

Sensory Cues and Memory in Lepidopteran Mud Puddling Behavior

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Abstract

Puddling is a form of supplemental feeding for nectivorous Lepidoptera to acquire necessary mineral nutrients, primarily sodium, that are otherwise absent from their nectar diets. For many species sodium is important for growth, nervous system function, and egg production. However, the mechanisms through which Lepidoptera locate puddling sites is unknown. I investigated three potential factors influencing puddling site selection: visual cues from landscape contrast, olfactory cues from bacterial volatiles, and memory. Knowing the factors that influence lepidopteran puddling site selection can help us better understand how they find the resources necessary to survive and reproduce, as well as provide insight to the learning and memory capacities of Lepidoptera. Landscape contrast had a significant effect on lepidopteran puddling site selection, with butterflies on average choosing spots lighter than the surrounding area. Temperature and shade also affected butterfly puddling, with butterflies across families showing a preference for warmer sites in direct sunlight. Between families, there were significant differences for puddling preferences for sites with certain temperatures and water contents. It is unclear if Lepidoptera use scent to find puddling sites. Overall, returns to specific puddling sites were rare and Lepidoptera do not seem to be using short term memory to relocate spots, but more data would need to be conducted to say anything conclusive.

Introduction

Puddling is a behavior observed in many species of Lepidoptera, where individuals aggregate at mud puddles, dung, carrion, sweat, and other mineral-rich sources to feed. This is thought to be a form of supplemental feeding to acquire essential nutrients that are otherwise rare in their plant-based diets (Lamie et al., 2025). In temperate climates where butterflies primarily feed on nectar, many species show a preference for sodium-rich puddling sites (Lamie et al., 2025). Boggs and Dau (2004), working out of Colorado, found that different species showed consistent preference for substrates with certain sodium concentrations (*Pieris macdunnoughii* [formerly *Pieris napi*] preferring lower concentration mud and both *Everes amyntula* and *Glaucopsyche lygdamus* preferring higher concentration carnivore dung). They also found that butterflies did not respond to other potential feeding cues tested, such as uric acid, urea, or ammonium. Other salts have also been tested but only sodium attracts Lepidoptera (Arms et al. 1974). In Lepidoptera, sodium is important for nervous system function, growth and reproduction (Arms et al., 1974; Snell-Rood et al., 2014).

Pivnick and McNeil (1987) found that in *Thymelicus lineola* the average egg complement contained more than 50% of a female's total body sodium at emergence. However, in many species, males are significantly more likely to be found puddling than their female counterparts. In *Thymelicus lineola*, Pivnick and McNeil found that males of the species passed on 32% of their abdominal sodium to the females during their first mating. This biased sex ratio at puddles

is consistent with many other puddling species of Lepidoptera, where the females likely acquire sodium through mating (Pivnick & McNeil, 1987; Sculley & Boggs, 1996).

Once one butterfly has landed at a puddling site more will follow (usually of the same species but some species will also respond to individuals of another), likely because, either intentionally or not, the first butterfly serves as a visual cue to others of beneficial nutrients (Ankola et al., 2021; Lamie et al., 2025; Scott, 1986). While butterflies will respond to seeing another butterfly puddling (even responding to pinned specimens (Boggs & Dau, 2004; Lamie et al., 2025)), what attracts the first individual is unknown. If selection is not random, it is possibly some other kind of visual cue that draws in the first butterfly, as it is already known they use sight to find sites with another butterfly. Adult butterflies have compound eyes made up of hundreds of ommatidia that can see the full range of color as well as in many species, being able to see ultraviolet and polarized light (Scott, 1986; Kelber et al., 2001). It is unlikely UV light is acting as a signal, as, while sodium is reflective on the ultraviolet spectrum, there is not a significant difference between puddling and non-puddling sites' UV reflectivity (due to how diluted the salt is) for it to be the sole visual cue (Walton, 2022). However, it is possible landscape contrast could contribute to butterflies locating viable puddling sites. Not only do puddling sites vary in color compared to the color of vegetation, but light would likely reflect differently off of viable puddling surfaces, depending on color, water content, salinity, and other factors (Sun et al., 2022).

It is known that butterflies will use a combination of visual and olfactory cues to locate host plants for laying eggs (Thompson & Pellmyr, 1991), so it is possible that they use a similar combination to locate puddling sites. Many insects respond to various volatile emissions from microbes for many different purposes including oviposition, host (plant and animal) location, and food location (Davis et al., 2013). Lepidoptera specifically have been shown to respond to the volatile emissions of fermented sugars (El-Sayed et al., 2005). Similar olfactory mechanisms may play a role in how they locate mineral-based feeding sources. Microorganisms that live off of carrion produce sulfides which attract many carrion insects (Weisskopf et al., 2021). Sulfides have another connection to salt sources, as dimethylsulfide is the reason for the distinct smell of the ocean (Stefels, 1997). If butterflies are more sensitive to these emissions they could be sensing a similar smelling compound that is associated with the ocean but at a much lower concentration.

Furthermore, it is unknown if butterflies are able to remember specific puddling spots and intentionally return to them. Some species of butterfly, most notably *Heliconius erato*, have displayed a capacity to learn spatial locations using broader visual landscape and celestial compass cues (Moura et al., 2024). This opens up the possibility that some species could learn where quality puddling sites are and return to them again using memory. Alternatively, it is also possible that the cues used for locating puddling sites are consistent enough to attract the butterflies to the same spot again and again, regardless of memory capacity.

Knowing the factors that influence butterfly puddling site selection can help us better understand how they find the resources necessary to survive and reproduce, as well as provide insight to the learning and memory capacities of butterflies. My study addresses three questions. 1) Does visual contrast of puddling sources compared to the surrounding area attract the first butterfly? Butterflies not only have excellent color vision, but light would also likely reflect differently off of puddling surfaces than it would off of vegetation. It is possible this

difference in reflectivity and contrast could serve as a visual cue for the quality of puddling sites. 2) Do the volatile emissions of bacteria on puddling sites attract the first butterfly? Butterflies will respond to chemical cues to locate egg laying sites and plant-based feeding sources, so it is possible they also use them to find puddling sites. 3) Will butterflies return to the same puddling sites? Not only will this help test for non-random selection (in theory if selection is non-random the same factors that initially attracted the individual to a specific site would do so again), but also test memory capacity. If there is a notable difference between initial landing/ sampling site and where the individual actually feeds from, and the individual returns to the feeding site (ignoring the initial sampling site), that would indicate that the individual remembers testing the initial site and determining the latter site was more desirable.

Methods

This study was conducted at the Rocky Mountain Biological Laboratory in Gothic, Colorado from June 29th to July 29th, 2025. Data was collected from the field between 1000 and 1300 MDT. This allowed for enough time to collect data on polarization in the morning, with the sunlight at a good angle, and around noon to collect data on returning site use. Data was collected at the mineral springs south of the Gothic town site (2870m asl) as well as from puddles along the Copper Creek trail (2926 to 2987 m asl) and sites within the Gothic town site (2899 m asl). Data was collected for any species present, with consideration for potential variation between families (different puddling preferences having already been recorded in Boggs and Dau (2004)).

Vision

A camera with a polarizing lens was used to take photos of places where butterflies landed but didn't initiate feeding, places where they did feed, and places they never landed at all. The rotation angle of the lens as well as the angle of the sun relative to where the butterflies are flying in from was also recorded, as that could affect how the polarized light appears. The photos were taken with the sun at the same horizontal angle as it was for the individual upon approach, so as to best approximate what the butterfly was seeing. However, vertical angle could not be controlled. Sampling and feeding spots were marked with flags of different colors. The flags were laid horizontally on the ground with the end pointing towards the spot, so as to avoid disturbing the soil. Unused spots were randomly selected by tossing pebbles over the shoulder with varying angle and strength. Feeding behavior, as opposed to sampling behavior, was defined by a feeding response greater than 2 seconds. Data on soil moisture was collected at each puddling spot using a VWC soil moisture meter. This is because not only will dryer substrates likely take more energy (and potential water loss from regurgitation and reimbining) for a butterfly to drink from, but might also affect the reflectivity of the surface as well as salt concentration. Butterflies are also sensitive to temperature and might be less likely to land at a cooler spot that would hinder their ability to take flight again. For this reason, temperature was recorded as well using a handheld thermocouple reader, shaded so it only recorded ground temperature and not sunlight. Furthermore, whether the spot was in direct sunlight or under cloud cover at the time of the butterfly landing was also recorded.

Olfaction

The olfaction experiment was conducted in the Gothic town site, away from any naturally occurring puddling sites so as to prevent any potential smell contamination. Beforehand, mud was collected from the mineral springs and separated into three treatment groups. The experimental treatment was autoclaved at 121°C for 20 minutes to kill any bacteria, placed in a drying oven at 60°C for about 20 hours, and then rehydrated using distilled water. The control treatment was dried in a drying oven at 60°C for about 20 hours, so as to not entirely kill off the bacteria, then rehydrated with distilled water. The second control (or wild treatment) was untampered-with mud so as to gain a baseline comparison for how the butterflies behave towards natural substrates as well as providing a way to control for the control treatment's drying process potentially killing some bacteria. For all trials both the experimental and control treatments' mud was collected the day before, so they had time to go through the drying oven, but the wild treatment was collected day off, to ensure it was as similar to the naturally occurring puddling source as possible. The treatments were placed in separate aluminum trays that were then placed 5 meters apart in a triangle formation. Initial trials used 6x3 in trays and later trials used 8x8 in to test if greater surface area would yield different results. The number of landings were recorded for each tray (feeding and sampling behaviors not being distinguished).

Memory

To test for random site selection, as well as short-term memory, a single butterfly was selected and startled off to record if they returned to the same spots in the mud puddle, different places, or didn't return at all. Specifically, I recorded whether they returned to the spots they initiated feeding from or reinvestigated sites they already rejected, indicating whether or not they remember or detect anew the spatial location of their initially preferred site. Startling was achieved by walking towards the butterfly (not running) so as to reduce the odds of the butterfly abandoning the site completely. An audio recording was started with the first step and I dictated when the selected butterfly took flight and when it landed or left my field of view. If they landed at a new spot, data was collected from there as well, using the same methods outlined under vision. If the butterfly returned to the spot, the time from initial flight to relanding was recorded. How many other butterflies were present at the site at time of startling was also recorded and if all butterflies startled off (meaning there were zero other butterflies remaining at that spot), that was recorded in the notes. This was to control for the possibility of a return being due to the presence of other butterflies rather than the cues being tested for. Memory data was initially collected at the mineral springs and a second smaller site along the Judd falls was added later to test if the size of a puddling site (i.e. reducing the amount of viable puddling area) would affect likelihood of an individual returning to a specific spot.

Data Analysis

The photos were converted to gray scale and analyzed using imageJ. Contrast was determined by calculating the mean shade of gray (0= total black, 255= total white) at the landing spot (defined by a 120x120 pixel box around the tip of the flag pole) and mean grey of the total nearby area (defined by a 600x600 pixel box centered around the landing area). The pole of the flag was removed from the image to prevent it from affecting the final values. The total gray was subtracted from the landing gray so that a positive contrast value indicated the

landing spot was brighter than the surrounding area and negative indicated it was darker. There were some photos where the flags were placed less precisely and in those cases I used my memory and best judgment to determine where exactly the butterfly landed (for example if the end of the flag was in a shadow but the shade_cloudCover was a no, I determined the butterfly landed on top of the lump causing the shadow). The contrast values were then analysed using a t-test. A generalized linear model was used to test for effects of temperature, soil moisture, and shade. The temperature and water content data were analysed with t-tests and shade data was analysed with a chi-square test. To determine if there were differences between families, the random selection data was filtered out and an ANOVA and Tukey's HSD test were performed on the remaining data for both temperature and water content. The olfaction experiments did not return enough data to analyse. The return data was analysed with a chi-square test to compare return rates for the larger Site 1 and smaller Site 2, and another to compare observed return rates to expected random return rates. Finally, a chi-square test was used to compare the return rates based on the presence of other butterflies puddling in the area.

Results

Vision

There was a significant difference between landing spots and random spots in landscape contrast (Fig. 1; $t = -3.21$, $df = 50.307$, $p = 0.002$). On average the butterflies landed at spots lighter than the surrounding area, compared to unused spots that on average were darker than the surrounding area. Angle of approach, relative to the sun (from the front, rear, left or right) significantly differed from expected 1:1:1:1 of random approaches (Table 1; chi-square= 24.62, $df = 3$, $p = 0.0001$). Combining front with behind and left with right showed butterflies were significantly more likely to approach a site with the sun in front of or behind them, rather than to the left or right (chi-square= 22.04, $df = 1$, $p > 0.0001$). Approaches with the sun in front and behind the butterfly did not significantly differ from each other (chi-square= 1.18, $df = 1$, NS).

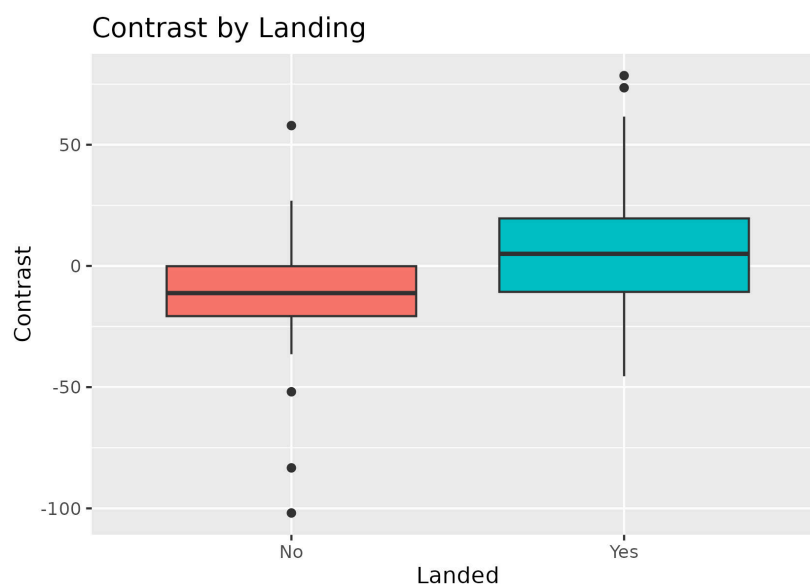


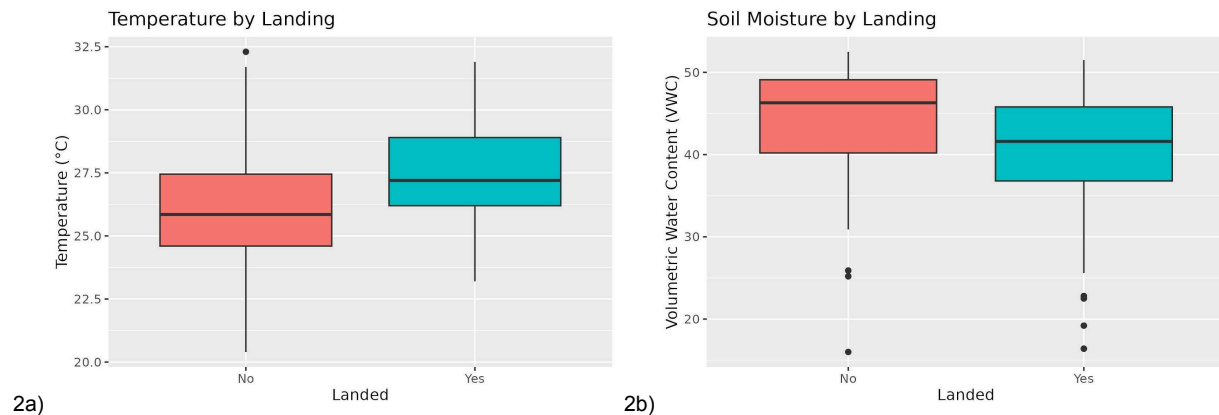
Figure 1: Contrast significantly affects likelihood of landing.

Number of Approaches by Sun Angle

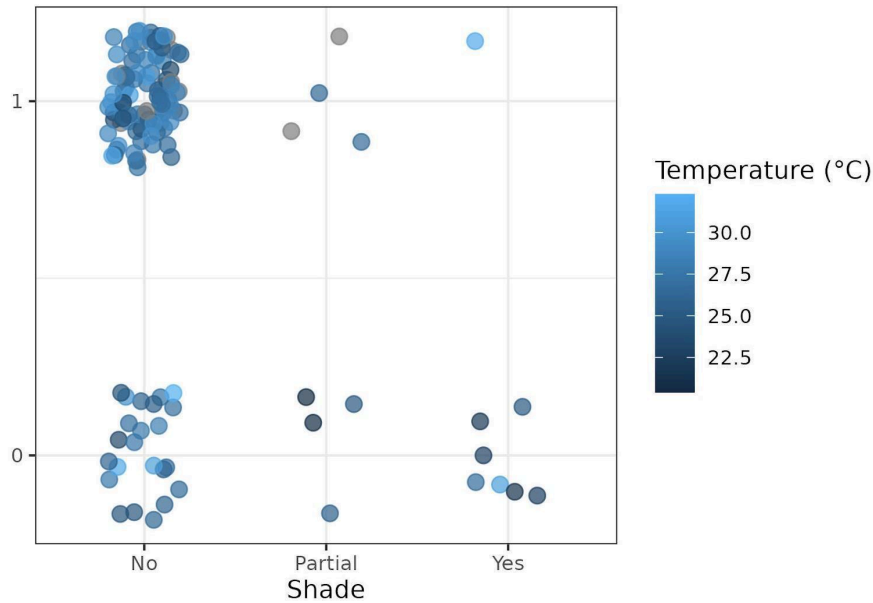
SUNANGLE	APPROACHES
behind	23
front	31
left	5
right	10

Table 1: Butterflies were significantly more likely to approach a landing spot with the sun in front of or behind them.

Temperature significantly affected whether or not butterflies would land at a site (Fig. 2a; $t = -2.60$, $df = 45.206$, $p = 0.012$), while water content did not (Fig. 2b; $t = 1.74$, $df = 49.307$, $p = 0.087$). Compared to randomly selected sites, butterflies selected sites with higher temperatures and no butterfly landed at a site below 23°C. However, when shade and cloud cover were added to the model, temperature became non-significant and shade was the significant variable affecting landing (Fig. 2c; chi-squared = 21.26, $df = 2$, $p = 2.408e-05$). While shade/cloud cover was the determining variable for landing, the best model was the one that accounted for all three variables (temperature, soil moisture and shade).



Relationship between Landing and Amount of Shade



2c)

Figure 2: Landing was a categorical variable with no indicating unused spots and yes indicating feeding or sampling spots. 2a) Temperature had a significant effect on landing, with butterflies overall preferring sites with higher temperatures. 2b) Soil moisture had a non significant relationship to landing. 2c) Shade had a significant relationship with landing, as butterflies preferred sites in direct sunlight.

Families differed significantly in site preference for both temperature (Table 2a; $F_{3,84} = 4.91$, $p = 0.003$) and soil moisture (Table 2b; $F_{3,85} = 3.96$, $p = 0.01$). A post-hoc test between families showed soil moisture of selected sites differed significantly between Pieridae and Nymphalidae. Nymphalidae had the highest average VWC of all families (43.5%) and Pieridae had the second lowest (38%). Lycaenidae had the lowest average VWC (37.5%) but also had the lowest number of observations (Table 2a). Temperature was significantly different between Papilionidae and the three other families, Papilionidae having the lowest average temperature (26.1°C)(Table 2b).

Family VWC Tukey's HSD Test

FAMILY	DIFF	LWR	UPR	P
Nymphalidae-Lycaenidae	6.008333	-0.5583308	12.5749975	0.0852129
Papilionidae-Lycaenidae	4.652273	-1.8598954	11.1644408	0.2477556
Pieridae-Lycaenidae	0.475000	-5.6180809	6.5680809	0.9969602
Papilionidae-Nymphalidae	-1.356061	-6.8921277	4.1800065	0.9180779
Pieridae-Nymphalidae	-5.533333	-10.5697349	-0.4969318	0.0254909
Pieridae-Papilionidae	-4.177273	-9.1424107	0.7878653	0.1302235

2a)

Family Temperature Tukey's HSD Test

FAMILY	DIFF	LWR	UPR	P
Nymphalidae-Lycaenidae	-0.04243421	-1.7153271	1.6304586	0.9998937
Papilionidae-Lycaenidae	-1.90056818	-3.5204799	-0.2806564	0.0147773
Pieridae-Lycaenidae	-0.27520161	-1.7928773	1.2424741	0.9643243
Papilionidae-Nymphalidae	-1.85813397	-3.4022313	-0.3140366	0.0117544
Pieridae-Nymphalidae	-0.23276740	-1.6692430	1.2037082	0.9740965
Pieridae-Papilionidae	1.62536657	0.2509555	2.9997776	0.0137723

2b)

Table 2: 2a) Effect of family on volumetric water content. Significant p-values are highlighted in green. 2b) Effect of family on temperature. Significant p-values are highlighted in green.

Olfaction

While there were butterflies present in the area, none of them displayed a response to any of the treatments in any of the olfaction trials. The first trial of the olfaction experiment was conducted with 6x3 tin trays and returned no results. Trial two similarly returned no response

from the butterflies. The third trial was conducted with 8x8 inch tin trays to see if expanding the amount and surface area of mud would trigger a response, but again no butterflies landed on the trays. In all trials there were occasionally butterflies that landed nearby and puddled directly on the dirt road, but not close enough to indicate they were responding to the tins themselves. To address the possibility that the reflections coming off of the rims of the tins were causing confusion in butterflies attempting to land, the mud was removed from the tins and placed directly on the ground, but still no butterflies landed on the mud nor displayed any investigative behavior (circling around site).

Memory

Returns were rare and did not vary as a function of site size. Site 1 had a total of 36 observations collected, only 3 of which were returns, while Site 2 had a total of 45 observations, 6 of which were returns. These ratios did not differ between sites (chi-square=0.13, 1 df, NS). Therefore, I combined the data for the two sites and tested against the null hypothesis of random probability of return, 1:1. The observed returns varied significantly from the expected 50/50. Of 86 total observations, 9 were returns (chi-square=31.86, 1df, $p < .00001$).

A butterfly was more likely to return to a site if there was another butterfly present. Of 73 observations with no other butterflies remaining at the initial site after startling, 6 returned. Of 4 observations where at least one butterfly remained on the initial site after startling, 3 returned (chi square= 10.6, 1df, $p=0.001$).

Discussion

Vision

Landscape contrast does affect butterfly puddling site selection. This indicates that they can rely on visual cues other than the presence of another butterfly to locate these mineral sources. This, in combination with shade and cloud cover also being a significant factor in site selection, provides support for the possibility that butterflies are using the light (potentially polarized) reflecting off of the surfaces of puddles to find them. Butterflies being significantly less likely to land at a spot that is shaded, and sites with darker contrast values, could be related to the absence of light reflecting off of that spot. More evidence supporting the use of polarized light in locating puddling spots is the fact that the butterflies were significantly more likely to approach their selected site with the sun in front or behind them, rather than to the side. The strongest horizontal polarization will occur when the butterfly is in line with the sun (Yadav & Shein-Idelson, 2021). Furthermore, if approaches were random, the surrounding habitat would have favored approaches from the side, as there were more flowers around the edges and the back of the mineral spring faded into forest. If these same cues also apply to other puddling sources like dung or carrion remains unknown. However, dung and carrion are more likely to have stronger scents. It could be that butterflies rely on different cues to locate different feeding sources, and this could be a contributing factor as to why the olfaction test (conducted with mud) did not yield results.

Temperature and shade affect butterfly puddling and there are differences between families for puddling preferences. This is consistent with expectations based on butterflies' sensitivity to temperature (Bladon et al., 2020). Furthermore, shade and cloud cover also had a

significant effect on landing. This is also consistent with expectations based on butterflies' sensitivity to temperature as shaded places are likely to be cooler. Papilionidae having a lower average temperature preference than the other families is consistent with general trends of larger butterflies with greater wingspans being better at thermal buffering (Bladon et al., 2020). It is strange there wasn't more of a significant difference in soil moisture between families based on previously described differences in salt concentrations in species (in theory as the water evaporates, it will leave dryer areas with increased salt concentrations). Lycaenidae having the lowest average VWC is consistent with the preference for higher salt concentrations of *Everes amyntula* and *Glaucopsyche lygdamus* described by Boggs and Dau (2004). And despite not being significant, the p-value for Lycaenidae-Nymphalidae was still quite low ($p=0.09$). Given Lycaenidae had the lowest number of observations (16 to other families' >20), it is possible with more observations that difference could become significant. However, Boggs and Dau (2004) also reported *Pieris macdunnoughii* as preferring lower concentrations, but my results showed Pieridae (most observations consisted of *Pieris macdunnoughii*) having the second lowest VWC. Though, without having tested samples for salt content I can't be sure as to the actual amount of salt present in the mineral spring.

Olfaction

It is unclear if butterflies use scent to find puddling sites, though it is strange there was no response at all to any of the olfaction treatments. Butterflies were puddling in the general area, indicating they were looking for puddling sites. Even if they do not respond to bacterial emissions, the mud itself was visually much darker than the surrounding dirt. However, this could have been to the experiment's detriment as the results from the contrast photos indicated that butterflies responded to lighter contrast values. As mentioned in the results, removing the mud from the tins was tested, though not as its own separate trials and not for as long. Potentially, the sun reflecting off of the rim of the tins was affecting the butterflies' ability to locate or land, and longer observation periods may have yielded a response (though the method of placing them directly on the ground would not be recommended for a full trial as it would contaminate the autoclave mud). Future experiments might explore using a different type of container (non-reflective) that would still be able to go through the autoclave and drying oven; or, as mentioned above, they might try using dung or carrion which would likely have a stronger scent.

Memory

Butterflies do not seem to be using short term memory to relocate spots, though there are some potential confounding factors at play and more data would be needed to say anything conclusive. There is increased room for error given that the return data for Site 1 had less than 5 observations in a category and therefore violates the chi-squared test's assumptions. Either way, short term returns were very rare for both sites and do not appear to be affected by area size. It does seem that the presence of another butterfly at the initial spot increases the odds a startled individual will return. Whether this is because the other butterfly serves as a strong visual cue for a good puddling spot (as if the selected butterfly is finding the site for the first time rather than a retuning behavior) or if the presence of the other butterfly serves as a signal that the initial feeding spot is safe to return to, is unclear. However, there is still increased room for

error due to low expected values. Though, even with the small sample size, the results are consistent with what we know about puddling being a social behavior. Given this pre-existing knowledge, it is not a stretch to conclude that the presence of another butterfly increases the likelihood the flighted butterfly will return.

Caveats and Future Directions

The contrast images were not taken at a consistent distance from the flag, meaning there was some variation in the amount of area the 120x120 and 600x600 pixel boxes covered. This could make a difference if the proportion of further photos was different between landed and unused spots. However, this is not likely as the ratio of close to far photos is fairly even for both used and unused spots (43 close: 42 far used and 18:16 unused). For the vision observations, random selection data was occasionally collected when cloudy and the butterflies weren't flying. This is a potential error as those data points would not accurately tell what butterflies weren't responding to because they were not flying at all, and therefore not able to respond or not respond to them. Future experiments could take photos without a polarizing lens and compare how the presence of polarized light affects the landing. In addition to this, a future experiment could also record the butterflies landing approach and calculate the exact angle of approach to see if it aligns with the angle where the most polarized light would be visible. For memory, it is possible that the low returns were due to the method of startling. Because I was the only person collecting data, I had to both be the one to startle them and keep track of them, making it hard to get away from the initial site (in relatively difficult terrain for Site 1 and part of Site 2) while also not losing sight of the selected individual. Given that the thing that startled them off also remained in the area for a time, rather than immediately moving through, it may have discouraged the butterflies from immediately returning. Furthermore, even at the smaller Site 2, the area of available puddling space was still quite large relative to the size of even the biggest butterfly, meaning it would be fairly easy to locate a new puddling spot rather than needing to return to a potentially compromised spot. In future experiments, I think it would be more fruitful to observe on a larger scale. Trying MRR on various puddles located very close to each other (well within a single butterfly's natural range) and recording if the same individuals return to the same puddles over a longer span of time (days or weeks), rather than very specific spots within one puddle that likely do not vary much from each other in quality, could be one way to approach this. This would also provide insight into how often young males will puddle (if they only do it once to get all the sodium they need or multiple times).

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