Bearding the scorpion in his den: desert isopods take risks to validate their ‘landscape of fear’ assessment

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Bearding the scorpion in his den: desert isopods take risks to validate their 'landscape of fear' assessment

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Animals balance the risk of predation against other vital needs by adjusting their spatial behavior to match spatiotemporal variation in predation risk. To map this 'landscape of fear', prey use evolutionary rules of thumbs that are associated with the activity and hunting efficiency of predators. In addition, prey acquire perceptual information about the presence, identity and state of potential predators and use these cues to focus their acute anti-predatory responses. Our goal was to explore if and how prey also use such perceptual information that decays with time to update their spatiotemporal risk assessment. We placed scorpions in freshly dug burrows and recorded the spatial activity and defense behavior of their isopod prey upon encountering the burrows straight after settling the scorpions and seven days later. To corroborate our understanding, we also examined the isopods' detailed reactions towards deserted scorpion burrows. The isopods reacted defensively to scorpion burrows during their first encounter. After seven days, proportionally more isopods approached the scorpion burrows on their way out for foraging and fewer isopods encountered it on their way back. No changes in the spatial activity were observed towards deserted burrows. In addition, on the eighth day, more isopods entered the risky area near the scorpion burrows when leaving their own burrow than on the first encounter. The results suggest that isopods used predator cues to readjust the 'landscape of fear'. Yet, rather than avoiding the dangerous areas altogether, the isopods implemented risky inspection behavior, validating whether the danger is actual. Our findings imply that inspection behavior toward predators can be used for future planning of prey spatial activity, offsetting possible 'information decay costs'.

Keywords: desert isopods, information decay costs, landscape of fear, predation risk, predator inspection, risk assessment

Introduction

A key question in animal ecology is how prey determine their spatial activity (Stephens et al. 2007, Gallagher et al. 2017). The dynamic environments which prey inhabit hold opportunities and threats that vary in space and time (Lima 1998a, Kohl et al. 2018). To balance the risk of predation against other vital needs, animals

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must adjust their spatial activity to match spatiotemporal variations in predation risk (Lima and Dill 1990, Lima 1998b, Palmer et al. 2017). To map this 'landscape of fear' (sensu Laundré et al. 2001), prey use evolutionary 'rules of thumbs' that are associated with predictable changes in the activity and hunting efficiency of predators (Laundre et al. 2010, Gallagher et al. 2017, Palmer et al. 2017, Gaynor et al. 2019). For instance, kangaroo rats alter their spatial activity in response to seasonal and lunar cycles that reflect changes in the activity and hunting efficiency of snakes and owls (Bouskila 1995). This probabilistic assessment provides general guidelines for lessening the risk of predation but entails a high degree of uncertainty concerning the predators' contemporary whereabouts.

While engaging in other activities, prey acquire perceptual information about the presence, identity and state of potential predators and use these predator cues to focus their acute anti-predatory responses (Lima and Steury 2005, Schmidt et al. 2010, Zaguri et al. 2018). Prey are hypothesized to also use this contemporary information for updating their spatiotemporal risk assessment, and consequently for adjusting their future spatial activity (Palmer et al. 2017). Predator activity is transient in space and time, hence the informational value of predator cues decays with time (Koops and Abrahams 2003). Therefore, basing future decisions on information that may no longer reflect the current risk levels can erroneously deny prey access to profitable areas (Stephens 1987, Koops 2004). These 'information decay costs' (IDC) can be substantial, especially for prey that have small home ranges. It is still unclear how prey resolve this conundrum of using time sensitive information to fashion future spatial activity.

Hypothetically, prey can use perceived information that implies high risk in two different ways: 1) to instantaneously assess risk without affecting future decisions, or 2) to classify the area as risky. In case of the later, prey can 2.1) register the patch as permanently risky and avoid it altogether or 2.2) classify it as temporarily risky, and actively try to validate their assessment by gathering new information. Determining which of these solutions are used is empirically challenging because it requires inferring complex cognitive considerations from behavioral reactions (Lima and Steury 2005). This challenge is even greater in field conditions where the need to eat and avoid being eaten are often confounded. For example, a prey may revisit a patch where it formerly encountered predation cues because this patch was not classified as permanently risky. Alternatively, it can revisit the patch to acquire indispensable resources despite the high risk, or to inspect whether the predator is still there.

Previous studies exploring the 'landscape of fear' associate prey activity with the spatial activity of their potential predators and with environmental variables (Arias-Del Razo et al. 2012, Latombe et al. 2013, Palmer et al. 2017). These studies provide important insights into how prey can solve the predator–prey-resources game on extended spatiotemporal scales. Other studies use experimental approaches to implicitly map the spatial projection of the 'landscape of fear' assessment and to identify how prey perceive and react to different predator cues (van der Merwe and Brown 2008, Mella et al. 2014). What remains largely unknown is 1) whether and how prey use predator cues to update their spatiotemporal risk assessments, and consequently their prospective spatial activity, and 2) whether prey deliberately take informed risks to validate this time sensitive information.

We explored these two questions in a system that comprised of the highly abundant desert isopod *Hemilepistus reaumuri* prey, and the Israeli golden scorpion *Scorpio palmatus* predator. We set scorpions in freshly dug burrows close to the isopods' natural burrows, creating a localized risky patch that provided no resources for isopods. We then recorded the isopods' spatial activity and behavioral reactions soon after settling the scorpions. During this time, the isopods had no prior knowledge about the scorpions' whereabouts. Therefore, the isopods' activity reflected their baseline spatiotemporal risk assessment. By comparing this to their spatial behavior seven days later, we could determine whether and how isopods used the perceptual information to adjust their future spatial activity. A similar number of isopod visits to the scorpion burrow during the first and eighth day would suggest that the patch was not classified as risky. Lower or higher numbers of isopod visits after seven days would mean that isopods classified the patch as risky but either decided to avoid it altogether or to deliberately inspect it for validating the risk, respectively. To corroborate our understanding, we also examined the isopods' detailed reactions upon encountering the scorpion burrows and compared the visit frequency and behavioral reactions to inhabited and recently deserted scorpion burrows.

Our work demonstrates that prey use predator cues to update their 'landscape of fear' assessment. Rather than avoiding the risky patches altogether, the isopods deliberately inspected them to validate their assessment. This attempt to offset 'information decay costs' highlights the need to consider 'information acquisition' as another fundamental determinant of the prey's spatial activity.

Methods

Study organisms

Isopods live in family groups that include the parents and their ~70 offspring, all residing within a single permanent burrow. They have poor eyesight and use their antennae's contact chemoreceptors to locate food, recognize kin, identify their burrow-specific scent and detect predation cues (Linsenmair 1985, Hoffmann 1990, Warburg 1993). Therefore, perception distances are considered to be of antennae length from the isopod's body (Zaguri et al. 2018). During the summer months, isopods forage for about two hours after dawn, and remain within their burrow for the rest of the day (Shachak et al. 1979). Isopods begin their morning activity by evacuating fecal-pellets from the burrow to a pile that surrounds the entrance, and then leave to forage in close proximity to the burrow for plant-litter and biological soil crust (Warburg 1993) (Fig. 1). Returning to the burrow is rapid and timed by the first sunrays that directly hit the foraging area. Lingering isopods risk dying from dehydration. Isopods use path integration to navigate back to their burrow (Alt 1995, Merkle et al. 2006). Their homing behavior starts with a straight return path to the fecal-pellet mound, followed by systematic search to locate the burrow entrance (Hoffmann 1983a, b).

Golden scorpions are strict ambush predators that hunt for isopods exclusively from within their own burrows. The entrance to the *Scorpio palmatus* burrow is typically crescent shaped with an excavated soil mound in front (Kotzman et al. 1990) (Fig. 1). The upper part of the burrow, called the 'platform', descends in a very moderate slope (Adams et al. 2016). Scorpions use the 'platform' to ambush their prey during the night and early morning (Shachak 1980, Shachak and Brand 1983). Scorpions use mechanoreceptor organs to perceive vibrations created by prey walking on the platform's roof (Barth and Wadepuhl 1975, Foelix 1985).

Experimental design

The experiment was conducted at the Avdat Research Station, Central Negev Desert, Israel (34°76′N, 30°78′E). During July–August 2017, we located 13 wild isopod burrows with similarly sized fecal pellet mounds (i.e. roughly similar number of isopods). To reduce chances of pseudo-replication we only selected burrows that were more than 5 m apart, the isopods' maximum foraging distance (Shachak et al. 1979). Soon after the isopods ceased their daily activity and returned to their burrows, we dug artificial scorpion burrows. Each artificial burrow was positioned in a randomly selected direction. We positioned the scorpions' burrows 30 cm away from a focal isopod burrow (Fig. 1). This distance is within the range of the direct path that isopods take after leaving their burrows as indicated by a straightness index (Benhamou 2004) 0.935 ± 0.08 (mean ± SD, n = 37) for the initial 40 cm following burrow departure. The artificial burrows were 10 cm deep and shaped like the upper part of a typical *S. palmatus* burrow. Near the burrows' entrances, we created an excavated soil-mound that was similar in shape and size to a scorpion soil mound. The entrances to all artificial burrows faced isopod burrows (Fig. 1). Thus, isopods leaving their burrow should initially meet the excavated soil mound in front of the scorpion burrow. To all artificial burrows we released field-trapped scorpions of similar sizes. To prevent escape, we placed an enclosure with a sponge base around each artificial burrow. In this way, we forced the scorpions to settle in their new burrows without disturbing the surrounding soil crust. On the following day (hereafter 'first day'), we removed the enclosure 30 min before dawn, right before the beginning of isopod aboveground activity. Consequently, during the first day of the experiment, all burrows housed live scorpions. The scorpions were left completely free for the following week. Of the 13 settled scorpions, five deserted their burrow on the first night following the enclosure removal (hereafter 'deserted burrows'). The remaining scorpions (n = 8) continued to excavate their burrows (hereafter 'inhabited burrows') and take up residence, as was evident by the expansion of the soil mounds at the eighth day. In a previous study, isopods responded defensively to artificial burrows that inhabit no scorpions. The responses were stronger when scorpion were present in those burrows (Zaguri et al. 2018).

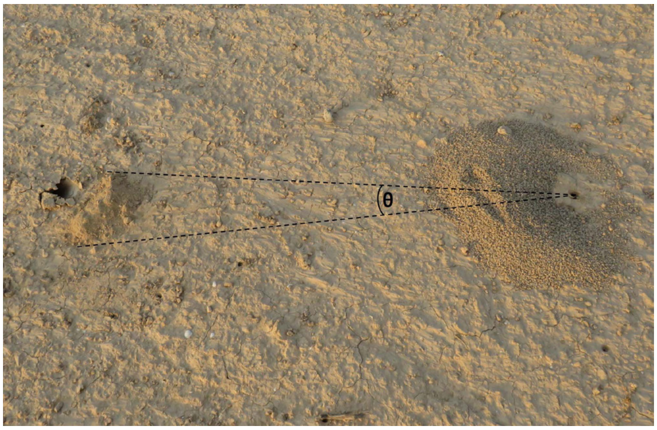

Figure 1. Spatial experimental design: The isopod burrow (at the right side of the figure) has a single circular entrance surrounded by a pile of fecal-pellets. Each scorpion was settled 30 cm away from the isopod burrow, and its burrow entrance was facing the isopod burrow. We used the angle θ between the isopod and scorpion burrows to calculate the isopods' probability to encounter the scorpion burrow by chance.

For all 13 burrows, isopod morning activity was filmed on the first and eighth days, in an area of about 1 m^2 that included both the isopod and scorpion burrows (for an example video see Supplementary material Appendix 1). The recordings started before the first isopod exited the burrow and lasted for about three hours, until aboveground isopod activity ceased. On the first day, the isopods had no previous knowledge regarding the scorpion presence and could identify the scorpion burrow just upon encounter. Thus, the isopods' spatial activity on this day reflected the spatiotemporal risk assessment that preceded our manipulation. We assumed that on the eighth day, most resident isopods were already aware of the scorpion burrows. Thus, by comparing isopod spatial behavior between the first and eighth day we could reveal how predator cues affect their spatiotemporal risk assessment.

Isopod behavioral analyses

We analyzed the movies using the VLC media player. We recorded the number of isopods that left their burrow, and the number of isopods that encountered the scorpion burrows either immediately after leaving their own burrow or during their rapid return. We did not consider other encounters because there was no way to confirm whether or not these isopods were residents of the focal burrows and not foragers from a distant burrow. By considering those two encounter types separately, we were able 1) to explore whether the isopods altered their spatial activity when leaving the burrow, and 2) to determine the consequences of this spatial decision on the probability of accidently encountering the scorpion burrow while heading straight back (using path integration) to their own burrow. We also recorded the isopods' detailed behavioral responses upon encountering the scorpion burrows. To classify all possible responses, and to reduce possible researcher bias, we developed a dichotomous decision-tree that corresponds with specified spatial projections (Fig. 2). The behavioral parameter at the base of the decision-tree was whether isopods stopped when encountering the treated area (i.e. stop), and then whether they entered this area (i.e. entry). For isopods that entered, we defined subsequent terminal behaviors. Isopods that entered either (a) stopped within the treated area, (b) crossed it or (c) promptly retreated (Fig. 2).

Statistical analysis

The number of isopods leaving their burrow to forage highly varied between days. Therefore, we used the fraction of isopods encountering the scorpion burrow from all the isopods that left the burrow during that day (i.e. encounter fraction) as our response variable. The scorpions continued to excavate their burrows during the experiment, thus increasing their soil-mound perimeter. Therefore, the probability of an isopod walking in the general burrow direction to accidently encounter the scorpion burrow was slightly higher on the eighth day. We corrected for those mound-size differences by dividing the encounter fraction by the angle (θ) between the isopods and the scorpion burrows (Fig. 1). Acute behavioral responses were calculated as the proportion of isopods that used each behavior upon encountering the scorpion burrow (for the original untreated data see Supplementary material Appendix 2 Table A1–A3).

To determine whether isopods' respond defensively to scorpion burrows, we used previously collected data of isopod reaction towards bare ground that was virtually marked during data analysis (Zaguri et al. 2018). We compared this reference data with isopods' reactions toward scorpion burrows from the first day of the current experiment, using Mann–Whitney U test. The corrected encounter fraction (CEF) and the proportion of behavioral responses were compared between the first- and eighth-days using Wilcoxon-signed rank tests. Results were separately analyzed for isopods leaving their

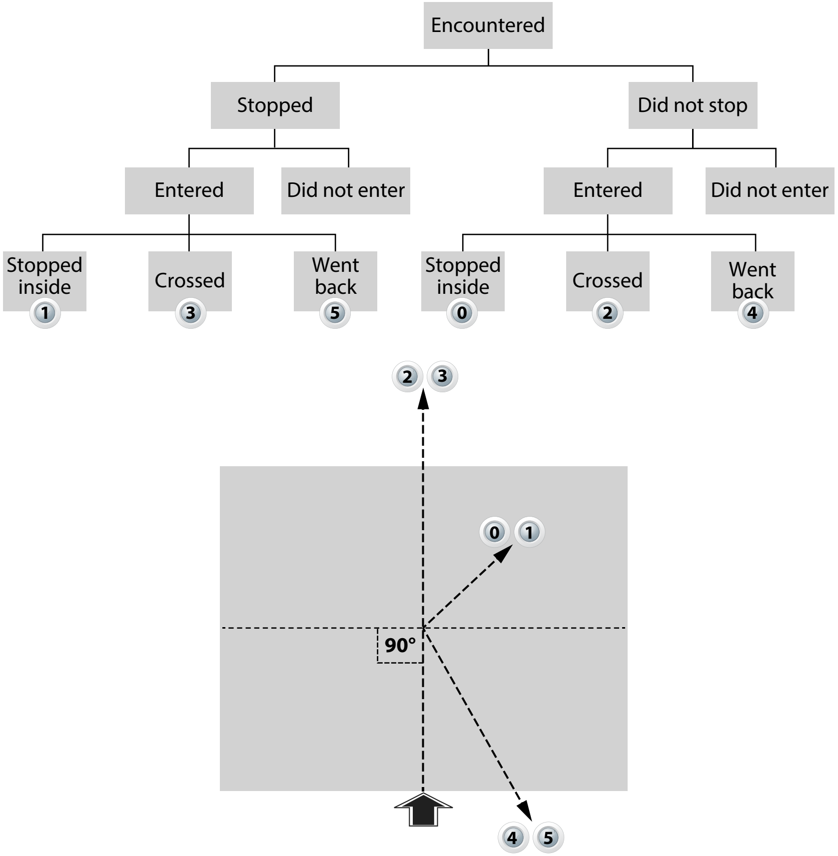

Figure 2. Decision-tree of the isopod's behavioral responses when encountering a scorpion burrow. At encounter, the first decision is whether to stop. This decision is followed by a second decision of whether to enter the burrow area, i.e. to climb on the debris mound. Entry could take place irrespective of the stopping decision. Isopods who entered could proceed in three ways: crossing the treatment area (2, 3), stopping inside it (0, 1) or running away ('went back' behavior; 4, 5).

burrows and those returning because we assumed that the return path was affected by the information acquired during prior encounters with the scorpion burrow. Similarly, we had to test the results for inhabited (eight burrows) and deserted burrows (five burrows) separately, because all burrows were inhabited during the first day. SPSS (ver. 21) was used for all statistical analyses.

Data deposition

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.5352kv8> (Zaguri and Hawlena 2019).

Results

All scorpion burrows were inhabited during the first day of the experiment. During this day, the proportion of isopods encountering a scorpion burrow did not differ depending on whether or not those burrows will later be deserted or not (Mann–Whitney U test; $z = -1.025$; $p = 0.354$, and $z = -1.317$; $p = 0.222$, for encounters upon leaving and return respectively). Similarly, on the first day there were no differences in the isopod's behavioral responses toward these two groups of scorpion burrows (Mann–Whitney U test; $z = -1.354$; $p = 0.182$, and $z = -0.480$; $p = 0.660$, for stop and enter, respectively).

Compared to their responses toward bare ground Control in a previous experiment (Zaguri et al. 2018), isopods stopped four times more upon encountering scorpion burrows (51.4% versus 12.8%) and enter the treatment area 30 times less (3.2% versus 95.9%; Mann–Whitney U test; $z = -3.882$; $p < 0.001$, and $z = 4.665$; $p < 0.001$, for stop and enter, respectively).

On the eighth day, larger proportions of the isopods on their way out of their burrows encountered the inhabited scorpion burrows than on the first day (Wilcoxon signed-rank test $z = -2.521$; $p = 0.012$, Fig. 3). This pattern was reversed when the isopods headed back to the burrow, with smaller proportions of isopods encountering the scorpion burrows on the eighth day compared to the first day (Wilcoxon signed-rank test $z = -2.100$; $p = 0.036$, Fig. 3). We found no differences in the CEF of deserted scorpion burrows between the eighth and first days for either approaching directions (Wilcoxon signed-rank test $z = -0.135$; $p = 0.893$, and $z = -0.135$; $p = 0.893$, for leaving and return respectively, Fig. 3).

The isopods' tendency to stop when arriving at the soil-mound edge of an inhabited scorpion burrow did not differ between the first and the eighth days, for either approaching direction (Wilcoxon signed-rank test $z = -0.210$; $p = 0.833$, and $z = -0.845$; $p = 0.398$, for leaving and return respectively, Fig. 4). Here too, the results were different for deserted scorpion burrows. On departing from their own burrows, isopods that encountered deserted scorpion burrows stopped less on the eighth day compared to the first day (Wilcoxon signed-rank test $z = -2.023$; $p = 0.043$, Fig. 4). No differences were found on the way back to their burrows (Wilcoxon signed-rank test $z = -0.405$; $p = 0.686$, Fig. 4).

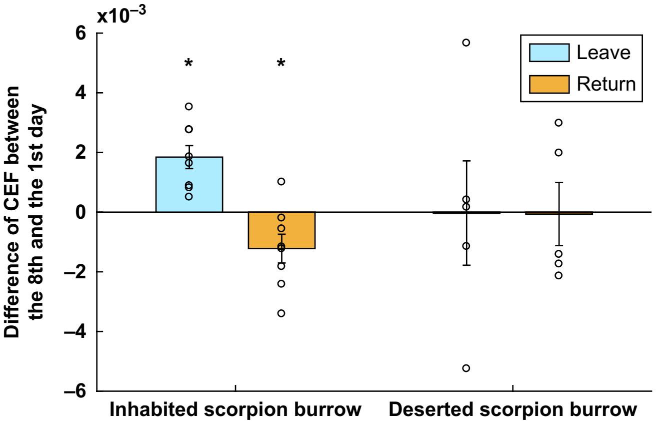

Figure 3. Comparison of mean (± 1 SE) differences of the corrected encounter fraction (CEF) between the first and the eighth day. The number of isopods encountering the scorpion burrows was calculated as the fraction from all the isopods that left the burrow during this day. This fraction was then corrected by dividing it by the angle between the isopods and the scorpion burrows which reflect the probability to encounter the scorpion burrow by chance (for the original data see Supplementary material Appendix 2). Encounters that happened on the isopods' way out of the burrow are depicted in light blue and those on their return are depicted in orange. Data is presented separately for inhabited and deserted scorpion burrows. Asterisks represent significant difference ($p < 0.05$).

On the first day, only 3.15% of the isopods that encountered scorpion burrows while departing from their own burrows climbed on the scorpion mound. A week later, this fraction was much bigger toward both inhabited (52.73%, Wilcoxon signed-rank test $z = -2.527$; $p = 0.012$, Fig. 4) and deserted burrows (43.47%, Wilcoxon signed-rank test $z = -2.032$; $p = 0.042$, Fig. 4). On their way back, proportionally more isopods entered the area of deserted scorpion burrows on the eighth day relative to the proportion that entered during the first day (Wilcoxon signed-rank test $z = -2.023$; $p = 0.043$, Fig. 4). However, no differences were found for returning isopods approaching inhabited scorpion burrows (Wilcoxon signed-rank test $z = -0.845$; $p = 0.398$, Fig. 4).

During the first day, isopods entered the area of scorpion burrows more on their way back to their burrow than on the way out (Wilcoxon signed-rank test $z = -2.407$; $p = 0.016$). This result is also true if we only consider scorpions that adopted their burrows (i.e. inhabited burrows; Wilcoxon signed-rank test $z = -2.207$; $p = 0.027$). In contrast, on the eighth day, isopods entered the inhabited scorpion burrow area more on their way out (Wilcoxon signed-rank test $z = -2.366$; $p = 0.018$).

On the first day, only a very small fraction of the isopods climbed on the scorpion mounds. This precluded us from analyzing subsequent behaviors. Instead, we used the results of a previous experiment that used this same methodology but with a larger sample size (Zaguri et al. 2018). In this previous

Figure 4. Comparison of mean (± 1 SE) percentage of isopods behavioral responses when approaching the scorpion burrow between the first and the eighth day. Data of stop and entry responses is divided according to the isopods' progress direction (leaving in beige and returning in brown). Data is presented separately for inhabited (a) and deserted (b) scorpion burrows. Asterisks represent significant difference ($p < 0.05$).

experiment, only 4.5% of the isopods that climbed on scorpion mounds changed their progress direction and withdrew ('went back'; Fig. 2, Supplementary material Appendix 1). On the eighth day of the current experiment, many more isopods (22.9 ± 3.2%) that climbed on soil mounds of inhabited scorpion burrows reacted this way.

Discussion

Animals adjust their spatial activity according to the distribution of vital resources and to spatiotemporal variations in predation risk (Lima and Dill 1990, Brown and Kotler 2004). Their 'landscape of fear' assessment is based on evolutionary 'rules of thumbs' that are correlated with predation risk (Lima and Steury 2005). Whether and how prey use predator cues to update their assessment remains unclear, most likely due to the empirical difficulty of inferring complex cognitive considerations from prey behavior. We addressed this challenge by setting scorpions in freshly dug burrows, and by comparing the spatial behavior of their prey isopods on their first encounter and after seven days. On the first day, the proportion of naïve isopods that accidently encountered the scorpion burrows reflected their landscape of fear assessment prior to our manipulation. Of these isopods, very few entered the risky zone surrounding the scorpion burrows. After seven days, a bigger proportion of isopods approached the inhabited scorpion burrows and more isopods also climbed on the excavated soil mound despite the imminent risk. Scorpion mounds provide no resources that may attract isopods. Thus, our findings support the hypothesis that desert isopods used predator cues to update their spatiotemporal risk assessment, and purposely entered the dangerous burrow areas to inspect them.

Prey of various taxa approach and follow predators, particularly when they are first encountered (FitzGibbon 1994, Godin and Davis 1995, Brown and Godin 1999). Inspection behavior seems paradoxical because prey individuals that approach a predator increase their chances to be killed. This puzzling behavior must entail substantial benefits that ameliorate the obvious costs (Dugatkin and Godin 1992). Inspection behavior can provide the information needed for fine-tuning the prey defense responses (Magurran and Pitcher 1987, Fishman 1999), deter predator attacks (FitzGibbon 1994, Godin and Davis 1995), provide warning for conspecifics (Pitcher et al. 1986, Magurran and Higham 1988), or enhance the inspector's own social status (Curio et al. 1983, Regelmann and Curio 1986). The last two mechanisms necessitate the presence of attentive conspecifics. This is obviously not the case here. Isopods forage individually, have poor eyesight and sense the environment primarily using their antennae's contact chemoreceptors (Linsenmair 1985). We can also evidently reject the hypothesis that isopods approached the active scorpion burrow to deter attack. *Scorpio palmatus* hunt for isopods exclusively from within their burrows. Therefore, isopod inspection behavior cannot induce scorpion withdrawal or change its ambush site location. Moreover, this hypothesis cannot explain why very few isopods entered the scorpion burrow on their first encounter and many more approached and entered the danger zone after seven days. Consequently, it is most likely that the isopods approached the scorpion burrows to update their information.

Studies that interpreted inspection behavior as a tool of gathering new information have focused predominantly on acute situations in which a predator has been recently detected (Dugatkin and Godin 1992, Cooper and Blumstein 2015). In these situations, the prey attempt to gather information about predator identity, state (Pitcher 1991, Brown and Godin 1999), and motivation to attack (Murphy and Pitcher 2005). Such detailed information can assist prey in adjusting their defense reactions to better match the particular risk. Our results do not support this classic explanation. In general, the isopods did not closely inspect the scorpion area on first encounter, but did so after seven days. Moreover, scorpions hunt for isopods exclusively from their burrows and therefore, the best way for isopods to minimize the risk of predation is to avoid the already identified scorpion burrow altogether. We hypothesized instead that isopods use inspection behavior to confirm the scorpions' presence.

Why are isopods willing to take risks to confirm the scorpions' presence? Isopods use path integration to navigate back to their burrow (Alt 1995, Merkle et al. 2006). In other words, isopods compute their return distance and direction vector from the vectors joining the locations on their route. The limited ability to modify the return route (Hoffmann 1985, 1990) may cause homing isopods to unintentionally bump into the danger zones surrounding scorpion burrows. Such encounters can be fatal if isopods unwarily approach the scorpion burrow from the roof side. Scorpions that ambush from within their burrows can detect the vibration caused by the advancing isopods while the isopod remains completely unaware of the threat. Indeed, in hundreds of potential encounters that we filmed, the only predation events were when isopods approached the scorpion burrow from its roof. Foraging isopods that distance themselves from the area near scorpion burrows substantially reduce the chances of mistakenly entering the risk zone when homing. Conversely, avoiding this section altogether based on information that is no longer relevant may unnecessarily decreases the isopods' already restricted foraging opportunities, resulting in substantial 'information decay costs' (IDC).

On first encounter, a new soil mound with scorpion odors clearly implies an active scorpion ambush-site that should be avoided. Indeed, about 97% of the isopods that encountered scorpion burrows on the first day circumvented the risk zone. As time progressed, chances increased that the scorpions abandoned the burrow (i.e. mortality or emigration). A way to lessen the IDC is to regularly check whether the scorpion is still present by inspecting the soil mound where predation cues are ample and the risk is relatively low. This inspection behavior is analogous to a fish that inspects a predator by approaching its tail to avoid the cone of attack (Magurran and Seghers 1994, Brown and Dreier 2002). Our findings support this explanation. On the eighth day, proportionally fewer isopods encountered the scorpion burrows on the way back than did returning isopods on the first day. Moreover, a larger proportion of the isopods that inspected the mound changed their movement direction compared to the proportion of isopods that inspected the mound on the first encounter in another study (Zaguri et al. 2018). Thus, it appears that isopods use inspection behavior to reduce the chances for later encounters with predators.

Isopod reactions toward deserted scorpion burrows further corroborated our findings. On the first day, there were no detectable differences in the ways isopods reacted to the burrows that would remain inhabited and those that would be deserted. Yet after seven days, the isopod behavioral responses toward these two burrow types differed substantially. The proportion of isopods that encountered deserted scorpion burrows did not differ between the eighth and first days for both approaching directions. This suggests that isopods have already identified the scorpion burrows as empty and ignored their presence. On the eighth day, isopods also entered deserted scorpion burrows more upon returning to their own burrows in comparison to the first day, implying that they did not try to avoid the foraging areas surrounding scorpion burrows. When departing from their own burrows, isopods that encountered deserted scorpion burrows stopped less on the eighth day compared to the first day. This finding contrasts with the behavior of isopods that approached inhabited burrows. The later tended to stop when encountering the scorpion soil mounds in similar proportions between the first and eighth days. Stopping behavior allows isopods to accumulate additional sensory information without increasing the risk (Zaguri et al. 2018). Thus, after seven days, isopods seemed to already perceive the deserted scorpion burrows as bearing no risk.

In summary, we empirically demonstrated that desert isopods take deliberate risks to validate their spatiotemporal risk assessment. We created scorpion burrows that provide no resources for isopods, and measured the isopods' reactions to these risky patches on their first encounter and after seven days. On the first encounter, isopods avoided the danger zone surrounding the scorpion burrow, but after seven days, they intentionally approached and entered this area, most likely to determine whether the scorpion was still present. We hypothesize that isopods employ this risky inspection behavior to lessen the 'information decay costs' (IDC) that are associated with spatial changes in the predator foraging behavior. To the best of our knowledge, this is the first example in which inspection behavior toward predators is used for the prey's future planning of spatial activity. Our study system is unique because it allows us to disentangle the confounding considerations that dictate prey spatiotemporal activity, and to unravel the value of information and its use. We believe that many other species use similar considerations to remap their 'landscape of fear' assessment. Overlooking the importance of 'information acquisition' may lead to incorrect interpretation of prey anti-predator behaviors thus ending with inaccurate projections of their 'landscape of fear' assessment.

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Author contributions – MZ and DH conceived the ideas and the experimental design, MZ executed the study and analyzed data, MZ and DH wrote the manuscript.

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Supplementary material (available online as Appendix oik-06477 at <www.oikosjournal.org/appendix/oik-06477>). Appendix 1–2.