the REBIOSH had more favorable conservation status than the surrounding area. This contributed to the declaration of the REBIOSH because in order to qualify to be designated as a biosphere reserve in Mexico, an area must be representative of a determined ecosystem and not significantly disturbed by humans (DOF 2021).

To compare the REBIOSH with its surroundings, we followed the method used by Figueroa et al. (2009) to assess the effectiveness of Mexican protected areas, with some modifications. Using QGIS (v.3.8.0), we divided the area surrounding the REBIOSH into two polygons, one to the north and one to the south, to account for the aforementioned landscape-scale differences. Each of these polygons was 1.1 km wide and had the same area like the REBIOSH polygon (59,076 ha). As sample units, within each polygon, we randomly placed 150 sampling points separated from each other by ≥ 1 km (Fig. 1c). To avoid confounding land-use effects with altitude, the sampling points were restricted to the elevational range shared among the three polygons, 759–1470 masl. We also ensured that points did not fall on irrigated croplands, buildings, greenhouses, or paved roads.

2.2. Study variables

Vegetation cover. We characterized the vegetation cover at each of the 150 sampling points in each polygon using the normalized difference vegetation index (NDVI) * 100 (i.e., converted to percentage). The NDVI has been used previously to characterize vegetation cover in studies of lizard ecology and conservation in arid ecosystems (Furnas et al., 2019). We obtained the rasters of the average NDVI for the hottest trimester of the dry season (March–May) and for the core months of the rainy season (July–September) in 1999 and 2020 at a resolution of 30m from Climate Engine (Huntington et al., 2017). We used the NDVI from the rainy season to compare vegetation cover among polygons because the NDVI is most sensitive during the most productive period in seasonal and semi-arid ecosystems (Guzmán et al., 2019). NDVI from the dry season was an input for the simulations of microclimate, thermal safety margin,

foraging duration, and metabolic rate (see below).

Simulated microclimate. We used the R package NicheMapR (Kearney and Porter 2017; 2020) to simulate the microclimate available to *S. horridus* lizards and to model its thermoregulatory behaviors, body temperature, foraging duration, and metabolic rate at each sampling point. To simulate the microclimate, we used the `micro_ncep` function of NicheMapR, which integrates the topography, incident solar radiation, and climate of a specified geographical point, during a specified interval of date and time, and at both extremes of a specified interval of perch height and shade percentage (this last calculated based on vegetation cover, leaf area index, and the leaf angle ratio) (Kearney and Porter 2017). There is no information about the home range size of *S. horridus* specifically, but the mean home range size of six *Sceloporus* species for which this information is available (1104.0 m², SD = 1440.5 m²; Table S1) is similar to the 30 m spatial resolution (i.e., 900 m² grid cells) utilized by NicheMapR. Thus, we considered the cell surrounding each sampling point to represent the home range of a single simulated *S. horridus* lizard (hereafter, “simulated home range”). The elevation, slope, and orientation of the terrain of the simulated home range were extracted automatically by NicheMapR from a digital elevation model. We were interested in understanding how microclimate was affected by changes in vegetation cover generated by 20 years of protection in the REBIOSH, rather than temperature differences between the specific years of 1999 and 2020. We therefore decided to separate the effect of vegetation cover from the effect of yearly weather fluctuations by using a single climate dataset for microclimate modeling. Constraints of the NicheMapR program did not allow us to use a composite climate dataset that averages the weather of the three hottest months of the dry season across the 20 year timespan, so we used climate data from a single year to run all microclimate simulations. We chose to use climate data from the year 2017 because it was the warmest year in Mexico since data became available in 1971 (CONAGUA 2017) and therefore represented a worst-case scenario for lizard thermoregulation under hot conditions. We used hour as the temporal scale and averaged the hourly records of microclimate temperature from 9 to 16h, the activity time of *S. horridus* (Bustos-Zagal et al., 2013) for the days of the study period in the dry

season (March–May). We calculated the microclimate at perch heights of both 3 cm and 120 cm since microclimate may be cooler higher above the ground in arid woodlands due to increased wind speed (Asbury and Adolph 2007). Using these perch heights allowed us to capture the daytime microclimates available to the lizards that move vertically to access cooler air temperatures and higher wind speeds (Ortega et al., 2017). NicheMapR can accurately describe the microclimate temperature at perch heights of 5 cm and 120 cm (root mean square error of 3.8 °C and 2.8 °C, respectively; Kearney et al., 2018). To characterize the dry season of the seasonally dry tropical forest in NicheMapR, we set the leaf area index to 1.5 (one-sided green leaf area per unit soil surface area; following Maass et al., 1995) and the albedo to 0.24 (following Barradas and Adem 1992). We set the leaf angle ratio to 0 given that nearly all trees in the seasonally dry tropical forest lose their leaves during the dry season. Finally, we set the minimum shade percentage to 0, and the maximum to the percent vegetation cover of the simulated home range.

Simulated body temperature and thermal safety margin. To simulate the body temperature, NicheMapR integrates into the ectotherm subroutine the microclimate simulated previously and the specified traits of the lizard (Kearney and Porter 2017; 2020; code available at https://github.com/mrke/NicheMapR/blob/master/R/ectoR_devel.R). We set the morphology to a “lizard-like object” of 35g of mass with diurnal activity (Bussjaeger 1971; Bustos-Zagal et al., 2013). As thermoregulatory behaviors, the simulated lizard could change its body orientation relative to direct insolation, move along the specified interval of shade percentage, and climb from 3 cm up to 120 cm perch height to attempt to maintain an average body temperature of 34.2 °C or to avoid body temperatures outside the interval of voluntary thermal tolerances (28.8 °C–36.4 °C). There are no published reports of VT_{min} for *S. horridus*, only of its VT_{max} (Lemos-Espinal et al., 1993), so we set its VT_{min} as the average body temperature of *S. horridus* in the field during the dry season (34.2 °C) minus 1SD (5.4 °C) (Bustos-Zagal et al., 2013). NicheMapR can accurately describe the observed body temperature in a seasonally arid shrubland similar to our study ecosystem (root mean square error of 3.9 °C; Kearney et al., 2018). We did not allow sheltering in burrows because *S. horridus* is not a fossorial or burrowing species, and males spend much of their time courting and defending their territories in open and conspicuous perches above the ground during the dry season (Bussjaeger 1971). *Sceloporus horridus* has been reported to be active between 9 and 16h during the dry season (Bustos-Zagal et al., 2013). We considered this reported activity time because it reflects the meteorological conditions that challenge the thermoregulation of *S. horridus* while it defends its territory during the dry season, generating a temporal trade-off between thermoregulatory and territorial behaviors. We also carried out simulations considering the daylight hours (from 7 to 19h in our study site) to account for the possibility of bimodal activity. The parameters used in the ectotherm model are in Table S3. We calculated the thermal safety margin for each simulated lizard as the species' VT_{max} minus the body temperature recorded every hour between 9 and 16h or 7–19h for each day of the dry season (March–May).

Foraging duration and metabolic rate. Foraging duration was calculated as the average of the total daylight hours per day when the simulated lizard's body temperature was within the species' voluntary thermal tolerance range (28.8 °C–36.4 °C) during the hottest trimester of the dry season (March–May). The code of NicheMapR to calculate the foraging duration is available at https://github.com/mrke/NicheMapR/blob/master/R/trans_behav.R. The basal metabolic rate was calculated based on the allometric relationship of the basal metabolic rate to body mass and body temperature of squamate reptiles, following equation number 2 of (Andrews and Pough 1985). The NicheMapR code to calculate the metabolic rate is available at https://github.com/mrke/NicheMapR/blob/master/R/ectoR_devel.R. We averaged the sum of the 24 hourly basal metabolic rate records generated each day during the dry season (March–May). The unit of the basal metabolic rate was transformed from consumed mL of O₂ to kJ in order to determine the

daily energy required by the simulated lizards to satisfy their basal metabolic rate under the different simulated conditions. We multiplied the O₂ mL/day consumed by the simulated lizard by 20.08 J/mL O₂ to obtain the kJ/day that the simulated lizards expended to maintain its basal metabolic rate (Benabib and Congdon 1992).

2.3. Statistical analysis

We determined whether parametric models were appropriate using the Shapiro-Wilk test of normality, Levene's test of homoscedasticity, normal quantile-quantile plots, and residuals-versus-fit plots. We compared the percent vegetation cover during the rainy season between 1999 and 2020 using Wilcoxon's rank sum test, and among the REBIOSH, NAA, and SAA using a Kruskal-Wallis test. To test for the interactions between year and polygon, we compared the percent vegetation cover during the rainy season among the REBIOSH, NAA, and SAA in 1999 and 2020 using a Kruskal-Wallis test considering six groups (three polygons in two years) with 150 sampling points each. If the Kruskal-Wallis tests were significant, we conducted *post-hoc* Dunn's tests with Bonferroni correction, and we reported effect size as Cliff's delta for significant comparisons. Cliff's delta ranges from -1 to 1, the number indicates the effect size, and the positive numbers indicate that the first group of the comparison is higher than the second. Whenever comparing among the six year-by-polygon groups, we only interpreted pairwise comparisons that were relevant to our main questions (between years within the same polygon and among polygons within the same year). We compared the difference in vegetation cover between years among polygons using an analysis of variance (residuals were normal and heteroscedastic). If the analysis of variance was significant, we conducted Tukey's *post-hoc* tests, and we reported effect size as Cohen's *d* for significant comparisons.

We compared the microclimate temperature of simulated home ranges, and the thermal safety margin, daily foraging duration, and daily basal metabolic rate of simulated lizards during the dry season using two-way analysis of variance considering polygon, year, and their interaction. Each group had a sample size of 150 sampling points. Whenever the interaction effect was non-significant, it was removed prior to performing *post-hoc* tests. We conducted Tukey's *post-hoc* tests and reported effect size as Cohen's *d* for significant comparisons. Since *S. horridus* can be found on the ground, on rocks, and on the trunk of trees and may use those surfaces to thermoregulate, we analyzed the available microclimate temperature at the 3 cm and 120 cm perch heights separately. However, since *S. horridus* frequently forages on the ground, we only analyzed the thermal safety margin, daily foraging duration, and basal metabolic rate at the 3 cm perch height. We did all analyses and constructed all figures in R (R Core Team, 2020). The raw data and R-code required to reproduce the below findings are available to download from (Valencia-Esquivel et al., 2015).

3. Results

3.1. Percent vegetation cover

The mean percent vegetation cover differed between years (Wilcoxon rank sum test, $W = 39823$, $P = <0.001$) and among polygons (Kruskal-Wallis test, $X^2 = 58.548$, $DF = 2$, $P = <0.001$). We found a significant difference in the percent vegetation cover among the six polygon-year combinations (Kruskal-Wallis test $X^2 = 315.88$, $DF = 5$, $P = <0.001$). *Post-hoc* Dunn's tests showed that in 1999, the mean percent vegetation cover was higher in the REBIOSH than in the NAA, and intermediate in the SAA (statistically similar to the REBIOSH and NAA; Fig. 2; Table 1). In 2020, the mean percent vegetation cover was lower in the NAA than in the REBIOSH and SAA, and similar between the REBIOSH and SAA (Fig. 2; Table 1). *Post-hoc* Dunn's tests showed that the mean percent vegetation cover was higher in 2020 than in 1999 for each of the three polygons (Fig. 2; Table 1). *Post-hoc* Tukey's tests

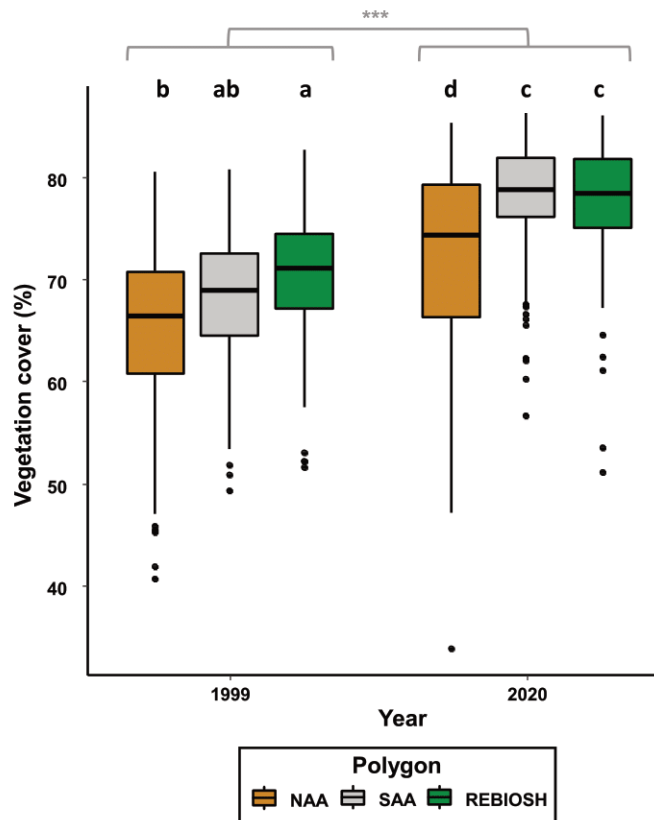


Fig. 2. Vegetation cover (NDVI converted to percentage) within the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected adjacent areas to the north (NAA) and south (SAA) in 1999 and 2020, during the core months of the rainy season (July–September). The color and order of the polygons is shown in the legend. Different letters denote significant differences ($P < 0.05$). Gray brackets denote differences between years (***) indicates a significant difference of $P \leq 0.001$). In the boxplots, the thick black horizontal line denotes the median, the box the interquartile range, the vertical lines 1.5 times the interquartile range, and the points are values outside that range. Each group has a sample size of 150.

Table 1

P -values from *post-hoc* Dunn’s test (Bonferroni-adjusted) and Cliff’s delta effect size comparing percent vegetation cover among the three polygons (REBIOSH, north adjacent area [NAA], and the south adjacent area [SAA]) in 1999 and 2020, and comparing percent vegetation cover between years in each polygon. P -values from *post-hoc* Tukey’s test (Bonferroni-adjusted) and Cohen’s d effect size comparing the change of percent vegetation cover between years in every polygon. Significant P -values are indicated in bold type.

| Comparison | Adjusted P | Effect size | |
|---|------------------|------------------|--------|
| Vegetation cover between polygons in each year | | | |
| 1999 REBIOSH | 1999 NAA | <0.001 | 0.372 |
| 1999 REBIOSH | 1999 SAA | 0.517 | 0.198 |
| 1999 NAA | 1999 SAA | 0.737 | -0.208 |
| 2020 REBIOSH | 2020 NAA | <0.001 | 0.382 |
| 2020 REBIOSH | 2020 SAA | 1.00 | -0.026 |
| 2020 NAA | 2020 SAA | <0.001 | -0.398 |
| Vegetation cover between years in each polygon | | | |
| 1999 REBIOSH | 2020 REBIOSH | <0.001 | -0.688 |
| 1999 NAA | 2020 NAA | <0.001 | -0.432 |
| 1999 SAA | 2020 SAA | <0.001 | -0.762 |
| Difference of the vegetation cover between years among polygons | | | |
| 1999 vs 2020 REBIOSH | 1999 vs 2020 NAA | 1.00 | 0.087 |
| 1999 vs 2020 REBIOSH | 1999 vs 2020 SAA | 0.0716 | -0.262 |
| 1999 vs 2020 SAA | 1999 vs 2020 NAA | 0.0080 | 0.349 |

showed that the difference in mean percent vegetation cover between 1999 and 2020 was similar between the REBIOSH and both adjacent areas, but the SAA gained significantly more vegetation cover than the NAA (Table 1).

3.2. Microclimate temperature

At 3 cm perch height, the mean microclimate temperature of simulated home ranges differed between years ($F_{1,894} = 28.37, P = <0.001$) and among polygons ($F_{2,894} = 5.79, P = 0.0032$), with no significant interaction effect ($F_{2,894} = 0.10, P = 0.9062$). The mean microclimate temperature decreased from 1999 to 2020 in all three polygons (Cohen’s $d = 0.355$; Fig. 3). Considering both years together, the mean microclimate temperature was higher in the NAA than in the REBIOSH and the SAA (NAA-REBIOSH *post-hoc* Tukey’s test $P = 0.0043$, Cohen’s $d = 0.229$; NAA-SAA *post-hoc* Tukey’s test $P = 0.0224$, Cohen’s $d = 0.218$), and similar between the REBIOSH and SAA (Fig. 3A).

At 120 cm perch height, the mean microclimate temperature of simulated home ranges was different across polygons ($F_{2,894} = 11.108, P = <0.001$) but not between years ($F_{1,894} = 0.967, P = 0.326$), with no significant interaction effect ($F_{1,894} = 0.003, P = 0.997$). Considering both years together, the mean microclimate temperature was higher in the NAA than in the REBIOSH and SAA (NAA-REBIOSH *post-hoc* Tukey’s test $P = <0.001$, Cohen’s $d = 0.385$; NAA-SAA *post-hoc* Tukey’s test $P = 0.0351$, Cohen’s $d = 0.203$), and similar between the REBIOSH and SAA (Fig. 3B).

3.3. Thermal safety margin

At 3 cm perch height during the reported activity time during the dry season (9–16h), the mean thermal safety margin differed between years

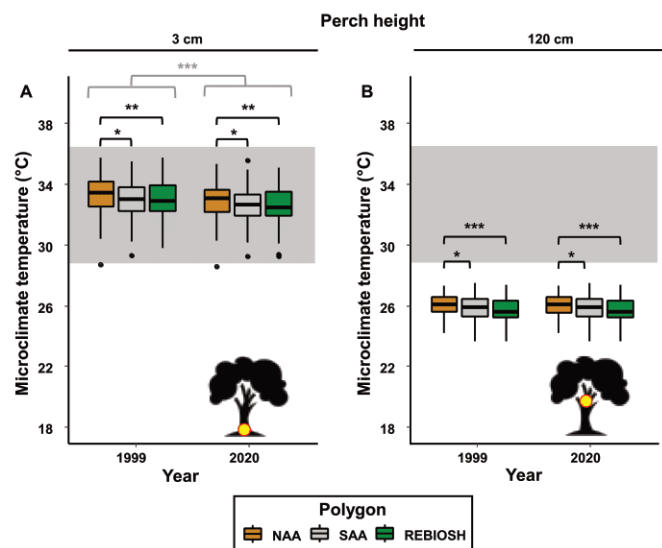


Fig. 3. Microclimate temperature of simulated home ranges within the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected adjacent areas to the north (NAA) and south (SAA) in 1999 and 2020, during the hottest trimester of the dry season (March–May), at 3 (A) or 120 cm (B) perch height. The color and order of the polygons is shown in the legend. Asterisks indicate significant differences between groups connected by brackets ($*P \leq 0.05, **P \leq 0.01, ***P \leq 0.001$). Gray brackets denote differences between years, and black brackets indicate differences among polygons within each year. Groups not connected by brackets were not significantly different. See text for full statistical results. Each group has a sample size of 150. The shaded region denotes the interval of voluntary thermal tolerances of *S. horridus* (28.8–36.4 °C). In the boxplots, the thick black horizontal line denotes the median, the box the interquartile range, the vertical lines 1.5 times the interquartile range, and the points are values outside that range.

($F_{1,894} = 38.218$, $P = <0.001$) and among polygons ($F_{2,894} = 3.381$, $P = 0.0345$), with no significant interaction effect ($F_{1,894} = 0.117$, $P = 0.8897$). The mean thermal safety margin was higher in 2020 than in 1999 in all three polygons (Cohen's $d = 0.413$; Fig. 4A). Considering both years together, the mean thermal safety margin was higher in the REBIOSH than in the NAA (*post-hoc* Tukey's test $P = 0.0398$, Cohen's $d = 0.199$) and intermediate in the SAA (statistically similar to the REBIOSH and NAA; Fig. 4A). The analysis considering the full daylight interval (7–19h) yielded similar results (between years: $F_{1,894} = 4.729$, $P = 0.0299$; among polygons: $F_{2,894} = 4.206$, $P = 0.0152$; interaction effect non-significant: $F_{1,894} = 0.6811$, $P = 0.5063$). As above, the mean thermal safety margin was higher in 2020 than in 1999 in all three polygons (Cohen's $d = 0.145$) and the thermal safety margin was higher in the REBIOSH than in the NAA (*post-hoc* Tukey's test $P = 0.0128$, Cohen's $d = 0.232$) and intermediate in the SAA (not statistically distinguishable from the NAA or REBIOSH; figure not shown).

Given that we found differences among polygons in both vegetation cover and thermal safety, we were interested in further exploring whether the thermal safety margin increased with the percent vegetation cover within each polygon and whether the strength of this relationship varied among polygons. Therefore, we performed a multiple linear regression of the thermal safety margin on the percent vegetation cover, the polygon, and their interaction. To simplify the analysis, we considered only the year 2020 since we were most interested in the current conditions. We analyzed the multiple linear regression with a two-way analysis of variance and found that there was a significant interaction effect between predictors ($F_{2,444} = 4.439$, $P = 0.0123$). Thus, we compared the relationship between the thermal safety margin and percent vegetation cover among polygons with the emmeans package. Thermal safety increased with percent vegetation cover for all three polygons (Fig. S2); the slope of the relationship was significantly higher in the REBIOSH than in the NAA (*post-hoc* Tukey's test $P = 0.0095$; Cohen's $d = 0.083$), and intermediate in the SAA (statistically similar to the REBIOSH and NAA). Removing one apparent outlier from the NAA (a simulated home range with unexpectedly high thermal safety; See Fig. S2) did not change these overall results (*post-hoc* Tukey's test $P = 0.0160$; Cohen's $d = 0.079$).

3.5. Foraging duration

The mean daily foraging duration differed between 1999 and 2020 ($F_{1,894} = 85.354$, $P = <0.001$) but not among polygons ($F_{2,894} = 1.088$, $P = 0.3375$), with no significant interaction effect ($F_{2,894} = 1.387$, $P = 0.2504$). The mean foraging duration was higher in 2020 than in 1999 (Cohen's $d = 0.616$; Fig. 4B) in all three polygons. Considering both years together, mean daily foraging duration was similar among the three polygons (Fig. 4B).

3.6. Basal metabolic rate

The mean daily basal metabolic rate expressed in kJ/d differed between 1999 and 2020 ($F_{1,894} = 39.771$, $P = <0.001$) and among polygons ($F_{2,894} = 4.285$, $P = 0.0141$), with no significant interaction effect ($F_{2,894} = 1.117$, $P = 0.3279$). The mean daily basal metabolic rate was higher in 1999 than in 2020 (Cohen's $d = 0.420$; Fig. 4C) in all three polygons. Considering both years together, the mean daily basal metabolic rate was higher in the NAA than in the REBIOSH and SAA (NAA-REBIOSH *post-hoc* Tukey's test $P = 0.0273$, Cohen's $d = 0.210$; NAA-SAA *post-hoc* Tukey's test $P = 0.0345$, Cohen's $d = 0.203$), and similar between the REBIOSH and SAA (Fig. 4C).

4. Discussion

We found partial support for our hypothesis that the REBIOSH has simulated home ranges with higher vegetation cover and cooler microclimate, and simulated *S. horridus* lizards with higher thermal safety margin, daily foraging duration, and lower daily basal metabolic rate compared to unprotected adjacent areas. The REBIOSH presented simulated home ranges with more vegetation cover and cooler simulated microclimate, and simulated *S. horridus* lizards with higher thermal safety margin and lower daily basal metabolic rate compared to the NAA. The SAA presented simulated home ranges with cooler simulated microclimate and simulated *S. horridus* lizards with lower daily basal metabolic rate than the NAA. Vegetation cover increased over time in all three areas, rather than the REBIOSH only, and microclimate

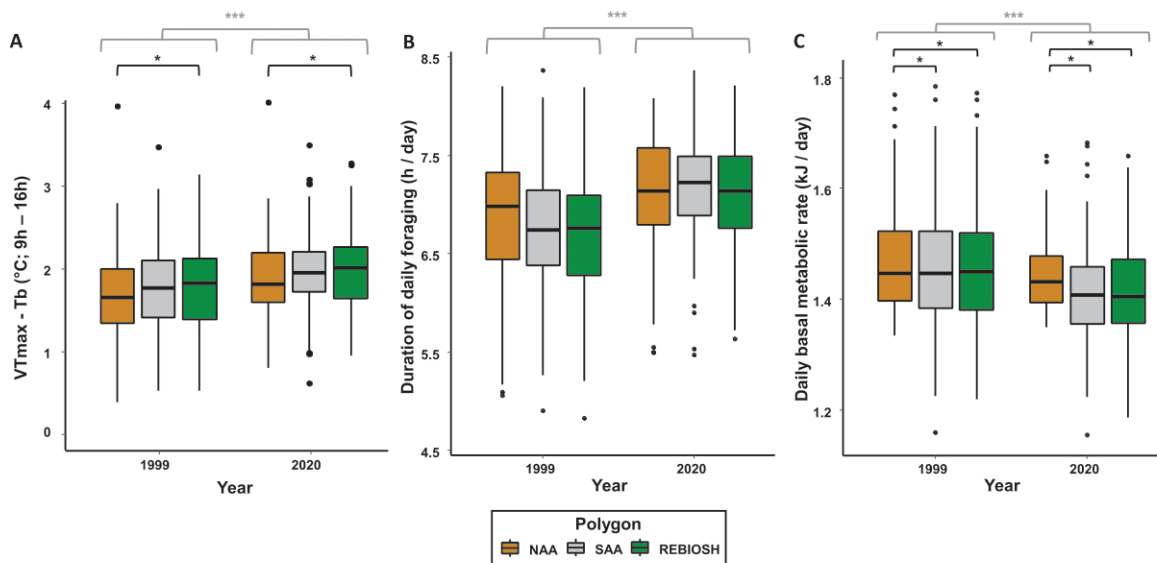


Fig. 4. Thermal safety margin ($VT_{\max} - T_b$; A), daily foraging duration (B), and daily basal metabolic rate (C) of simulated lizards within the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected adjacent areas to the north (NAA) and south (SAA) in 1999 and 2020, during the hottest trimester of the dry season (March–May), at 3 cm perch height. The color and order of the polygons is shown in the legend. Asterisks indicate significant differences between groups connected by brackets ($*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$). Gray brackets denote differences between years, and black brackets differences among polygons within each year. Groups not connected by brackets were not significantly different. See text for full statistical results. Each group has a sample size of 150. In the boxplots, the thick black horizontal line denotes the median, the box the interquartile range, the vertical lines 1.5 times the interquartile range, and the points are values outside that range.

temperature was higher, thermal safety margin lower, daily foraging duration lower, and daily basal metabolic rate higher in 1999 than in 2020. Thus, our findings suggest that in our study area, *S. horridus* lizards currently experience cooler conditions that allow them to thermoregulate better, reduce their energetic cost of life, and increase their foraging duration compared to when the REBIOSH was declared 20 years ago.

4.1. Vegetation cover

Vegetation cover increased from 1999 to 2020 in the REBIOSH as expected; it also, unexpectedly, increased in the two adjacent areas. Although it was not our initial prediction, increasing vegetation cover in areas surrounding protected areas is a repeated pattern, and the mechanisms behind this trend are the subject of ongoing research (Fuller et al., 2019). It is possible that the vegetation cover of the REBIOSH increased due to its protected status and the implementation of temporary employment opportunities (López-Medellín et al., 2017). Increased vegetation cover within the REBIOSH could augment the production of propagules, pollinators, and/or seed dispersers which may disperse into adjacent areas (sinks; Hansen 2011) and thus increase vegetation cover there through natural succession. It is also possible that larger-scale shifts in conservation attitudes, legislation, and enforcement positively impacted vegetation cover in the region or country. Studies of vegetation cover change over time at larger geographic scales are needed to clarify the mechanisms and scales of this increase in vegetation cover.

The lower vegetation cover in the NAA in both years was probably due to its proximity to tourist developments, cities, and large areas of agricultural fields, all of which were facilitated by its relatively flat terrain (CONANP 2005). In contrast, mountainous terrain has been previously shown to improve conservation status by hampering agriculture and urban activities (Mouillot et al., 2020). Therefore, the REBIOSH and the SAA could share similar percentages of vegetation cover since both are in mountainous terrain. Even though vegetation cover increased in both adjacent areas, this increase was stronger in the SAA than the NAA. It is possible that the REBIOSH influenced this differential increase by acting as a barrier, preventing disturbance from spreading from the NAA to the SAA.

Even though the results of our comparison of vegetation cover among the polygons were clear, NDVI has some limitations in representing the structure of the vegetation and the opportunities it provides for lizard thermoregulation. The vegetation cover estimated using NDVI in the dry season (which we used to simulate microclimates and body temperatures) may be underestimated compared to real vegetation because NDVI considers only active photosynthetic tissue, which is largely reduced during the dry season when woody plants lose their leaves (Singh and Chaturvedi 2018; Guzmán et al., 2019). Even so, NDVI is a realistic and informative marker of vegetation since it correlates with vegetation structure variables such as leaf area index and fractional vegetation cover (Carlson and Ripley 1997) and vegetation function variables such as photosynthetic capacity and net primary production (Pettorelli et al., 2011). Completely excluding dead or non-photosynthetic plant structures using the NDVI could mean that the actual microclimate during the dry season may be cooler than was estimated by our simulation for the three polygons, since real lizards can climb on or take refuge under fallen dead trees or standing leafless trees to thermoregulate. This is partially accounted for in our simulation because the simulated lizards were allowed to ascend to 120 cm perch height to thermoregulate. Also, the NDVI does not differentiate between rain-fed crop fields and native vegetation of the seasonally dry tropical forests during the dry season; however, we determined that it was appropriate to consider these crop fields in our simulations because *S. horridus* does bask and forage there during the dry season (IVE, pers. obs.).

4.2. Microclimate temperature

At 3 cm perch height, simulated lizards experienced cooler microclimates in 2020 compared to 1999 in the entire study area, but at 120 cm perch height, the microclimates were similar between years. This could be due to differences in the interaction between the forest vegetation cover and the atmospheric boundary layer at 3 versus 120 cm perch height. The vegetation cover of forest patches buffers the effects of the background environmental conditions, for example by intercepting solar radiation and decreasing wind speed. This buffer is stronger closer to the ground and further from patch borders due to the accumulation of vegetation above and surrounding the point of interest (Ewers and Banks-Leite 2013; Davis et al., 2019). Thus, the cooling of the microclimate at 3 cm perch height from 1999 to 2020 directly mirrored the increase in vegetation cover from 1999 to 2020. Meanwhile, the meteorological conditions at 120 cm were likely more directly affected by background environmental conditions, which are determined by factors that operate on longer time scales, such as topography, soil type, and wind direction (Oliver 2005). The meteorological conditions at 120 cm perch height thus seemed to reflect the local climate more than the more labile microclimate. Finally, our simulation models were deterministic; they did not consider sources of information or randomness of the inputs (as probabilistic models would). Using probabilistic models in future studies could improve our understanding of the biological relevance of vegetation cover change on the temperature of terrestrial ectotherms and their habitats.

Within each year, simulated lizards at both perch heights experienced cooler microclimates on average in the REBIOSH and SAA than in the NAA. This generally followed the vegetation cover differences among polygons, which is expected since higher percentages of vegetation cover generate cooler microclimates (Davis et al., 2019; this study). However, we must consider that although adult lizards use covered sites to exploit their cool microclimates, lizards cannot simply move to areas with increasingly thicker vegetation to avoid the risk of overheating; too much shade may generate environments that are too cold for lizards to sustain their thermal performance (Huey 1982) or the proper development of embryos (Monasterio et al., 2011). Specifically, the performance of lizards increases directly with body temperature up to surpassing its optimal temperature range (Huey 1982) and the embryos of *Psammotromus algirus* take longer to hatch and hatch with poorer body condition at temperatures colder than their optimum. Finer aspects of microclimate dynamics under the canopy could impact lizard thermoregulation and could be explored in future research using more sophisticated modeling tools such as microclimc (Maclean and Klingle 2021).

4.3. Thermal safety margin

The thermal safety margin was higher in 2020 than in 1999 in the entire study area, almost certainly due to the aforementioned increase in vegetation cover and consequent decrease in microclimate temperature. Within each year, considering the reported activity time of *S. horridus* or the daytime hours, the simulated lizards were safer from overheating in the REBIOSH than in the NAA, and intermediate in the SAA (statistically similar to both the REBIOSH and NAA). These results are consistent with previous findings. For example, *S. horridus* lizards had higher mean body temperatures during the dry season of the year in Mexican seasonally tropical dry forests (Bustos-Zagal et al., 2013), and *Uromastyx aegyptia* lizards had higher mean maximum body temperatures during the driest season of the year in disturbed sites with less vegetation cover in the Kuwait desert (Al-Sayegh et al., 2020). These findings demonstrate that thermoregulatory behaviors cannot completely buffer habitat warming during the dry season. The microclimate temperature differed more strongly between polygons than the thermal safety margin. This makes sense given that thermoregulatory lizards like *S. horridus* utilize behavioral thermoregulation to maintain constant body temperatures,

buffering spatial and temporal differences in microclimate temperature (Bustos-Zagal et al., 2013). This finding shows that the thermoregulatory tactics we simulated did partially modulate the effects of microclimatic changes between years and polygons on body temperatures of the simulated lizards.

The buffering capacity of thermoregulatory tactics depends on multiple factors and assumptions, some of which cannot yet be integrated into computational models (Fey et al., 2019). For example, our model assumed that the simulated lizards had the same probability of climbing to thermoregulate in every simulated home range regardless of its vegetation cover. However, territories with lower vegetation cover have fewer bushes and trees to climb, which could make climbing costlier and/or force lizards to utilize other thermoregulatory tactics such as modifying activity times or increasing use of shaded microhabitats. Even though there were simulated home ranges with low vegetation cover in all three polygons, they were more frequent in the NAA, such that the thermal safety margin difference in the NAA could be even stronger than estimated by our models. Indeed, if the vegetation cover of the NAA continues to diminish due to deforestation and fragmentation, the thermal safety margin difference could increase even more, risking in turn the capacity of the landscape north of the REBIOSH to function as a thermal buffer. Another limitation of our model, but a fruitful opportunity for future research, is that we were unable to account for the ecological costs that lizards pay for moving to the shade and climbing to higher perch heights to cool down (Huey and Slatkin 1976). However, there are studies under laboratory conditions that show that thermoregulatory behaviors incur costs on growth, distance moved (Brewster et al., 2013), and travelling time (Basson et al., 2017). Finally, our model did include one of the thermoregulatory tactics used by lizards in hot and arid environments to avoid overheating—a bimodal activity pattern in which lizards are more active in the morning and evening than at midday (Lara-Reséndiz et al., 2014). This occurs in several lizard species that inhabit seasonally dry ecosystems, such as *Phrynosoma munitzei* (Lara-Reséndiz et al., 2014) and *Uromastix aegyptia* (Al-Sayegh et al., 2020) which both avoid the hottest hours at midday by concentrating their activities in the morning and evening. In our simulations, in addition to considering the hours of activity that have been previously reported for this species (9–16h; Bustos-Zagal et al., 2013), we also considered the full daylight interval (7–19h) in order to allow the possibility of a bimodal activity pattern. The thermal safety margin considering the full daylight interval was on average 1 °C higher than when considering the reported activity time, but the differences among polygons were unchanged. These lizards may concentrate their daily activities more frequently in the morning and evening (bimodal activity pattern) in the face of the expected increasingly warmer conditions of their habitats (a result of climate warming). However, such changes in their activity time could increase ecological costs such as interspecific competition, territorial defense, foraging, and predation risk. Field observations of real lizards in dry environments that consider vegetation structure, the thermal conditions of the habitat, the full repertoire of thermoregulatory behaviors, and life history trade-offs will be required to determine how accurately our simulations describe real thermoregulatory ectotherms. Such observations could provide valuable information for designing more complex, flexible, and accurate modeling techniques.

It is also important to consider that different species may respond differently to the same environmental conditions. It is most common to assess environmental quality using species that have low to intermediate stress tolerance (Carignan and Villard 2002). *Sceloporus horridus* is an intermediate heat-tolerant species whose mean body temperature is near the median among 28 lizard species from dry and seasonally dry forests (Table S2). This species could therefore indicate a maximum thermal safety margin for less heat-tolerant species, as well as a minimum thermal safety margin for more heat-tolerant species that inhabit dry or seasonally dry forests.

4.4. Relationship between thermal safety margin and vegetation cover

Thermal safety margin increased with vegetation cover in all three polygons. However, this relationship was stronger in the REBIOSH than the NAA, and intermediate in the SAA (statistically similar to both the REBIOSH and NAA). In general, patches with higher vegetation cover within landscapes with more continuous vegetation cover are more resilient to microclimate warming and have a lower edge effect (Arroyo-Rodríguez et al., 2017). Given that vegetation cover was higher within the simulated home ranges of the REBIOSH than in those of the NAA, the vegetation cover of the former could also be more continuous than in the latter. Therefore, the stronger relationship in the REBIOSH could be the consequence of the vegetation cover being higher within its simulated home ranges and more continuous among them. This emphasizes the importance of habitat connectivity in the planning of protected areas.

4.5. Foraging duration and metabolic rate

We found that simulated lizards were able to dedicate more time of the day to foraging in 2020 than in 1999 and that they foraged a similar number of daily hours among the polygons. The time of thermal restriction (i.e., the time during which an individual must thermoregulate rather than carry out other activities such as foraging) has been previously shown to correlate positively with vegetation loss (Kearney, 2013) and habitat warming (Sinervo et al., 2010). Our results suggest that the lower vegetation cover in 1999 led to higher temperatures, which increased the amount of time that lizards were required to thermoregulate, at the expense of time they could spend feeding. At the same time, we found that the daily basal metabolic rate was higher in the NAA than the REBIOSH and SAA, as well as being higher in 1999 than in 2020. In ectotherms, ingestion efficiency (the energy the animal gains by ingestion minus the energy lost to metabolism) decreases with habitat warming because the metabolic rate increases with increasing body temperature, and can decrease even further if the rate of ingestion cannot increase quickly enough to keep pace with the increased metabolic rate (Rall et al., 2010). Our simulations suggest that lizards in the NAA are subjected to a higher basal metabolic rate, which increases the amount of food they require, but they do not have more time available to forage compared to the REBIOSH and SAA, which likely limits the ability of NAA's lizards to acquire more food to compensate. An insectivorous diet provides 23.276 kJ/g of dry mass (Golley 1961), of which 83% is actually assimilated by *Sceloporus* lizards (19.3 kJ/g; Pough, 1973). Given that the simulated lizards in the NAA, SAA, and REBIOSH consumed 1.44 kJ/d, 1.41 kJ/d, and 1.42 kJ/d in average, respectively, during 2020 conditions; therefore, the lizards in the NAA must consume on average 0.001 more grams of an insectivorous diet than the lizards in the REBIOSH and 0.002 more than in the SAA under 2020 conditions.

4.6. Protected areas as thermal refuges against climate warming

Climate warming could decrease the thermal safety margin of lizards, risking the viability of their populations. Direct effects of climate warming can modify life history traits of lizard populations and threaten their population persistence. For example, *Zootoca vivipara* lizards in field enclosures 2 °C warmer than the mean ambient temperature had an accelerated life cycle and lower adult survival, leading to the prediction of their local extinction in the near future (Bestion et al., 2015). A similar trend was suspected to have occurred as a consequence of climate changes over the past several decades, leading to the local extirpation of several lizard species of *Sceloporus* in Mexico (Sinervo et al. 2010). Sinervo et al. (2010) proposed that the disappearance of previously documented populations between 1975 and 2010 was related to the hours of restriction of activities like foraging, when lizards had to retreat to thermal refuges to avoid overheating. Direct effects of climate warming or temporal costs of thermoregulatory behaviors are unlikely

to decrease sufficiently to compensate for climate warming even if heat tolerance increases through mechanisms such as plasticity or adaptive evolution. For example, acclimation led to a heat tolerance increase of 1.8 °C at most for multiple species of lizards (Clusella-Trullas and Chown 2014) and CT_{max} increased by only 0.51 °C after 16 generations in *Drosophila subobscura* (Mesas et al., 2021). This degree of tolerance is clearly insufficient to cope with the mean temperature increase of 4.2 °C during March–May that is projected by the year 2080 in Morelos, Mexico under business-as-usual climate projections (Bolongaro et al., 2006). Furthermore, directional selection on the adaptive evolution of heat tolerance traits such as physiological increases in CT_{max} could be slowed down by the buffering effect of behavioral thermoregulation (Huey et al., 2003). Given the evident importance and flexibility of behavioral thermoregulation, it is therefore critical to decrease lizards' thermal exposure in their habitats through management activities such as protected areas. Protected areas can provide cooler microclimates which ectotherms may exploit to decrease their risk of overheating in tropical ecosystems (like in this study), and as always, protecting tree biomass and preventing land use change and habitat loss are important strategies to promote biodiversity, ecosystem services, and carbon sequestration and storage (Imorou et al., 2021).

The buffering capacity of habitats in protected areas could decrease if vegetation cover is lost within or adjacent to protected areas. Therefore, we must protect the percentage of vegetation cover of protected areas to ensure that lizards have access to shade where they can avoid stressful temperatures in order to assure the sustainment of their hours of diurnal activity (Kearney 2013). Secondly, we must address the disturbance in the surroundings of protected areas (Laurance et al., 2012). For example, we must control and manage the anthropization in the NAA since disturbance in adjacent areas tends to creep into the edges of protected areas, especially regarding climatic attributes, vegetation cover, and deforestation (Laurance et al., 2012). Finally, although it is important to increase the total area dedicated to protected areas, it is important that this expansion be strategic, protecting the sites that can maintain the most favorable conditions for populations persistence in the face of climate warming scenarios (Prieto-Torres et al., 2021). Our simulations show that in addition to a number of considerations such as biological interactions and existing anthropogenic disturbance (Mora 2017), thermal biology must be taken into account, especially when considering the conservation of ectotherms in hot, dry environments that will only be further stressed as the climate continues to warm. In the case of the REBIOSH, our simulations suggest that it would be highly valuable to extend the protection of the REBIOSH into the SAA. The SAA presented cool microclimate temperatures, similar to those of the REBIOSH, which allowed simulated lizards to spend less energy to fulfill their daily basal metabolic rate than in the NAA. Furthermore, the western portion of the SAA has already been tagged as a priority terrestrial region for conservation, the Sierra Taxco-Huautla (Arriaga et al., 2000), and its eastern portion is part of a proposed protected area, the Mixteca Baja Poblana Biosphere Reserve (Valenzuela-Galván et al., 2013). Our study emphasizes the importance of considering thermal biology of the habitats and native species at the microclimate scale when evaluating the effectiveness of protected areas. A valuable next step would be to test our predictions in the field, as well as to carry out similar simulations using projected conditions under different climate change scenarios to better pinpoint which areas are most likely to continue to have favorable microclimate and prioritize the protection of those areas.

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Data and code

The raw data and R-code required to reproduce the below findings are available to download from <https://doi.org/10.17632/882j9btjk9.1> (<https://data.mendeley.com/datasets/882j9btjk9>).

Declaration of interest

The authors declare that they have no conflicts of interest.

CRediT authorship contribution statement

Israel Valencia-Esquivel: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Lynna Marie Kiere:** Conceptualization, Formal analysis, Investigation, Writing – review & editing, Supervision. **Marcela Osorio-Beristain:** Conceptualization, Investigation, Writing – review & editing, Supervision, Funding acquisition, All authors contributed to the interpretation of results.

Data availability

I have shared the documents of our dataset and R-code at the Attach File step and the url link where you can find the dataset: <https://data.mendeley.com/datasets/882j9btjk9>

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Appendix A. Supplementary data

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DISCUSIÓN GENERAL

Actualmente los reptiles terrestres están enfrentando el calentamiento de sus hábitats, lo que puede incidir sobre su temperatura corporal (Ortega et al. 2016; Díaz et al. 2022) y, por ende, sobre el desempeño de sus procesos termosensibles (*revisado en Huey 1982*). Los reptiles terrestres termorregulan explotando la oferta térmica de su hábitat mediante conductas termorreguladoras (*revisado en Huey 1982*). La inversión de energía y tiempo del reptil terrestre en conductas termorreguladoras disminuye ambos recursos para otros procesos fisiológicos y actividades esenciales, así como puede aumentar la frecuencia de riesgo de depredación (*revisado en Angilletta 2009*). El aumento de la inversión y exposición asociados a conductas termorreguladoras plantea *trade-offs*, los cuales son clave para entender cómo el calentamiento del hábitat afecta la viabilidad poblacional de animales terrestres (*revisado en Cahill et al. 2013*). Por lo tanto, debemos ahondar en el funcionamiento y alcances de las conductas termorreguladoras de reptiles terrestres con el fin de entender su vulnerabilidad frente al calentamiento.

La vulnerabilidad de los reptiles terrestres asociada al calentamiento climático se debe con menos frecuencia a los efectos letales del sobrecalentamiento (*revisado en Cahill et al. 2013*). Por otro lado, la vulnerabilidad de los reptiles terrestres asociada al calentamiento climático se debe con más frecuencia a ambos, el cambio en las interacciones tróficas (*revisado en Cahill et al. 2013*) y el aumento de tiempo en conductas termorreguladoras a costa del resto del horario de actividad (Sinervo et al. 2010). Para entender los *trade-off* de las conductas termorreguladoras debemos conocer y entender sus costos asociados. Ha habido

múltiples avances en el conocimiento de los costos asociados a las conductas termorreguladoras (Blouin-Demers and Nadeau 2005; Angilletta 2009; Vickers et al. 2011; Fey et al. 2019; Cunningham et al. 2021). No obstante, carecíamos de una revisión sistematizada que englobara los costos de energía, tiempo y seguridad de las conductas termorreguladoras, que incluyera múltiples especies de reptiles terrestres y que considerara su contexto ecológico.

Los resultados de la revisión sistematizada fueron que ninguno de los costos de conductas termorreguladoras fue más estudiado que otro. Previo a esta revisión sistematizada, se proponía que el estudio de los costos de las conductas termorreguladoras estaba dominado por un acercamiento fisiológico, específicamente energético (*revisado en Angilletta 2009*). En consecuencia, se sugirió aumentar el esfuerzo de investigación en costos no-energéticos, como la pérdida de oportunidades o el riesgo de depredación (*revisado en Angilletta 2009*). Los costos energéticos no explicaban por sí solos las estrategias termorreguladoras realizadas por los reptiles terrestres (*revisado en Blouin-Demers and Nadeau 2005*). En la presente revisión sistematizada encontramos una gran diversidad de estudios relativos a los costos de las conductas termorreguladoras. Ninguno de los tres tipos de costos dominó en frecuencia, lo que indica que se está nivelando el conocimiento entre los tres tipos de costos.

La frecuencia de estudios varió entre los contextos ecológicos considerados. Encontramos que hubo menos estudios sobre costos de conductas termorreguladoras de reptiles terrestres en ambientes cálidos que en frescos, así como menos estudios en latitudes tropicales que en latitudes subtropicales y templadas. Esto es grave por tres razones. Primero, los reptiles terrestres de

ambientes cálidos, como los de bajas elevaciones, son más vulnerables al calentamiento climático que los de ambientes frescos, como los de mayores elevaciones (*revisado en* Wiens 2016). Segundo, los reptiles terrestres de latitudes tropicales son más vulnerables al calentamiento climático que los de latitudes templadas ya que su temperatura corporal esta más próxima a su VT_{max} (*revisado en* Kearney et al. 2009; Sunday et al. 2014). No obstante, hay menos información sobre los costos de conductas termorreguladoras para los reptiles terrestres más vulnerables al calentamiento, es decir, los de ambientes cálidos y latitudes tropicales. Tercero, latitudes tropicales cuentan con mayor riqueza de reptiles terrestres (*revisado en* Winter et al. 2016), no obstante, también cuentan con menos estudios sobre costos de conductas termorreguladoras en comparación con latitudes templadas donde es menor la riqueza de reptiles terrestres.

La frecuencia de estudios entre los costos de conductas termorreguladoras varió al considerar el contexto ecológico de los reptiles terrestres. Por un lado, se planteó que el calentamiento del hábitat podía aumentar el tiempo que reptiles terrestres se refugiaban en refugios térmicos en ambientes cálidos (*revisado en* Sinervo et al. 2010; Kearney 2013; Díaz et al. 2022). Por otro lado, se planteó que los escondites fríos podían disuadir a múltiples especies de reptiles terrestres de escapar a sus escondites frente a un intento de depredación en ambientes frescos (Polo et al. 2005; Radzio and O'Connor 2017). No obstante, previamente no se había considerado ni puesto a prueba la hipótesis de que los costos de las conductas termorreguladoras podían diferir entre especies de ambientes cálidos y frescos, así como entre zonas latitudinales. Nosotros encontramos que el número de estudios sobre costos de seguridad fue mayor que el de costos de energía en

ambientes frescos y latitudes templadas al considerar el contexto ecológico de los reptiles terrestres. Nuestros resultados tienen implicaciones para diferenciar la forma en que los reptiles de condiciones cálidas o frescas son afectados por el cambio en sus condiciones microclimáticas de sus hábitats. Nuestros resultados colaboran para acercarnos al estudio comparativo de los costos y *trade-offs* conductuales de las conductas termorreguladoras en reptiles.

Abordamos vacíos en el conocimiento sobre *trade-offs* entre el automantenimiento y la reproducción en reptiles terrestres de ambientes cálidos en el capítulo dos. El *trade-off* entre el automantenimiento y la reproducción es central en la teoría de historias de vida (Stearns 1992), pero aun así es poco explorado en reptiles de ambientes cálidos. Hay algunos estudios de este *trade-off* con hembras grávidas de reptiles terrestres, la mayoría en ambientes frescos (Shine 1980; Amo et al. 2007; Herczeg et al. 2008; Foster et al. 2009; Lorioux et al. 2013) y uno en ambientes cálidos (Beltrán et al. 2021). En consecuencia, nosotros planteamos y comprobamos un *trade-off* de tiempo entre conductas territoriales y termorreguladoras de machos territoriales de *S. ochoterenae* durante su época de apareamiento en la estación seca de un BTES. Explicamos el *trade-off* considerando el porcentaje de cubierta vegetal y temperatura microclimática de los diferentes territorios, así como el tiempo que un intruso conespecífico duraba dentro del territorio del macho focal. Planteamos tres objetivos particulares. Primero evaluamos el supuesto de que los machos territoriales desplegaban flexiones con más frecuencia en puntos soleados que en puntos sombreados. Segundo, evaluamos si existía una relación negativa entre las conductas territoriales y termorreguladoras en los machos focales. Tercero, planteamos tres hipótesis

generales para explicar el *trade-off*: en territorios con menor cubierta vegetal, y por ende con una mayor temperatura y visibilidad, los machos focales priorizaban (1ª) evitar el riesgo de sobrecalentarse, (2ª) evitar el riesgo de perder su territorio o (3ª) evitar el riesgo de depredación.

Encontramos tres resultados principales. Confirmamos que los machos territoriales sí desplegaban flexiones con más frecuencia en puntos soleados que en puntos sombreados, lo cual sugiere que los machos focales usan los puntos soleados para aumentar la eficacia de sus flexiones. Encontramos que sí existía una relación negativa entre las conductas territoriales y termorreguladoras en los machos focales, lo que concordó con la existencia de dicho *trade-off* para animales terrestres. Nuestros resultados sugieren que los territorios con menor cubierta vegetal presentaban temperaturas microclimáticas más elevadas, en las que los machos focales pasaban más tiempo realizando flexiones a expensas de resguardarse menos tiempo en puntos sombreados. Los machos focales pasaban más tiempo realizando flexiones cuanto más tiempo estuvieran presente un intruso. Los intrusos pasaban más tiempo en territorios con menor cobertura vegetal y temperaturas microclimáticas más altas.

La priorización de las conductas termorreguladoras sobre las territoriales y viceversa pueden intervenir en el riesgo de extinción de reptiles terrestres en ambientes cálidos. El aumento en la temperatura de zonas áridas se asoció positivamente con la extirpación de múltiples poblaciones de lagartijas *Sceloporus* spp. (Sinervo et al. 2010). La priorización de las conductas termorreguladoras frente a otras actividades esenciales para evitar los efectos letales del sobrecalentamiento fue el mecanismo propuesto, lo cual representamos en una de nuestras hipótesis

generales y ha sido observado en otros animales terrestres (*revisado en* Cunningham et al. 2021). No obstante, nuestro estudio y otros realizados con animales acuáticos muestran que algunas especies territoriales priorizan conductas territoriales sobre termorreguladoras en ambientes cálidos (Bohórquez-Herrera et al. 2014; Darnell et al. 2020). Por ejemplo, machos de cangrejos *Austruca mjoebergi* priorizaron conductas territoriales en puntos soleados a expensas de conductas termorreguladoras en puntos sombreados, a pesar de experimentar altas temperaturas y escases de fuentes de alimento (Darnell et al. 2020). Entonces, priorizar conductas reproductivas sobre termorreguladoras en ambientes cálidos también podría afectar la extirpación termogénica de reptiles terrestres. No obstante, la conservación de la cubierta vegetal podría reducir el calentamiento del hábitat en ambientes cálidos y, con ello, disminuir los costos de conductas termorreguladoras.

La vulnerabilidad al calentamiento de los reptiles terrestres podría reducirse mediante la disminución de su exposición al calentamiento. La vulnerabilidad al calentamiento de un organismo se compone de los factores que lo exponen o resguardan del calentamiento, como la cubierta vegetal, de sus caracteres intrínsecos asociados a su resiliencia, como su termorregulación conductual, y de las obras antropogénicas realizadas para disminuir su exposición o aumentar su resiliencia, como designar áreas protegidas (*sensu* Williams et al. 2008). Las áreas protegidas son espacios para la conservación de la biodiversidad a largo plazo (IUCN 2018). La mayoría de los estudios muestran que la riqueza de especies está aumentando o se está perdiendo más lentamente dentro de las áreas protegidas (*revisado en* Geldmann et al. 2013b). La efectividad de las áreas protegidas para

lograr dicho cometido se ha evaluado con base en la estructura de la vegetación, en atributos de poblaciones (*revisado en* Geldmann et al. 2013b) y comunidades (*revisado en* Gray et al. 2016), y en grupos funcionales de animales y plantas (*revisado en* Laurance et al. 2012). Aunque tenemos una imagen clara de la efectividad de las áreas protegidas, falta información sobre los mecanismos responsables.

El desconocimiento de los mecanismos responsables de la efectividad de las áreas protegidas puede estar basado en la falta de estudios a nivel de individuo, así como en la falta de estudios a escalas y de caracteres biológicos asociados a ese nivel de organización. El estudio de estos mecanismos nos permitiría proponer o identificar algunos de los atributos de las áreas protegidas que explican su efectividad. Esto sería útil para hacer más eficiente el uso de los recursos destinados para la evaluación de las áreas protegidas ya existentes y la planeación de aquellas por designar.

El estudio desarrollado en el capítulo 3 aportó evidencia sobre la efectividad de un área protegida a nivel de individuo. Nosotros estudiamos el porcentaje de cubierta vegetal de rangos hogareños de lagartijas simuladas de *S. horridus* durante la estación seca del BTES mediante imágenes satelitales. Evaluamos su efecto sobre la temperatura microclimática experimentada por las lagartijas simuladas, la capacidad de éstas para termorregular y, en consecuencia, mantener temperaturas apropiadas para forrajear y evitar el aumento de su tasa metabólica basal mediante un modelo mecanístico de distribución de especies. Comparamos estas variables entre el interior del área protegida y sus alrededores y entre 1999, cuando fue declarada el área protegida, y 2020, 20 años después. Nuestros resultados sugieren

que una parte de la efectividad del área protegida de BTES se basó en su capacidad para mantener e incluso aumentar el porcentaje de la cubierta vegetal, proveer los microclimas necesarios para la termorregulación del reptil terrestre y, con ello, mantener el desempeño de sus procesos fisiológicos.

La regulación de la temperatura aun no es considerada al evaluar la efectividad de las áreas protegidas. La cubierta vegetal y la termorregulación conductual intervienen en la exposición y sensibilidad al calentamiento, por lo cual se están considerando con más frecuencia debido al calentamiento climático cada vez más intenso y olas de calor cada vez más frecuentes (*revisado en* Kearney 2013; Scheffers et al. 2014; Rusch et al. 2018). No obstante, los servicios ecosistémicos como la regulación de la temperatura aun no son considerados al evaluar la efectividad de las áreas protegidas (*revisado en* Laurance et al. 2012; Geldmann et al. 2013b). La biología térmica tampoco no ha sido empleada para estudiar la efectividad de las áreas protegidas, aun cuando puede proveer información sobre la historia de vida de reptiles terrestres, la sobrevivencia de los individuos y la viabilidad de sus poblaciones (*revisado en* Angilletta et al. 2004; Kingsolver and Huey 2008; Sinervo et al. 2010). La capacidad de las áreas protegidas para controlar la exposición al calentamiento y mediar la sensibilidad al calentamiento de los reptiles terrestres debería formar parte de la evaluación de su efectividad.

Debemos considerar medidas de mitigación al calentamiento al estudiar la relación entre la termorregulación conductual y la evolución de la resistencia al calentamiento. Hay evidencia de que las conductas termorreguladoras podrían no ser suficientes para compensar el calentamiento del hábitat derivado del

calentamiento climático (Sinervo et al. 2010; Díaz et al. 2022), que podrían ralentizar la evolución adaptativa de caracteres asociados a la tolerancia al calentamiento (Huey et al. 2003), o que sus costos en términos de energía, tiempo y seguridad podrían plantear *trade-offs* (Angilletta 2009; Fey et al. 2019; Cunningham et al. 2021). Dicha evidencia no considera la disminución de la exposición al calentamiento a escala local por medio de la cubierta vegetal (Kearney 2013), así como a escala de paisaje por medio de áreas protegidas (Valencia-Esquivel et al. 2023). En este sentido, las áreas protegidas, en comparación con áreas no protegidas, podrían proveer la cubierta vegetal y los microclimas necesarios para que múltiples poblaciones de reptiles terrestres puedan disminuir los efectos subletales del calentamiento del hábitat, así como disminuir los costos de sus conductas termorreguladoras.

Conclusiones generales. Esta tesis ahonda en el tema de la vulnerabilidad de reptiles terrestres al calentamiento del hábitat. Brinda tres aportes principales. Primero, nos da una visión más clara y organizada de los costos que las conductas termorreguladoras suponen para los reptiles terrestres de ambientes frescos y cálidos. Esto nos permitirá avanzar en la aplicación y planteamiento de los *trade-offs* asociados a conductas termorreguladoras de reptiles terrestres. Segundo, muestra el funcionamiento de un *trade-off* temporal no registrado previamente para reptiles terrestres entre conductas territoriales y termorreguladoras. Esto permitirá aumentar nuestro entendimiento acerca de los impactos del calentamiento del hábitat sobre la biología conductual y poblacional de reptiles terrestres del BTES. Tercero, demuestra por primera vez la importancia de las áreas protegidas para

conservar la calidad térmica del hábitat y coadyuvar en la termorregulación de los reptiles terrestres. Esto permitirá evaluar la capacidad de las áreas protegidas para disminuir la exposición al calentamiento y disminuir la sensibilidad al calentamiento de reptiles terrestres en comparación con las áreas adyacentes no protegidas.

Sistematizamos la evidencia acerca de los costos de las conductas termorreguladoras en reptiles terrestres mediante una revisión sistematizada. Encontramos que los tres costos de las conductas termorreguladoras se estudian con la misma frecuencia, de tal manera que la perspectiva fisiológica del tema está abriendo lugar a la perspectiva ecológica. Que las conductas termorreguladoras generan costos de seguridad con más frecuencia que de energía en ambientes frescos y latitudes templadas. Que prácticamente no hay información sobre los costos de conductas termorreguladoras para especies de latitudes tropicales en comparación con especies de latitudes templadas, a pesar de que la riqueza de especies de reptiles es mayor en los trópicos.

Abordamos un *trade-off* entre caracteres de reproducción y automantenimiento no registrado previamente para reptiles terrestres. Demostramos que los machos territoriales de *S. ochoterenae* priorizan las conductas territoriales sobre las termorreguladoras durante su época de apareamiento en la estación seca del BTES. Observamos que dicho *trade-off* es afectado por el porcentaje de cubierta vegetal, temperatura microclimática y presencia de intrusos conespecíficos. La cubierta vegetal afectó a los otros predictores, así como al *trade-off* en cuestión, de tal manera que es una variable que considerar al momento de estudiar los *trade-off* asociados a las conductas termorreguladoras de reptiles terrestres.

Evaluamos el papel de la protección de la cubierta vegetal en un área protegida sobre la exposición al calentamiento de lagartijas simuladas de *S. horridus*. Demostramos que el porcentaje de cubierta vegetal de la REBIOSH y también de sus alrededores aumentó de 1999 a 2020. Que el porcentaje de cubierta vegetal fue mayor en la REBIOSH que en el área adyacente más perturbada. Que la temperatura microclimática del hábitat, así como la temperatura corporal y el metabolismo basal de las lagartijas simuladas fueron más bajos en la REBIOSH que en el área adyacente más perturbada. Esto sugiere que el área protegida fue eficaz para conservar y aumentar su porcentaje de cubierta vegetal con dos beneficios asociados, aumentar el porcentaje de cubierta vegetal de sus alrededores no protegidos y proveer de las condiciones microclimáticas necesarias para la termorregulación de lagartijas.

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ANEXO 1

Oecologia

Temporal trade-off between territorial and thermoregulatory behaviors of a generalist lizard in a dry forest --Manuscript Draft--

| | | |
|------------------------------|---|------------------------------------|
| Manuscript Number: | OEEO-D-23-00239 | |
| Full Title: | Temporal trade-off between territorial and thermoregulatory behaviors of a generalist lizard in a dry forest | |
| Article Type: | Behavioral ecology –original research | |
| Corresponding Author: | Jose Israel Valencia-Esquivel, M.D. Universidad Autonoma del Estado de Morelos Cuernavaca, MEXICO | |
| Order of Authors: | Jose Israel Valencia-Esquivel | |
| | Lynna Marie Kiere | |
| | Marcela Osorio-Beristain | |
| Suggested Reviewers: | <p>M. Zachary Darnell, Dr. Associate Professor, University of Southern Mississippi zachary.darnell@usm.edu He has researched the trade-off between territorial and thermoregulatory behaviors with semi-aquatic animals in hot environments. Therefore, he has deep experience in this topic.</p> <p>Snow Bian, Dr. Adjunct Research Officer, La Trobe University S.Bian@latrobe.edu.au She has experience in assessing the effect of the environment, such as vegetation cover, on the effectiveness of mobile visual signals in animals such as push-ups.</p> <p>Jimena Bohórquez-Herrera, Dr. Full-time Professor, Universidad de Cartagena jbohorquezh1@unicartagena.edu.co She has researched the trade-off between territorial and thermoregulatory behaviors with semi-aquatic animals in hot environments, i.e., with elevated temperatures and intense solar radiation. Therefore, she has deep experience in this topic.</p> <p>Susan Cunningham, Dr. Senior lecturer, University of Cape Town susan.cunningham@uct.ac.za She has extensive knowledge about the opportunity and energetical costs of thermoregulatory behaviors in terrestrial animals in front of hot environments, even in terms of survival, growth, and reproduction.</p> <p>Kika Tuff, Dr. Founder of Impact Media Lab, Impact Media Lab kika@impactmedialab.com She has developed a framework for integrating thermal biology into fragmentation research that allow us to explore the physical and biological consequences of habitat loss in hot environments</p> | |
| Opposed Reviewers: | | |
| Funding Information: | Consejo Nacional de Ciencia y Tecnología (National Scholarship Program 2018–2022 (CVU: 664584)) | MSc. Jose Israel Valencia-Esquivel |
| Abstract: | Avoiding dangerously hot body temperatures is important for survival, but animals may perform reproductive behaviors at the expense of behaviors used to cool down (or vice-versa), resulting in a thermoregulation-reproduction trade-off. Although this trade-off has been demonstrated in semi-aquatic animals, it has not been studied in terrestrial ectotherms. This is an important research gap given the importance of | |

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survival-reproduction trade-offs in evolutionary ecology and the pace of habitat warming due to vegetation loss and global climate change. We explored this trade-off in territorial males of the lizard *Sceloporus ochoteranae*, which mates during the hot-dry season in seasonally dry tropical forest. We first confirmed the existence of a temporal trade-off between performing push-ups (a territorial behavioral display) versus sheltering in the shade (thermoregulatory behavior), then used confirmatory path analysis to explore how it is affected by vegetation cover, microclimate temperature, and the presence of a conspecific intruder. We found that territories with less vegetation cover had higher microclimate temperatures, where focal males spent more time performing push-ups at the expense of sheltering in the shade. Focal males also spent more time performing push-ups the longer an intruder was present, who was also affected by the environmental variables. Territorial males spent more time in sunny spots when performing push-ups despite the potential for overheating, perhaps because the display is more effective when performed in the open. The potential effects of continued habitat warming on this trade-off vary widely, including intensifying it, driving lizards to change their daily activity rhythms, and chronic overheating.



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DES de Ciencias Naturales
Doctorado en Ciencias Naturales



Cuernavaca, Morelos, a 15 de junio del 2023.

VOTOS APROBATORIOS DE TESIS

Los integrantes de la Comisión Revisora de la tesis titulada: **“Compromisos de la termorregulación conductual en hábitats perturbados de un ecosistema cálido”**, que presenta el **C. José Israel Valencia Esquivel**, del Programa de Posgrado Doctorado en Ciencias Naturales, bajo la dirección de la DRA. MARÍA MARCELA OSORIO BERISTAIN, han determinado que el documento reúne los requisitos académicos para su defensa oral en el examen de grado, por lo que emiten su **VOTO APROBATORIO**.

Comisión Revisora de tesis (firma electrónica)

DRA. MARIA MARCELA OSORIO BERISTAIN (directora de tesis)

DRA. LYNNA MARIE KIERE

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DRA. ELSAH ARCE URIBE



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