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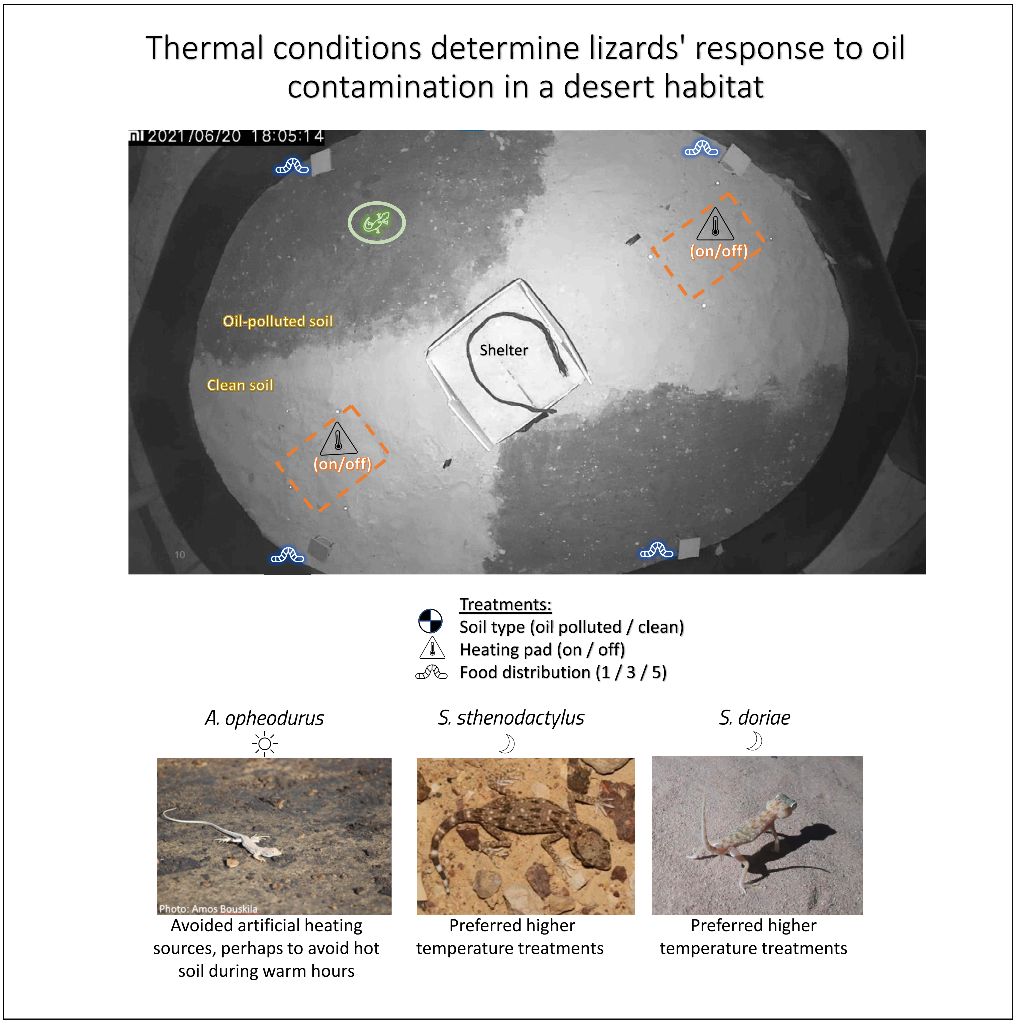

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Highlights

A hyper-arid nature reserve in southern Israel was polluted by crude oil in 2014

Past field studies found that some lizard species avoided the oil and others did not

We found that thermal conditions drive habitat preference in an oil-polluted habitat

Attraction to oil-polluted soil may lead to an ecological trap

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Thermal conditions determine lizards' response to oil contamination in a desert habitat

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SUMMARY

A unique, hyper-arid habitat in southern Israel was polluted by crude oil in 2014. Surveys following the event found that some species of local lizards avoid the oil, while other species were found more frequently in polluted plots. These results raised the question: why do species react differently to oil-polluted soil? We evaluated how soil type, thermal conditions, and food availability interacted to shape habitat preferences of three lizard species. Generally, thermal conditions determined habitat selection and preferences for contaminated or clean soils, while the effects of food availability were weak. The diurnal *Acanthodactylus opheodurus* avoided artificial heating sources, perhaps to avoid hot soil during warm hours. Both nocturnal *Stenodactylus* species showed a preference for higher temperature treatments. While crude oil is considered harmful, ectotherms may not recognize it as a danger and may be attracted to it due to its thermal properties, which may create an ecological trap.

INTRODUCTION

Human-induced rapid environmental changes (HIREC)[1] may lead to novel situations that organisms have neither experienced in their lifetime nor in their evolutionary history. In most cases, the initial reaction of animal species to such changes is behavioral, and when the behavioral reaction is not congruent with the properties or rate of environmental changes, the consequences may be harmful. Moreover, HIREC may lead to instances of behavior that has once led to positive outcomes, but now produce different outcomes in the altered habitat, possibly leading to a maladaptive response, termed an evolutionary trap,[2] or in the case of maladaptive habitat selection, an ecological trap.[3] Thus, understanding how animals behaviorally react to a rapidly changing environment may be central to our ability to predict the impact that HIREC will have on animal populations, making it an important tool that can help prevent biodiversity loss.[4,5] One extreme, though not uncommon, example of habitat alteration caused by HIREC is the case of oil contamination.

To date, the majority of research into the impacts of oil pollution has focused on oil spills in marine environments. These events have both short-term and long-term impacts on various marine habitats. For example, marine reptiles are highly affected by petroleum contamination. When a sea turtle in an oil-polluted marine habitat reaches the sea surface to breathe, it is covered by the oily substances that float on the water, causing health damage and changes to diving patterns and respiration.[6] Another example is the case of oil pollution on Santa Fe island, which was thought to be contained, but in fact caused a massive 62% local mortality to marine iguanas (*Amblyrhynchus cristatus*) in the year following the event.[7] Much less information is available regarding oil spill events in terrestrial habitats and even less on oil-polluted arid habitats.[8] This lack of information creates a gap in our understanding of the impacts of oil pollution on desert ecosystems and can lead to unhelpful and perhaps even harmful recovery efforts.

Body temperature is a fundamental factor in the ecology of ectotherms, and desert reptiles are known to behaviorally thermoregulate. Specifically, desert lizards are often active at temperatures that are close to their critical thermal maximum temperature — temperatures above which can be lethal for them.[9] Oil-polluted soil heats faster and retains its heat longer than uncontaminated soil,[10] and differs from natural soil in its chemical components, accumulation of toxins,[11] and long-term alteration of hydrophobic properties.[12] In addition, oil pollution can lead to changes in resource distributions and the contamination of food resources. These may cause broad behavioral cascades[13,14] since as one species changes its behavior, it may affect the behavior of other species in the community. All these changes to the soil's characteristics

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Figure 1. ***Rhagerhis moilensis*** **on a patch containing oil-polluted soil next to clean soil in 'Avrona Nature Reserve (Photo: Nitzan Segev)**

and to animal behavior following oil contamination could be especially critical for ectothermic species that constantly need to balance their thermal and dietary needs.

Oil pollution in an arid habitat was shown to change the physiological and behavioral characteristics of diurnal lizards (*Acanthodactylus scutellatus*) in Kuwait. Male lizards in a contaminated habitat had larger body size, most likely due to earlier morning emergence, extended basking periods, and more efficient foraging behavior, perhaps as a consequence of polluted soil characteristics, such as rapid heating.[15,16] However, prolonged exposure to oil pollution also led to increased accumulation of contaminants and was shown to cause severe liver damage to lizards and other organisms.[17] This example shows that terrestrial oil pollution leads to both positive and negative consequences for lizards: on the one hand, oil pollution may increase ground temperatures, altering the environmental conditions and providing an additional source of heat for reptiles. In addition, the darker color of the soil may also provide improved camouflage for some species. However, the negative consequences include impaired health due to toxin accumulation, along with the consequences of the cascading multi-species effects in the polluted habitat.

In December 2014, 'Avrona Nature Reserve in southern Israel was contaminated by approximately five million liters of crude oil from a damaged pipeline (operated by Europe Asia Pipeline co.). The contaminating oil flowed in several channels along the reserve, creating contaminated soil in the streams and clean areas in the banks (Figures 1 and 2). As a result, animals in this habitat were presented with the choice of occupying contaminated or clean, natural habitats. Starting from 2016, surveys were conducted regularly, over the course of five years, to estimate the effects of the oil spill on various components of the 'Avrona ecosystem, including the local reptiles. It was found that while *Stenodactylus sthenodactylus*, a nocturnal gecko that lives in stony and sandy habitats, was seen more on oil-polluted soil rather than on natural, clean soil, *Stenodactylus doriae*, a nocturnal gecko that lives in sandy habitats, was seen in both oil-polluted and clean habitats. In addition, *Acanthodactylus opheodurus*, a diurnal lizard, was found more often on clean soil.[18] These findings raised the question: What drives these species to react differently to the same disturbance in 'Avrona Nature Reserve?

Several non-mutually exclusive processes may potentially explain this behavioral dissimilarity among species: (1) Different species may have different physiological sensitivities to the toxic compounds found in the polluted soil.[11] (2) Different species may have different thermal needs. Oil-polluted areas reach high temperatures earlier in the morning, compared to clean soils, and remain warm until later hours in the evening. This can lead to longer activity hours for ectotherms, such as lizards, that are highly affected by ground temperature. (3) The distribution of the lizards' food resources may change due to oil effects on arthropod species. Terrestrial arthropods are highly sensitive to oil exposure and the presence of oil in the ground may have long-term impacts on them.[19] However, because the environmental changes due to terrestrial oil spills are less investigated, it is still hard to predict the consequences of such changes. Since many lizard species, e.g., *S. sthenodactylus*, are insectivores,[20] changes to arthropod distribution may have a dramatic effect on the lizards' habitat selection (i.e., the change in lizards' behavior may be the result of cascading effects in the food web).

Figure 2. 'Avrona Nature Reserve 2014 oil spill event (Photo: Nitzan Segev)

In this article, we report on an experiment that we have conducted in semi-natural settings to examine what affects the habitat selection of lizards in oil-polluted arid habitats. Our experimental design is aimed at reflecting the choices that lizards have in nature, since the crude oil flowed in the channels of 'Avrona Nature reserve, allowing local lizards to choose between adjacent clean and oil-polluted areas.

RESULTS

Temperature measurements

Oil-polluted soil tended to be warmer than clean soil and heated clean soil (heating pad areas), reaching a peak temperature of ~55°C–60°C around 14:00. Heated clean soil was warmer than non-heated clean soil and cooler than oil-polluted soil, reaching a peak temperature of ~50°C–55°C around 14:00. Non-heated clean soil reached a peak temperature of ~45°C–50°C. The shelter in each arena provided a thermal refuge (Figure 3).

A. opheodurus

Observations per square meter varied between micro-habitats ($X^2_{(df = 5)} = 132.48$, $p < 0.001$), showing a preference for the areas above the heating pads in the clean quarters regardless of whether they were on or off. In addition, the interaction between micro-habitat selection and time was significant ($X^2_{(df = 17)} = 175.72$, $p < 0.001$, Figure 4), suggesting a time-dependent change, where toward noon a preference for heating pad areas (shaded and non-shaded) decreased and preference for shaded oil habitat increased. The rest of the examined factors and interactions were not significant: position of arena (east or west, $X^2_{(df =1)} = 0.87$, $p = 0.351$), seasonality ($X^2_{(df =1)} = 0.0023$, $p = 0.962$), the interaction between habitat selection and heating pad condition ($X^2_{(df =6)} = 3.201$, $p = 0.783$), and the interaction between habitat selection and feeding treatments ($X^2_{(df =12)} = 7.696$, $p = 0.808$).

S. doriae

The number of observations per square meter (log-transformed) differed between micro-habitats ($X^2_{(df = 2)} = 14.91$, $p = 0.050$), as there was a preference for the areas above the heating pads in the clean quarters regardless of whether the pads were on or off. Moreover, the interaction between micro-habitat and heating pad condition was significant ($X^2_{(df =3)} = 21.77$, $p < 0.01$), with more observations per square meter on heating

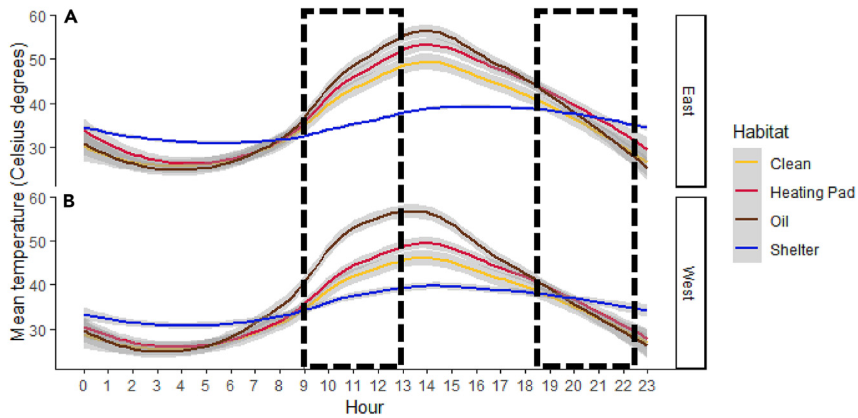

Figure 3. Mean temperatures along the hours of the day while heating pads were on, taken along six days during the fall run of the experiment using iButton sensors

X axis represents the hours of the day, y axis represents the mean temperature measured, yellow line represents temperatures measured in clean areas excluding heating pad areas, red represents temperatures measured in heating pad areas, brown represents temperatures measured in oil-polluted areas, and blue represents temperatures measured in the entrance to the shelter. Gray areas stand for 95% confidence intervals.

(A and B) (A) represents measurements taken in an east-row arena and (B) represents measurements taken in a west-row arena. Dashed rectangles mark the time-windows for which habitat selection data were analyzed in this study.

pad areas when heating pads were on (Figure 5A). In addition, the position of each arena (west or east) had a significant effect ($X^2_{(df = 1)} = 10.55$, $p < 0.01$), with more observations in heating pad areas on west-sided arenas. The rest of the examined factors and interactions were not significant: seasonality ($X^2_{(df = 2)} = 3.56$, $p = 0.059$), the interaction between habitat selection and time ($X^2_{(df = 9)} = 16.24$, $p = 0.062$, Figure 6A), and the interaction between habitat selection and feeding treatments ($X^2_{(df = 6)} = 10.79$, $p = 0.095$, Figure 7A).

S. sthenodactylus

Observations per square meter differed between habitats, as there was a preference for heating pad areas regardless of whether the pads were functioning or not ($X^2_{(df = 2)} = 16.73$, $p < 0.01$). In addition, the interaction between micro-habitat selection and time was significant as well ($X^2_{(df = 9)} = 86.41$, $p < 0.001$), suggesting an increasing preference for heating pad areas as the night progressed (Figure 6B). Preference for oil-polluted habitats was lower than for clean areas in the first examined hour (18:30 in fall or 19:30 in spring). Moreover, the interaction between micro-habitat selection and heating condition (whether heating pads were functioning or not) was significant ($X^2_{(df = 3)} = 29.75$, $p < 0.01$), with a higher tendency to be in the heating pad areas and a lower tendency to be in the oil-polluted habitats, when the heating pads were turned on (Figure 5B). The rest of the examined factors and interactions were not significant: arena position (east or west, $X^2_{(df = 1)} = 0.11$, $p = 0.74$), seasonality ($X^2_{(df = 1)} = 1/42$, $p = 0.23$), and the interaction between habitat selection and feeding treatments ($X^2_{(df = 6)} = 9.08$, $p = 0.169$, Figure 7B).

DISCUSSION

HIREC place many species worldwide in unfamiliar situations.[1] In 2014, an oil spill in the 'Avrona Nature Reserve in Israel dramatically altered the environmental conditions in the reserve. However, the impacts of the spill are yet to be understood completely.[8,21,22]

Habitat selection

All species in this study displayed a habitat selection behavior that was dependent on their thermal needs, but the behavioral patterns varied between species. In general, the thermal preference of *A. opheodurus* depended on the time of the day, while both *Sthenodactylus* spp. preferred a heated clean alternative to oil when the heated soil was available.

During earlier morning hours, *A. opheodurus* showed a preference for heating pad areas, located in the center of clean quarters, regardless of whether heating pads were functioning or not (which is probably an experimental artifact, see below). In later, warmer hours, *A. opheodurus* preferred oil-areas in the shade.

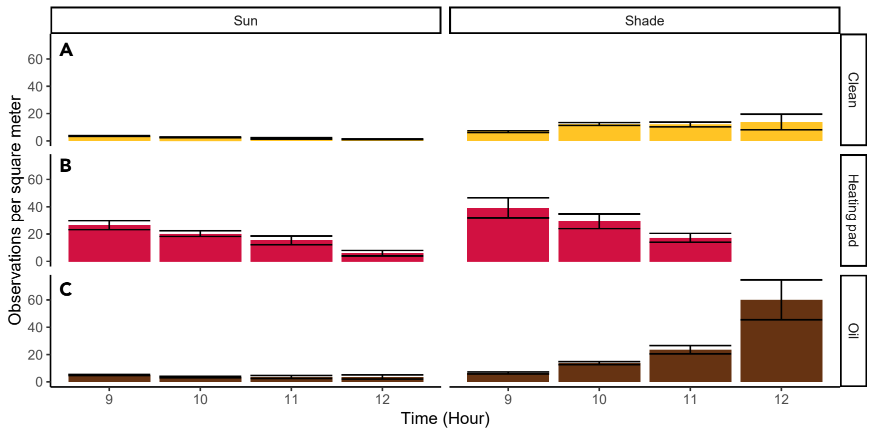

Figure 4. *A. opheodurus* - habitat selection along the examined hours

X axis represents each examined hour (9 refers to 09:00-10:00 and so forth). Y axis represents the number of observations per square meter. Each row refers to a different area of the arena: (A) yellow bars stand for observations in clean areas excluding heating pad areas, (B) red bars represent observations in heating pad areas, and (C) brown bars represent observations on oil-polluted soil. Each column indicates whether the observation was in the shade (on the right panel) or in the sun (on the left panel). Error bars represent one standard error.

This may indicate a preference for warmer temperatures, but at the same time an avoidance of direct sun radiation toward noon. The combination of direct radiation with high air and soil temperatures can reach extremely high temperatures (as seen in Figure 3). Since heating pad areas are located in the center of the arena and provide no shade during the late morning, lizards may prefer hotter oil-polluted areas that are shaded (i.e., closer to the sides of the arena). Thus, while we did not find direct evidence for the effects of heating pad treatments on *A. opheodurus* behavior, it is still highly probable that habitat selection in this species was affected by thermal conditions, albeit in a more complex way.

In the surveys conducted following 2014's oil spill event in 'Avrona, it was found that *A. opheodurus* was seen more in clean areas rather than contaminated areas.[18] However, it is important to note that the current study followed the lizards for longer hours than those examined in the surveys. Perhaps in nature (at the hours examined in the surveys), oil-polluted areas did not provide sufficient ground temperatures for these lizards. Our results suggest that *A. opheodurus* shows a heat-dependent habitat selection, affected by thermoregulation requirements that change along the hours of the day.

In the case of the nocturnal *S. sthenodactylus*, most observations per square meter occurred on heating pad areas. However, when heating pads were functioning, the number of observations per square meter greatly increased in these areas and the number of observations per square meter in oil-polluted quarters was reduced. Thus, *S. sthenodactylus* clearly showed a thermally driven behavior, with a preference for conditions with higher temperatures, which corresponds very well to the results of the field surveys[18] in which *S. sthenodactylus* was found more in oil-polluted areas rather than in clean areas. Our current study provides a potential explanation for this observation, suggesting a preference for warmer areas as provided by oil-polluted soils. However, our results also suggest that when given the choice between polluted and clean habitats with high temperatures, *S. sthenodactylus* prefers clean soil. Nevertheless, choosing a habitat with a higher temperature is this gecko's first priority. This finding might suggest an ecological trap, where *S. sthenodactylus'* natural habitat selection behaviors (such as attraction to warm areas due to thermoregulation needs) may lead to negative outcomes due to human interference (such as health problems from interacting with crude oil, an unfamiliar threat caused by humans).

S. doriae's tendency to stay in heating pad areas was the highest, regardless of whether it was on or off. However, more observations occurred on heating pad areas when they were on. In addition, habitat selection was affected by the location of the arena (east or west). More observations occurred on heating pad areas on west-sided arenas when heating pads were on. This behavior is unclear as the west and east sides did not differ in temperatures during the evening (Figure 3). Moreover, this behavior was not shown for *S. sthenodactylus*, and thus further research is required to explain this preference.

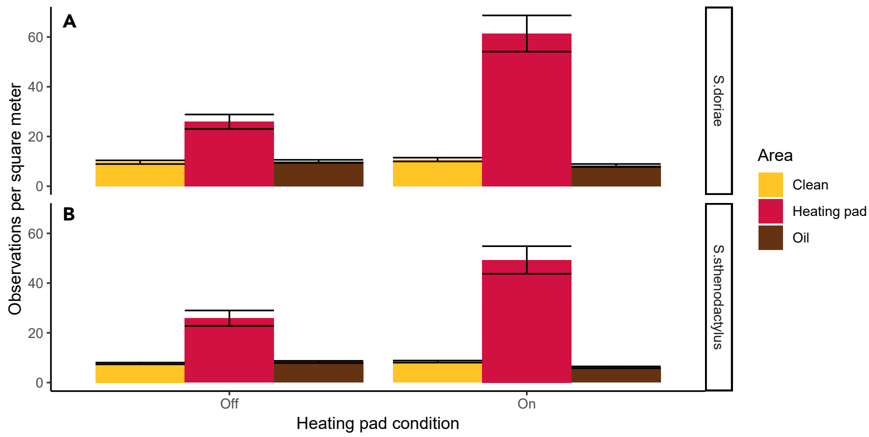

Figure 5. *Stenodactylus* spp. habitat selection of *S. doriae* (top panel, A) and *S. sthenodactylus* (bottom panel, B) with regards to heating treatments

X axis represents the heating pad condition (on/off), and y axis represents the number of observations per square meter. Yellow bars represent observations in clean areas excluding heating pad areas, red represents observations in heating pad areas, and brown represents observations in oil-polluted areas. Error bars represent one standard error.

In the field surveys, *S. doriae* was found on both oil-polluted and natural, control areas without showing a preference for one over the other,[18] which may suggest that this species did not have a preference between these two habitats. However, in the current study, *S. doriae* exhibited a habitat selection behavior based on thermal needs, with a preference for heated, clean areas when they were available. This suggests that this species' behavior is influenced by its thermal requirements and perhaps by other unrelated factors such as the availability of burrowing sites or other relevant resources.

When comparing the results of this study to other experiments investigating the effects of oil pollution on lizards' behavior, we can see both similarities and dissimilarities. For example, a study conducted in an oil-polluted desert habitat in Kuwait, Al-Hashem & Brain (2009)[16] found larger body-sized males in oil-polluted (tar and soot) habitats rather than control, clean sites. The authors suggested that the reason for this observation is related to greater availability of food, or that the food itself includes larger amounts of fat, increasing lizards' body size. This could also be related to early morning emergence.

A similar phenomenon was found in snakes spending time during early evening on asphalt roads that warm up during the day in the sun.[23] On the one hand, the warm surface provides an advantageous habitat in terms of temperature. On the other hand, this decision is followed by novel disturbances, such as vehicle traffic, that snakes are not familiar with. This is therefore an ecological trap, as a decision that once led to a certain outcome (i.e., a snake chooses to stay in a warm surface for thermoregulation needs) is not as beneficial as it used to be, and can lead to reduction of fitness (i.e., a snake killed by a vehicle). This situation is quite similar to the lizards in the current study that were attracted to a warm surface that is likely to reduce their fitness.

Amadi et al. (2020)[24] investigated the behavior of *Agama agama,* a diurnal lizard known to demonstrate great ecological plasticity in relation to artificial heat sources in an urban environment in Nigeria. Specifically, they investigated the lizards' retreat site selection and movement ecology in relation to electric panels. They found that some *A. agama* individuals tended to retreat next to electric panels at night, as these artificial heating sources provided a temperature in the nocturnal refuge similar or higher than the minimum preferred body temperature. These individuals moved further the next day than lizards which spent the night on bushes or trees, showing better movement performances. However, that behavior may lead to higher predation risk.[24]

Preference for heating pad locations

Surprisingly, all lizards showed a clear preference to the heating pad areas in the clean quarters, regardless of whether it was on or off. While this preference did not hinder our ability to detect heat preference by the

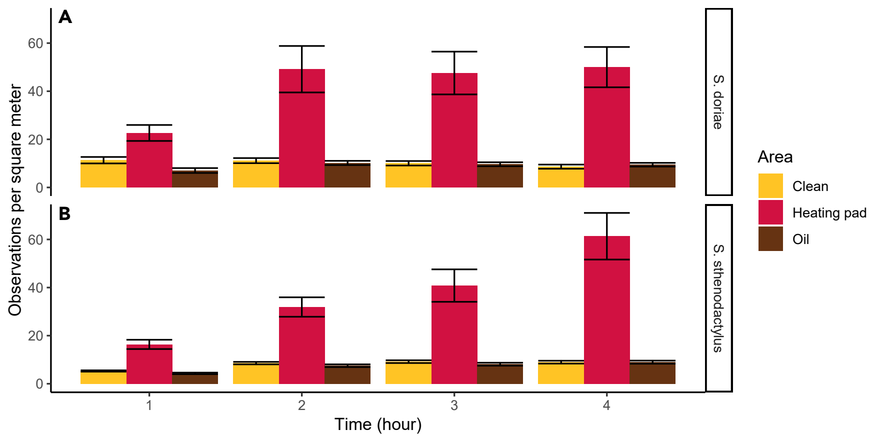

Figure 6. *Stenodactylus* spp. Habitat selection of *S. doriae* (top panel, A) and *S. sthenodactylus* (bottom panel, B) along the examined hours

X axis represents the examined hours (4 h: 18:30-22:30 in spring experimental run, 19:30-23:30 in fall experimental run), y axis represents the number of observations per square meter. Yellow bars represent observations in clean areas excluding heating pad areas, red represents observations in heating pad areas, and brown represents observations in oil-polluted areas. Error bars represent one standard error.

lizards (by comparing the lizards' behavior when the heating pads were turned off or on), it is likely to be an artifact created by our experimental setup and which we did not anticipate. One might suggest that this preference for the heating pad locations is because lizards have learned that these areas can be hot, and thus anticipate the heating even when the heating pads were turned off. However, we compared the behavior of lizards that have experienced the heating treatment in the first days of the experiment with the behavior of lizards that have experienced the heating treatment in the last days of the experiment (and thus cannot associate the heating pad areas with heat), and found no difference in their preference for the heating pad areas when the heating pads were off (results not shown). Thus, the ''anticipation of heat'' hypothesis has been ruled out. An alternative explanation for this preference may be that lizards prefer to stay in open areas, near the center of the arena, as these locations may provide a better line of sight, which can be advantageous either as an antipredator strategy or to improve foraging efficiency.[25,26] This hypothesis has yet to be tested. Nevertheless, the fact that the lizards preferred these central locations on clean soil, even though they equally occur also on contaminated quarters, suggests that there is a preference for uncontaminated soil, when there are no thermal considerations.

Conclusions

In this study, we found evidence for heat-dependent habitat selection behavior in lizard species in an oil-polluted arid habitat and showed that different lizard species react to oil pollution in a different manner. Hopefully, the knowledge about this reaction may enable us to predict which habitat will these lizards select in nature and perhaps can even serve as an indicator for the state of the polluted habitat.[5]

Behavioral alteration due to human-induced rapid environmental changes may hold benefits and costs. In this study, we investigated the behavior of three species in relation to oil pollution, while providing an artificial heating source. However, we did not investigate the long-term physiological consequences and costs. A preference for artificial, human-made heating source, such as contaminated soil, might provide a beneficial thermal source during certain hours of the day or the night. Nevertheless, the benefit might be accompanied by increased mortality due to the toxicity of chemicals in the soil or in the insects that come in contact with the contaminated soil, and thus might form an ecological trap.[3] Thus, when approaching the conservation or restoration of an oil-polluted desert habitat, the thermal attraction of reptiles to the thermal conditions provided by the new polluted environment should be taken into consideration.

Oil pollution can have complex and far-reaching impacts on the environment and its inhabitants. While crude oil is generally considered harmful and toxic, some animals may not recognize it as a danger and may even be attracted to it, as seen in the case of lizards being drawn to warm, oil-contaminated soil in 'Avrona Nature Reserve. This behavior can lead to negative consequences over time due to the toxic nature

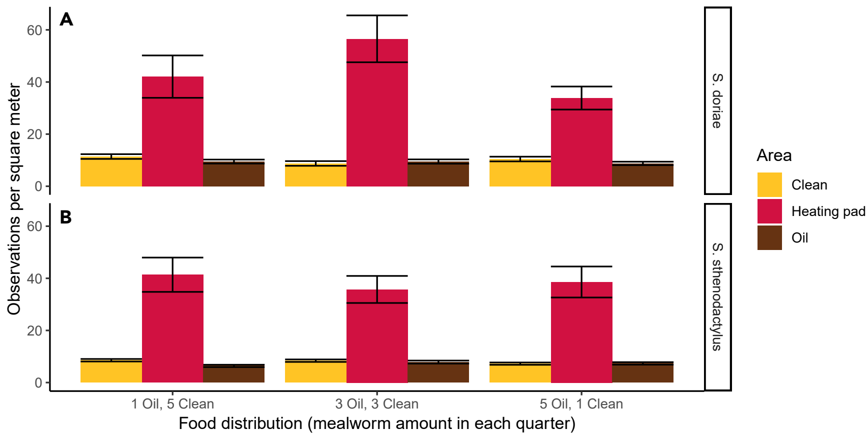

Figure 7. *Stenodactylus* spp. habitat selection of *S. doriae* (top panel, A) and *S. sthenodactylus* (bottom panel, B) with regards to food distribution treatments

X axis represents the number of mealworms put in each quarter, and y axis represents the number of observations per square meter. Yellow bars represent observations in clean areas excluding heating pad areas, red represents observations in heating pad areas, and brown represents observations in oil-polluted areas. Error bars represent one standard error.

of crude oil.[17] To fully understand the long-term effects of habitat selection in oil-polluted, terrestrial, arid environments, a long-term field study is necessary.

Limitations of the study

- Surprisingly, all lizards showed a clear preference to the heating pad areas, regardless of whether it was functioning or not. While this preference did not hinder our ability to detect heat preference by the lizards (by comparing the lizards' behavior when the heating pads were turned off or on), it is likely to be an artifact created by our experimental setup and which we did not anticipate.
- We acknowledge the fact that a more complete design would have included heating pads under the contaminated soil as well. However, due to logistic constrains (i.e., a limited number of arenas and a desire to reach a sufficient sample size for a robust statistical analysis), we opted to only place heating pads in the clean soil. Note that the goal of the heating pads in the clean soil was to create a habitat that would compete with the contaminated soil as a source of heat for the lizards. As detailed previously, the lack of heating pads in the contaminated soil did not fundamentally hinder our ability to infer the role of thermal preference in the lizards' habitat choice.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- RESOURCE AVAILABILITY
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  - Materials availability statement
  - Data and code availability
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Study species
- METHOD DETAILS
  - Experimental design
  - The experiment
  - Image analysis
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2023.107411.

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AUTHOR CONTRIBUTIONS

S.G., A.B., and O.B.T. designed the study; S.G. performed the experiments, analyzed the videos, performed statistical analysis and visualizations, and wrote the first draft of the manuscript; T.N. provided video analyses, data analysis, and validation; A.B. and O.B.T. secured the funding for the study and contributed to the writing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as a gender minority in their field of research. One or more of the authors of this paper self-identifies as living with a disability. We worked to ensure sex balance in the selection of non-human subjects.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the preparation of this work, the author used chatGPT for grammar-proofing. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Stenodactylus doriae	Wild	N/A
Stenodactylus sthenodactylus	Wild	N/A
Acanthodactylus opheodurus	Wild	N/A
Deposited data		
Raw data	This paper	https://doi.org/10.6084/m9.figshare.23303744
Software and algorithms		
R v4.1.2	R Core Team 2021[27]	r-project.org
ImageJ	Schneider et al.[28]	ImageJ.org
TimeLapse2 v2.2.3.7	Greenberg et al.[29]	saul.cpsc.ucalgary.ca/timelapse/pmwiki.php
Original code	This paper	https://doi.org/10.6084/m9.figshare.23303744

RESOURCE AVAILABILITY

Lead contact

Further information and request for resource should be directed to and will be fulfilled by the lead contact, Shahar Gofer (gofersh@post.bgu.ac.il).

Materials availability statement

This study did not generate new unique reagents.

Data and code availability

- Original datasets has been deposited at Figshare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Original code has been deposited at Figshare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional data in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Study species

We examined three lizard species, native to ʼAvrona Nature Reserve:

1. *Stenodactylus doriae,* a nocturnal desert gecko, is known to be found on sandy surfaces. Its distribution extends throughout the Arabian Peninsula, eastward to southern Iran, and westwards toward Syria and Israel. In Israel, its distribution is limited to sand patches along the ʼArava valley. *Stenodactylus doriae* is known to meticulously choose the location of its burrow, and typically seals and camouflages it upon entering by sweeping motions of the tail.[30] The excavation of the burrow necessitates soil crusts that prevent the collapse of the sand at the entrance.[31] Its reproductive season occurs in the summer. This gecko tends to prey on insects, and reproduces around five times every season, laying one to two eggs each time.[32]
2. *Stenodactylus sthenodactylus*, a nocturnal desert gecko, is known to be spread in north Africa and southeastern Asia. In Israel, it is distributed in various soils including sand in the coastal plain, Negev desert, and ʼArava valley. During the day it shelters in burrows that other animals have excavated. S. *sthenodactylus* tends to prey on insects and other arthropods. Females typically lay one to two eggs per clutch several times during the summer.[32]

3. *Acanthodactylus opheodurus,* a diurnal lacertid, is known to be widespread in the Arabian peninsula, Kuwait, Iraq, Jordan, and Israel (central Negev desert and Arava valley). It is found in dry riverbeds and desert surfaces, in coarse-sands soils, and amidst vegetation. It is active also during warm hours and is known to be less fearful than many other species of the genus. It burrows next to the base of shrubs. *A. opheodurus* tends to prey actively on invertebrates. Females lay four eggs per clutch several times during the summer. [32]

Lizards for the experiments were captured outside 'Avrona Nature reserve, at the edges of nearby agricultural fields. We assumed that the captured individuals had no contact with oil-polluted habitats prior to this study. We captured the lizards by noose or by hand one or two days prior to the experiment, and kept them in designated cloth bags and terraria under controlled temperature. At the end of each experiment run, we released each lizard in the same location in which it was caught.

METHOD DETAILS

Experimental design

The experiment took place in Hai-Bar Yotvata, 20 km north of 'Avrona Nature Reserve. We built 12 elliptic arenas (3.40m*2.20m) comprised of two opposing quarters filled with clean soil (10 cm depth) and two opposing quarters filled with the same amount of oil-polluted soil (Figure 1). Oil-polluted soil was brought from a location inside 'Avrona Nature Reserve (29.666928N, 35.012549E). Clean soil was taken from a site close to the Nature Reserve (29.893204N, 35.068852E), near kibbutz Yotvata. Though not taken from the same exact location, both soil types are similar desert soils that characterize the Arava Valley. The fence of each arena was made from 4 mm black polypropylene (Polygal™), buried 10 cm into the ground, and protruded 50 cm above it. At the center of each arena, we placed shelters comprised of two artificial burrows, made of plastic pipes buried 45 cm under the surface with four concrete blocks on top, to provide better isolation and prevent excessive overheating. A shrub was placed on the shelter in the first run of the experiment (September – October 2020) and was removed in later runs to facilitate image analysis.

We placed heating pads (43*28 cm) under the centers of the unpolluted clean soil quarters, one heating pad per quarter, at a depth of 3 cm. The area above the heating pad comprised approximately 10% of the entire quarter area. In the first three days of the experiment, heating pads were functioning in six arenas and shut down in the other six arenas. These were switched in the second half of the experiment.

We placed four feeding plates, one in each quarter, containing varying quantities of larvae of the beetle *Tenebrio molitor*, which is considered a preferred food for insectivorous lizards kept in captivity. The food remaining in the plates was replaced each morning and evening. During the experiment, the arenas were divided into three feeding treatments: (1) equal amounts of mealworms were placed on all feeding plates in the four arenas; (2) more food was placed on clean soil and less food on oil-polluted soil; and (3) less mealworm were placed on clean soil feeding plates and more food on polluted soil feeding plates (Table S2). The total number of larvae was always identical – only the distribution among the quarters changed. No natural food resources were available during the experiment, as the walls of each arena prevented animals from entering or exiting the arenas. This experimental design enabled us to examine how patch use and habitat selection are affected by food availability.

The arenas were built in two rows (east and west). East-sided arenas were adjacent to another fenced corral, creating a different shade regimen from the west-sided arenas during the morning. This factor was included in the statistical model.

To sample the temperatures in the arenas, we placed temperature sensors (thermocouples and iButton® Thermocron® data logger) in two arenas – one facing east and one facing west. We assumed that these measurements represent the temperatures in the rest of the arenas. Sensors were placed in each habitat (oil quarter, clean without heating, and above heating pads in clean quarters), and inside the shelter. Temperatures were measured every 10 minutes for the entire experimental run.

To eliminate the effects of predation risk, a transparent net was placed over the entire experimental site, preventing birds from entering.

The experiment was filmed continuously (using Mi Home Security Camera Basic 1080p). In addition, a snapshot was automatically taken every minute.

The experiment

The first experimental run took place between 24/09/2020 and 10/10/2020. The second run was between 25/05/21 and 31/05/21, and the third run was between 17/06/21 and 24/06/21.

Moon phases are known to affect animal behavior and activity,[33] and therefore have a considerable effect on the arid ecosystem. This is primarily due to changes in the anti-predator behavior of prey species, as prey is more vulnerable to visual predators during high moon illumination.[34] For example, *S. doriae* is known to be affected by moonlight and was found to be more active when illumination is higher.[35] To reduce behavior variation due to the phase of the moon, all experimental rounds of this experiment centered around the full moon.

We placed one diurnal lizard (*A. opheodurus*) and one nocturnal gecko (*S. sthenodactylus* or *S. doriae*) in each arena. As happens in natural habitats,[18] there is no overlap between the activity time of the diurnal and the nocturnal lizards, and we assume that there was no effect of one species on the behavior of the other. Moreover, lizards were not active at the same time during the examined hours. The experiment started following a 24 hours acclimation period. During acclimation, heating pads were shut off and three mealworms were put in each feeding plates. Each lizard experienced all possible combinations of heating and feeding regimes in the course of six days (Table S2). Overall, we tested 24 *A. opheodurus,* and 18 of each gecko species. The treatments order was determined according to a Latin square design.

Image analysis

Considering the main activity hours of each species, we focused on four hours each day (09:00 – 13:00) and four hours each night (18:30-22:30 in fall runs, 19:30-23:30 in spring runs). The location of each lizard was determined by the first frame of each 1-minute video (i.e., we checked for the location of each lizard 60 times every hour).

Using TimeLapse2 software (version 2.2.3.7),[29] we marked lizards' locations (if observed): Is the lizard located in oil-polluted soil, clean soil, or heating pad areas on clean soil; is it located in the shade or in the sun; whether it excavates a burrow and other remarks. If a lizard was not observed, we assumed it was inside the shelter.

More than 103,000 one-minute videos were analyzed manually.

QUANTIFICATION AND STATISTICAL ANALYSIS

We examined a question related to the decision-making of the lizards: how do different treatments affect the lizards' habitat selection?

To check how different treatments affected the habitat selection behavior of the lizards after leaving the shelter, we defined three different habitats during the night (clean soil, heating pad area on clean soil, oil-polluted soil), and six different habitats during the day (each of the three habitats could be in the sun or in the shade, and the area of the shaded parts was updated on an hourly basis using ImageJ[28]). Since the habitats were not of equal sizes, we divided the number of hourly observations by the area of the habitat, resulting in observations per square meter. We used a linear mixed model (''lmer'' function from ''lme4'' R package[36]) with a gaussian distribution. The dependent variable was the hourly number of observations per square meter, log transformed so the data will be normally distributed. We examined the effects of the following factors: habitat chosen by a lizard (three or six habitats, depending on whether it was a nocturnal of diurnal lizard), the interaction between habitat choice and heating treatments (whether heating pad was on or off), the interaction between habitat choice and the examined hours (T1-T4), and the interaction between habitat choice and food availability treatments (more / less / equal amounts of mealworms in each quarter). We also examined the effect of the orientation of the arena (west / east) and seasonality (spring / fall). We used individual (ID) as a random factor. Due to the complexity of the statistical analysis, only particular factors and interactions were selected. We used type III ANOVA (''Anova'' function from ''*car*'' R package[37]) to analyze LM results.

All analyses were performed in R version 4.1.2[27] using RStudio.