

An experimental assessment of polarized light's role in avian behavior toward  
water: implications for collisions with PV solar panels

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## APPROVAL PAGE

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## ABSTRACT

The number of solar panel installations in the United States has grown quickly in the past decade and is expected to continue rising. While solar power is an important component of our energy portfolio, there are some ecological concerns associated with increasing commercial sites. Bird mortality at solar panel sites has been observed and recently begun to be investigated. This phenomenon is still poorly investigated, and many questions remain to be answered, including what attracts birds to solar sites.

The “lake effect” hypothesis is that birds collide with solar panels as they mistake solar panels for waters because both surfaces reflect polarized light. Birds may be attracted to linear polarization (hereafter “polarization”), which is created in high levels by both solar panels and water. There is some evidence that birds use environmental polarization as a decision-making cue. For example, migrating birds appear to use skylight polarization to help them orient during takeoff and recent research suggests that birds are more attracted to small water sources (bird baths) with higher polarization. There are no studies that have directly addressed whether polarization might drive solar panels collisions.

To test whether polarization might be used by birds to direct them toward water, we created an operant conditioning experiment where domesticated zebra finches (*Taeniopygia guttata*) were trained via both positive and negative reinforcement to move towards water. Birds were trained in a testing arena with two choices, a bowl of water and an empty bowl. Once trained, as assessed by a success rate of 80%, we tested birds with an unreinforced version of the training stimuli, as well as with two more sets of polarization stimuli: a set of water bowls where one produced higher polarization, as modified by a set of films; and a set of light sources where one had higher polarization. The objective was to assess whether: 1. Birds preferred water with higher polarization, and 2. Whether this preference carried over to non-water sources of polarization.

Although birds passed through the training criteria, they did not perform better than chance when tested with the training stimuli. These results suggest that operant conditioning training was not successful, possibly because reinforcement was not compelling enough. Birds also did not show a preference for higher polarization in either of the subsequent tests. As training was not successful, these results of these tests can be considered in the context of having no previous exposure to these polarization stimuli. The results of this study are contradicted by other studies, that showed a preference for higher polarization when making foraging decisions. It could suggest that polarization vision is highly context dependent, taxonomically contingent or used only in conjunction with related cues. Few studies and conflicting evidence suggest that there is still much to be learned in how birds use environmental polarization, particularly as it could have important ecological consequences in the form of solar panel collisions.

## TABLE OF CONTENTS

Acknowledgements	ii
List of Figures	iii
Chapter 1. An experimental assessment of polarized light's role in avian behavior toward water: implications for collisions with PV solar panels	1
Bibliography	25

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## LIST OF FIGURES

1. Visualization of How Light Becomes Polarized	3
2. Schematic and Photograph of Testing Arena	7
3. Visual Guide of the Training and Testing Protocol	9
4. Example Polarimetry Images with a Polarizing Film	12
5. Proportion Correct per Test Type	16
6. Spearman Rank Correlation Results	17

## *Introduction*

Due to the impacts of greenhouse gas emissions on natural, physical, and economic systems of the planet (Rosenzweig & Parry 1994; Darwin 2004), there is a need to shift a greater proportion of energy production to low-carbon sources. Solar energy is an increasingly important component of that energy-producing portfolio. Because of this importance, there are global and national calls for the installation of more utility-scale photovoltaic (PV) solar panels.

As installation costs fall, particularly for commercial usage, the number of solar panels in the United States are expected to grow at an ever-increasing rate. A projected 38% increase in solar capacity for energy generation is predicted from 2023 through the end of 2024, and by first quarter 2024 solar energy already accounts for 75% of new energy generation installations (Antonio 2024).

While expanding green energy sources is a laudable pursuit, some ecological concerns have been raised - including increased avian mortality. Research at PV solar panels at utility-scale solar installations, particularly a report by Kagan in Southern California that investigated bird deaths, have described bird collisions (Kagan et al. 2014). It is unclear whether this phenomenon is common and/or restricted to particular landscape settings, such as Southern California desert. In the few studies that have been performed, only a small number of carcasses were found per site (Visser et al. 2019; Kosciuch et al. 2020); however, few observed mortalities per location may underplay the cumulative effect of collisions across commercial sites.

There are several critical components of avian collisions with PV panels that still need to be investigated. Firstly, cause of death at solar panel sites can be unclear and collision monitoring techniques may undercount mortality, leading to collision deaths being underestimated. Secondly, it is unknown if collision risk varies among species or other taxonomic groups. And lastly, the factors that cause solar panel collisions have yet to be determined.

PV solar panel sites can contribute to avian mortality in several ways beyond solar panel collisions: predation of stunned or injured animals, powerline electrocution, vehicle collisions (Kagan et al. 2014). With the rarity of powerline electrocution and vehicle collisions, predation and solar panel collisions appear to be drive most of the mortality; however, cause of death was not able to be determined in over 70% percent of cases. Current methodology for measuring mortality also contributes to obscuring the total effect of collision deaths. The current monitoring standard is performing site searches for carcasses once a day in the mornings, where search efficiency has been estimated between approximately 35% and 85% (Morrison 2002). Misses can be attributed partially to size, as small birds are missed more frequently, as well as underestimating due to birds colliding later in the day and being removed by humans or predators.

Taxonomic patterns of collisions have been poorly described. In Southern California, waterfowl carcasses were overrepresented at a PV solar site near a large body of water (Kagan et al. 2014). Establishing taxonomy-based mortality rates is difficult as there have been few peer-reviewed studies – two papers covering ten sites as of 2020 (Kosciuch et al. 2020).

Thirdly, it is unknown what factors cause solar panel collisions. Collisions with other man-made structures, such as windows, buildings and powerlines are better documented and are commonly observed (Brown & Drewien 1995; Loss et al. 2014); however, solar panels are horizontal rather than vertical structures, and we do not know if horizontal PV solar panels attract birds as a result of the same or different cues as vertical surfaces such as windows.

The leading explanation for PV solar panel collisions is that birds mistake the panels for water surfaces and attempt to land on them (Kagan et al. 2014) — i.e., the “lake effect hypothesis.” Central to this explanation is that PV panels reflect high levels of linear polarized light (hereafter “polarized light”). Polarized light is created when light reflects off shiny, non-metallic surfaces, changing from oscillating randomly to oscillating parallel to the struck surface (Fig. 1). The amount of polarization is described by degree of polarization (DOP), which refers to the percentage of reflected light that is polarized. Water is the greatest polarizer in nature (Horváth & Dezsö 2004), producing up to 70% polarization at optimal angles (Horváth et al. 2010). Solar panels can produce an even greater DOP, with levels ranging from 90 to 100% (Horváth et al. 2010).

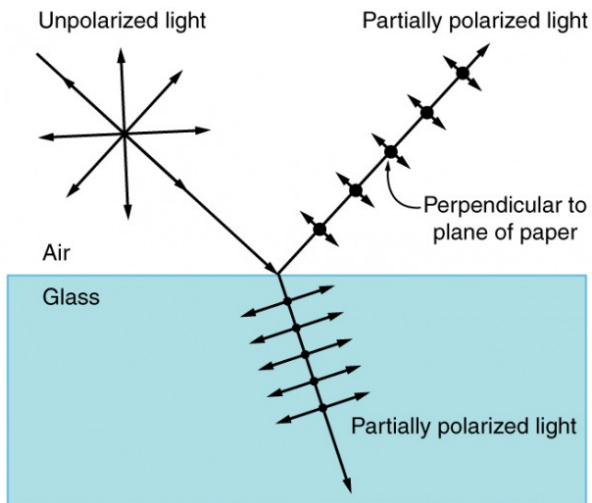


Figure 1. Unpolarized, or randomly polarized, light becomes polarized when striking a non-metallic surface such as glass or water. Light particles that are horizontal (parallel to the surface) reflect while light particles in other directions may refract or be absorbed into the surface. The light particles that reflect are said to be “polarized” (Urone & Hinrichs 2012).

Polarization sensitivity has been documented in several taxa. Many vertebrates, such as some reptiles, fish (Waterman & Forward 1970) and birds (Able 1982), have shown some form of polarization response. The mechanism of polarization vision is still under investigation, but double cones, pairs of cones found in all three of these groups, are a strong candidate (Chetverikova et al. 2022). Humans and other mammals have lost these photoreceptors, which is likely why polarization-sensitive vision is not present in these taxa.

Birds perceive polarized light in certain contexts, particularly as skylight polarization during migration orientation (Able 1982; Muheim et al. 2006); however, this response is still not well understood. Zebra finches (*Taeniopygia*

*guttata*) respond to skylight polarization in conjunction with magnetoreception (Muheim et al. 2016), but did not respond to vertical polarization even when reacting to other visual stimuli (Melgar et al. 2015). It is unclear if birds are attuned to horizontal polarization sources. Recent studies indicate that some avian species might use polarization cues when detecting artificial sources of food and water. For example, black-capped chickadees (*Poecile atricapillus*) and tufted titmice (*Baeolophus bicolor*) presented with higher and lower polarized water sources (bird baths) and food sources (bird feeders), showed a greater preference for more highly polarized resources (B. Robertson, personal communication, May 18, 2023).

Some species known to be attuned to polarized light from water are also attracted to man-made sources of polarization. Mayflies prefer to oviposit on both asphalt, another source of high DOP (Kriska et al. 1998) and solar panels (Horváth et al. 2010) over water. It is possible that birds also find solar panels highly attractive, and that this attraction contributes to solar panel related mortality. Solar panels are one of the strongest polarizers documented to date. This could make solar panels an “ecological trap,” which occurs when a once adaptive cue becomes linked to a less adaptive or deleterious outcome and poor habitat selection (Dwernychuk & Boag 1972). In this case, solar panel collisions may be the result of a preference for highly polarized horizontal stimuli. If polarization is a primary cue in water identification, birds may even prefer PV solar panels over water sources when presented with both.

## Objectives

In this study we investigated the assumptions of the “lake effect” hypothesis by determining: (1) If linear polarization cues are used by a model bird, the domesticated zebra finch (*Taeniopygia guttata*), when moving towards water; and (2) if finches also exhibit attraction to non-water sources that similarly polarize light.

## Overview of experimental approach

We used operant conditioning to train a set of zebra finches to perch over a water source, as opposed to an empty dish, and then presented them with a set of polarization cues to assess the role of polarized light in their preferences. If birds use polarized light to identify water, then birds will also prefer more highly non-water polarized cues because it is inherently associated with water sources. A preference for less polarized cues would suggest that birds could perceive polarization but did not necessarily associate it with a water source or that birds were paying attention to an alternative cue. No preference for either high or low polarization would suggest that birds either could not perceive polarized light or had no preference for it, particularly when searching for water.

## *Methods*

### Study subjects

We used ten adult male domesticated zebra finches in this experiment. These birds were arbitrarily selected from a larger population housed at the

William & Mary aviary. We banded birds with small, numbered aluminum leg bands and/or colored bands to allow for individual recognition. For this study, birds were housed in pairs in (75.5 x 45 x 45 cm cages) on racks within a windowless experimental room (4.3 x 4.3 m) on a 10:14h (light:dark) photoperiod with full spectrum lighting turning on at 0800 and off at 1800. Birds had ad libitum access to food (Volkman Super Finch seed blend) and drinking water. Birds were maintained in same-sex pairs as zebra finches are social and lack investigative behaviors when kept alone.

During experimental trials, we designated one male as the “focal” bird while the other was considered a “companion.” We determined experimental roles during the acclimation period based on food motivation, interest in feeders and water bowls, and degree of movement around the testing arena. Once designated to be a focal or companion bird, an individual did not take on the other role, nor were they paired with any other birds. A maximum of three pairs of birds (one block) were trained and tested at any given time. Each block was housed on a single rack.

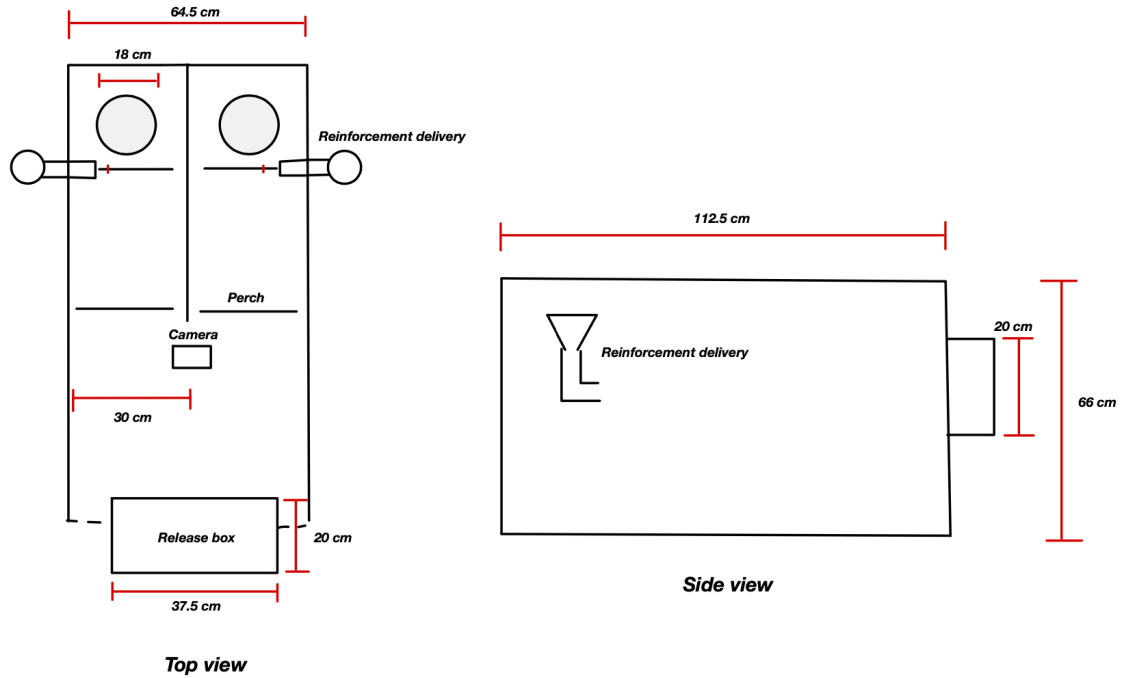


Figure 2. A schematic (a) of the testing area and a front interior view (b) of the area as photographed from the perspective of the release box. The middle line represents a separation between the left and right chambers. The circular openings were used to present the polarization cues, which were recessed under

the testing arena. The lower perch is closer to the release box while the higher perch is below the feeder and above the polarization cues.

### Testing arena

The testing arena was situated in the center of the experimental room. Birds not experiencing an experimental trial were distributed relatively equally on left and right sides of the room to equalize the spatial occurrence of acoustic cues. The testing arena was developed in part by referencing a similar arena created by Melgar et al. (2015). The interior space was 1.13 x 0.65 x 0.66 m, and the inside was painted dark gray to minimize polarization not coming from the presented cues (Fig 2.). Plexiglass was placed over the top of the testing arena to help diffuse overhead light. A GoPro Hero7 (30 fps, 720 resolution) camera was placed in the box to observe the feeder and choice-making, as well as the visual cues below. The GoPro was connected via micro-HDMI to a monitor (Dell model 2408WFPb) which provided live observation of behaviors inside the box with minimal lag.

## Training and testing protocol

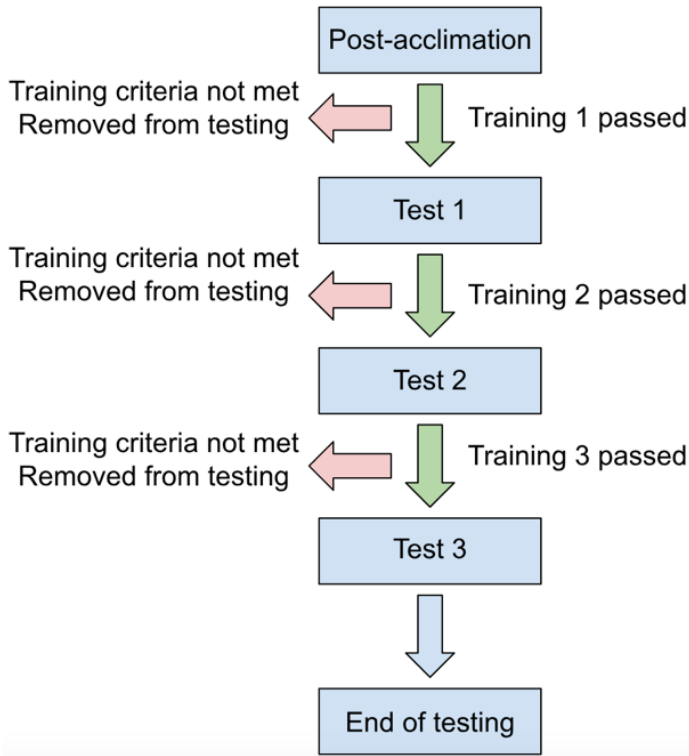


Figure 3. Schematic diagram of the training and testing protocol. After acclimation was completed, birds passed through rounds of training until they either passed the training criterium or were removed due to lack of participation or mistakes.

## Acclimation trials

We acclimated birds to the testing arena on three occasions before training began. On each day of acclimation, all birds in a block (three pairs) were placed in the testing arena for 2 h with both feeders filled with food and two black bowls filled with water (below). Behaviors during this period were noted to assess feeding drive. Acclimation was typically completed between 0900 and 1100.

## Training trials

Birds experienced training trials in a block of three pairs at a time, though only one pair was in the arena during a trial. We conducted two training trials per pair per day, with the order of pairs randomized. Training was typically performed six days a week, with training starting between 0858 – 1030.

The polarization cues used in training trials were randomly assigned to the left or right chamber of the arena (see fig 2.) in each trial thereby reducing side biases. We placed birds in a release box and allowed them to observe the cues for approximately 30 seconds. Upon release of the pair of birds, we tracked their movements and behavior through the monitor connected to the GoPro camera.

Once the focal bird displayed a choice of stimulus, by passing over an approximately 0.5 cm thick line placed 3 cm away from a feeder on the choice perch, we applied a reinforcement. If the focal bird chose the “correct” side, it experienced a positive reinforcement reward of the delivery of approximately 3 g of seed into the relevant feeder. If the focal bird made the “incorrect” choice, we engaged a negative reinforcement consisting of a puff of compressed air. An air compressor was kept in the experimental room and run between trials to maintain pressure. A hose was fed into the feeder, and a quick puff (around 0.5 sec) was applied after an error was made. We kept air pressure approximately at a level that resulted in the flight of birds from the perch during pilot research.

A trial ended when the “correct” choice was made, or the maximum length of the trial (45 mins) was reached. We recorded the number of errors (i.e.,

“incorrect” choices), the length of the trial, and whether a correct choice was made for each learning trial.

We continued training trials for a pair until the focal bird reached the predetermined passing criterion: four correct choices for every five consecutive completed trials. Participation in trials was required for trials to be counted, so that in determining whether passing criterion was met only trials ending in a correct or incorrect choice were included. Once a focal bird reached the passing criteria, they (along with their companion bird) experienced unreinforced test trials (see below). Following the unreinforced test trials, the pair experienced further reinforced learning trials until the focal bird met the passing criterion again and could proceed to the subsequent type of unreinforced test trials (Fig 3.).

Removal from training occurred if excessive mistakes were made (over 25 mistakes in three out of four consecutive trials) or a lack of participation was observed (participation in fewer than 75% of trials). Passing and removal criteria were assessed at the end of each day.

### Test trials

The general protocol for a test trial was identical to a learning trial except for the stimuli used and that no form of reinforcement was presented to the birds. Once a focal bird had met the learning criterion (described above), the pair experienced three unreinforced test trials with different stimuli.

The first type of test trial used identical stimuli as the learning trials (water vs empty bowl). This first test type was designed to assess whether the learned

responses resulted in reliable movement to water. The second test type used two bowls of water, one with a polarizing filter and the other with non-polarization film, such that one side showed much greater linear polarization than the other. This test ascertained whether the learned response to move to water was associated with a preference for a stronger polarization cue. In the third test type, we used these polarizing and non-polarizing films over standardized light sources to examine whether the previously learned preference for water was associated with a preference for strong patterns of linear polarization even in the absence of water.

A test trial ended when the “correct” choice was made by the focal bird, or the time limit (45 min) was reached. We recorded the number of errors per test trial, length of trial, and whether the focal bird made the “correct” or “incorrect” choice on their first response to the stimuli.

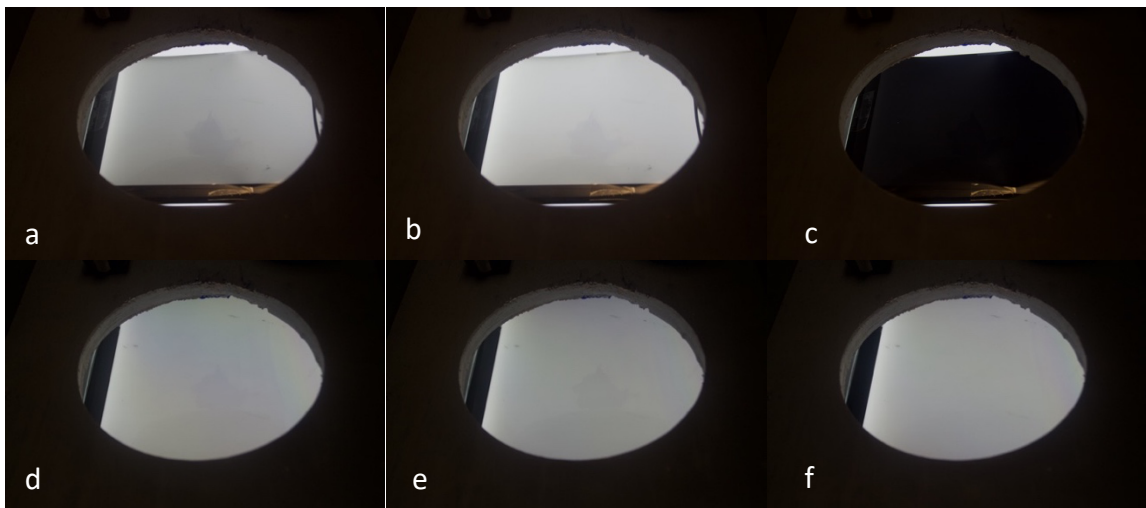


Figure 4. Example polarimetry images with a polarizing film (a, b, c) and non-polarizing film (d, e, f) over a light box. Photographs were taken consecutively with a change only in the angle of the polarizing lens. A dark film (as seen in c) is

due to a lack of light passing through to the camera and thus denotes high polarization.

### Polarization cues

Three sets of polarization cues were used in this study. These cues were developed to present the greatest variance in DOP. Maximum DOP was determined using a DSLR (Canon EOS Rebel T4i) with a modified lens. The camera was tilted to Brewster's angle to measure maximum polarization. Images were taken with the lens at three angles ( $135.5^\circ$ ,  $18.7^\circ$  and  $82.9^\circ$ ; Fig 4.) to capture the degree and orientation of polarization. The subsequent images were entered into AlgoNet©, which calculated polarimetry using a custom system created by Bruce Robertson from Bard College. Three factors of the testing environment affect the amount of polarization produced by the cues: color of the bowl, presence or absence of water, and film type.

Training and the first test type used two black bowls, one with water and one without. An extremely black matte paint (Black 2.0 created by Stuart Semple) was chosen to decrease polarization as much as possible. A black matte bowl produces low levels of polarization which is increased by adding water. The bowl filled with water had a DOP between 33-43% while the empty bowl had levels between 8-12% (much less than expected by a still water source).

The second test type used two water-filled white bowls, one covered with a linear polarizing filter (RENIAN polarized film sheets) and the other with a non-polarizing film (Optix Smoke Black Light Headlight Taillight Tint). A white matte

bowl produces extremely low levels of polarization, around 0.3–1%. Adding water does not increase polarization by a large amount, producing levels around 3-6%, which allows for polarization to be modified primarily by film type. The bowl with the polarizing filter showed a DOP around 93% and the bowl with the non-polarizing film showed levels between 10-42%.

The third test type presented the same films, polarizing and non-polarizing, over light boxes (LitEnergy A4 LED copy board light tracing box) at maximum brightness. The light box with the polarizing film showed a DOP around 99% while the light box with the non-polarizing film showed levels around 10%.

We performed reflectance light spectrometry (Ocean Optics USB 2000) to confirm that the combination of filters and light boxes produced near identical reflectance patterns from the external surface of each film. Hence, the films did not differ in color parameters that could be perceived by the birds but did differ substantially in patterns of polarization.

#### What happened to birds after they exited the study?

Birds not actively undergoing acclimation, training, or testing trials were housed in the experimental room. In addition, the next block of three pairs of experimental birds were housed in the experimental room at the same time. Once pairs of birds finished their sequence of trials or exited the study due to failure to reach criterion, they were returned to the main colony in a different room.

### Ethics and welfare statement

All procedures were followed in conformance to William & Mary's Institutional Animal Care and Use Committee (IACUC protocol #2022-0067 and IACUC protocol #2022-0059).

### Statistics and data analysis

For each test type, the proportion of test trials correct was calculated and compared to a chance result (0.5) using a one-sample t-test. Spearman rank correlations were also run to compare training performance (number of trials and number of "correct" training trials) with the results of test one.

### *Results*

Of the ten birds that began the study, six completed all rounds of testing while two were removed before test 1 and another was removed before test 3, due to failure to pass criterion for the next step of the study. The final bird completed test one but did not pass the second round of training due to time constraints. Consequently, eight birds completed test 1, seven birds completed test 2 and six birds completed test 3.

The minimum number of trials required by a bird to meet the criterion for passing to the next stage of the study was four and the maximum was 47. Qualitatively, birds showed adequate interest in the PVC feeders and food, with the majority eating after food was presented during each training trial. They also

showed interest in the presented cues, as evidenced by head tilting behaviors on the perch above the cues.

Following the initial round of training for each focal subject, we did not find sufficiently consistent evidence that birds had learned to move toward the dish containing water (i.e. the predicted choice) in the first set of unreinforced test trials (one-sample  $t_7 = 0.61$ ,  $p = 0.56$ ; Fig. 4). However, there was a trend that skewed in the predicted direction which suggests that the reinforced learning trials helped some birds choose the water dish in these test trials.

On the second and third series of unreinforced tests, there was also a slight trend for movement toward the predicted side (test 2,  $t_6 = 1.11$ ,  $p = 0.31$ ; test 3,  $t_5 = 1.11$ ,  $p = 0.32$ ). Note the small sample sizes in all these tests and the large overlap in the data with random behavior (i.e., 50% probability of the predicted response, Fig 4.).

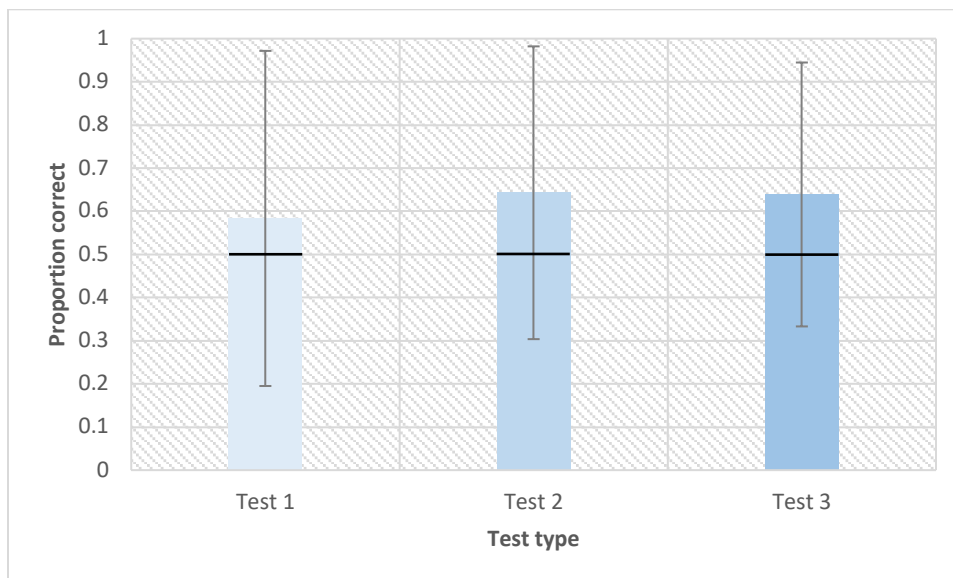


Figure 5. Proportion of trials correct for test types 1, 2 and 3. Test 1 presented an empty and a water-filled black matte bowl, test 2 presented two water filled bowls (one with a polarizing film and one with a non-polarizing film) and test 3 presented two light boxes (one with a one with a polarizing film and one with a non-polarizing film). Error bars represent standard deviation. A horizontal bar shows what proportion would be expected (50%) if selection was random.

Spearman rank correlations were performed to assess whether individual performance in training was correlated with better performance on the first test (Fig 5). Neither the number of trials required to pass training ( $r_s = -0.30, n = 8, p = 0.47$ ) nor the proportion of correct trials during training ( $r_s = 0.15, n = 8, p = 0.72$ ) were correlated with better testing performance.

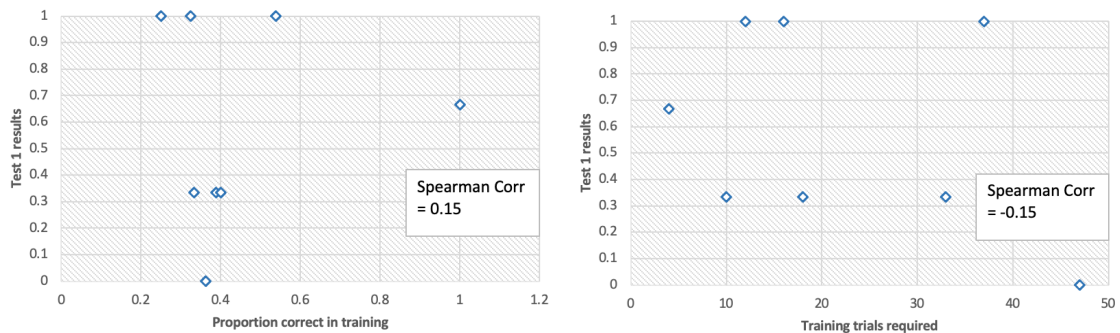


Figure 6. Raw data of the (a) proportion of correct trials during training in comparison to the proportion of correct trials in test 1 and (b) the number of trials required to pass training with corresponding Spearman rank correlation.

### Discussion

While birds passed the learning criteria, i.e., chose the bowl of water in 4 out of five consecutive trials, there was not adequate evidence that birds associated water with the reward consistently enough to choose water over an empty bowl in the first unrewarded trial. The first test type was used to assess the efficacy of the training and while birds chose the “correct” choice, the bowl with water, slightly more frequently than the empty bowl, this difference was not statistically significant. This result suggests that operant conditioning was not sufficient to train birds to move towards water. There was also no evidence that birds performed better on the first test if they passed through training more quickly or with a greater proportion of total correct trials, meaning that individual differences in performance could not explain this inconsistent result among birds. There appears to have been some association between the feeders and food, but it less clear if there was an association between a feeder with food and the water cue.

Operant conditioning is commonly and successfully performed with zebra finches, particularly for song preference studies (see Adret 1993, Coleman et al. 2019, among others). Responses to visual cues, such as color, have also been successfully trained (Melgar et al. 2015). There may have been methodological issues in this study that inhibited successful conditioning. It is possible that the puff of air applied when an incorrect choice was made was not a strong enough deterrent. While birds would fly away in response to the negative reinforcement, there were several cases where birds would fly to the incorrect perch up to 75 times in one training trial rather than choosing the other perch. This repetition of

incorrect choices suggests that the promise of a reward and risk of negative reinforcement were not sufficient to train birds to make a careful decision. It is also possible there was an issue with cue presentation; Water may have been difficult to see in the extremely black bowls which could have made associating water with a reward more difficult.

We found no evidence for a high polarization preference. All three tests showed a slightly greater frequency in choosing the “correct” side but none of these trends were statistically different from the null hypothesis of no preference. Based on this result, if any learning occurred it did not seem to transfer to tests of preferences for highly polarized cues. Without substantial learning, the subsequent test types (2 and 3) can be considered the presentation of novel polarization cues. A recent study has found that birds seem to show a preference under similar conditions. Wild birds in non-experimental conditions prefer small, polarized water sources (bird baths) over less polarized counterparts (B. Robertson, personal communication, May 18, 2023). However, the lack of clear preference exhibited by birds in the present study suggests that there was no novel preference for high polarization, particularly based on the third test type where there was extremely large polarization variance between the two stimuli (around 10% compared to almost 99% DOP).

A lack of response to polarization in the test birds could be due to several factors. It could be that zebra finches are not responsive to certain kinds of polarization cues. There have been few studies on zebra finch polarization responses and none that have used horizontal polarization as seen from above.

Vertical polarization responses have been observed, but the results are not conclusive. In a controlled environment, zebra finches did not show a response to vertically presented polarization, even when learning to respond to other visual stimuli (Melgar et al. 2015). On the other hand, zebra finches do appear to respond to skylight polarization but this is only in conjunction with magnetoreception and not polarization vision alone (Muheim et al. 2016). It is important to note that zebra finches are non-migratory, and therefore could respond differently to skylight/vertical polarization than migratory species.

There is the potential for polarization vision to have some taxonomic patterns. In an observational preference study, black-capped chickadees (*Poecile atricapillus*) and tufted titmice (*Baeolophus bicolor*) were found to make foraging decisions (from both bird feeders and fake spiders made from polarizing and non-polarizing film) in response to high levels of polarization (B. Robertson, personal communication, July 10, 2024). While both birds responded to polarization, tufted titmice had a strong preference for highly polarizing spiders while chickadees preferred their non-polarizing counterparts. Although more the polarization responses of more species would be required to assess taxonomic difference, variety in preference between two closely related species could suggest that polarization responses may be affected by even subtle behavioral or ecological differences between among birds.

It is possible that other cues in the testing arena interfered or altered how the polarization cues were perceived. As discussed above, skylight polarization is speculated to be tied closely with magnetoreception. Aquatic polarization may

also be intrinsically tied to other cues associated with water (e.g., specular reflection, water movement, smell etc.). Although these features were consistent throughout the study and between competing cues (i.e., test 2 where two bowls of water were presented with varying polarization), filters may have obscured or distorted essential information required for polarization to be used. Isolating and controlling polarization is difficult, particularly because it is not visible to researchers without specialized equipment.

Based on these results, there is no evidence that polarization makes horizontal structures appear water-like to birds. While the lack of statistical evidence that associative learning had occurred during training makes it difficult to determine whether polarization is linked to water identification, the lack of preference for higher polarization cues does suggest these birds did not have an inherent preference for high polarization sources.

The lack of preference for highly polarized cues does not allow us to reject the “lake effect hypothesis” as an explanation for avian collisions with solar panels. It is possible that other features of solar panels (e.g., size, color, shape, reflectance) make solar panels appear similar to water. It is also possible that the statistical power of the present study, due to high variability and low sample size, was too low to provide an adequate test of the hypothesis. There has been evidence from other studies suggesting that polarization does play a key role in water and food identification. Birds have also been shown to prefer small water sources (bird baths) that produce greater levels of polarization (B. Robertson, personal communication, May 18, 2023), and appear to use polarization in

foraging decisions, as discussed above. Potentially, a repeated study with different species, such as black-capped chickadees and tufted titmice that have been shown to respond to polarization stimuli, would lead to a different result.

The broader role of polarized light in bird behavioral responses is still unclear. Skylight polarization responses have been observed for decades, albeit debated due to being confounded or used in tandem with magnetoreception (Phillips & Waldvogel 1988; Muheim et al. 2016). It is possible that polarization vision is primarily used in the context of skylight polarization and that other uses are secondary or intertwined with other cues.

Birds are thought to be broadly capable of perceiving polarized light. Current research suggests that double cones are the most likely the site of polarization vision (Chetverikova et al. 2022), a type of photoreceptor cell found in almost all birds (Martin & Osorio 2008). It is possible that attunement to polarization differs depending on taxonomic or ecological differences such as the importance of behavioral interactions with water. Waterfowl, known to be found in greater proportions compared to other birds near PV solar panel sites next to large bodies of water (Kagan et al. 2014), may suggest a stronger response to high polarization than other birds or a higher reliance on polarization due to greater water usage.

A lack of conclusive evidence makes evaluating the “lake effect” hypothesis difficult. Conflicting studies suggest that polarization responses in birds are complex and may be dependent on context, taxonomy, or ecological circumstance. However, the potential avian mortality consequences of solar

panels become more pressing as installations continue at a rapid pace. Understanding the role of polarization in these collisions may be critical to reducing that mortality and maintaining avian biodiversity in those regions.

## *Bibliography*

- Able KP. 1982. Skylight polarization patterns at dusk influence migratory orientation in birds. *Nature* **299**:550–551. Available from <http://www.nature.com/articles/299550a0> (accessed March 5, 2023).
- Adret P. 1993. Operant conditioning, song learning and imprinting to taped song in the zebra finch. *Anim. Behav.* **46**:149–159.
- Antonio K. 2024, January 16. Solar and wind to lead growth of U.S. power generation for the next two years. Available from <https://www.eia.gov/todayinenergy/detail.php?id=61242> (accessed July 20, 2024).
- Brown WM, Drewien RC. 1995. Evaluation of two power line markers to reduce crane and waterfowl collision mortality. *Wildlife Society Bulletin (1973-2006)* **23**:217–227. [Wiley, Wildlife Society]. Available from <https://www.jstor.org/stable/3782794> (accessed November 10, 2022).
- Chetverikova R, Dautaj G, Schwigon L, Dedek K, Mouritsen H. 2022. Double cones in the avian retina form an oriented mosaic which might facilitate magnetoreception and/or polarized light sensing. *Journal of The Royal Society Interface* **19**:20210877. Available from <https://royalsocietypublishing.org/doi/10.1098/rsif.2021.0877> (accessed March 5, 2023).
- Coleman M, Saxon D, Robbins A, Lillie N, Day N. 2019. Operant Conditioning Task to Measure Song Preference in Zebra Finches. *Journal of Visualized Experiments* DOI: 10.3791/60590.
- Darwin R. 2004. Effects of greenhouse gas emissions on world agriculture, food consumption, and economic welfare. *Climatic Change* **66**:191–238. Available from <http://link.springer.com/10.1023/B:CLIM.0000043138.67784.27> (accessed July 20, 2024).
- Dwernychuk LW, Boag DA. 1972. Ducks nesting in association with gulls—an ecological trap? *Canadian Journal of Zoology* **50**:559–563. Available from <http://www.nrcresearchpress.com/doi/10.1139/z72-076> (accessed November 27, 2022).
- Horváth G, Blaho M, Egri A, Kriska G, Seres I, Robertson B. 2010. Reducing the maladaptive attractiveness of solar panels to polarotactic insects. *Conservation Biology* **24**:1644–1653. Available from <http://conbio.onlinelibrary.wiley.com/doi/10.1111/j.1523-1739.2010.01518.x> (accessed November 10, 2022).
- Horváth G, Dezső V. 2004. *Polarized light in animal vision: polarization patterns in nature*. Springer.
- Kagan R, Viner T, Trail P, Espinoza E. 2014. Avian mortality at solar energy facilities in Southern California: A preliminary analysis. *National Fish and Wildlife Forensics Laboratory*:1–28.
- Kosciuch K, Riser-Espinoza D, Gerringer M, Erickson W. 2020. A summary of bird mortality at photovoltaic utility scale solar facilities in the Southwestern U.S. *PLOS ONE* **15**:e0232034. Available from

- <https://dx.plos.org/10.1371/journal.pone.0232034> (accessed November 8, 2022).
- Kriska G, Horváth G, Andrikovics S. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *The Journal of Experimental Biology* **201**:2273–2286.
- Loss SR, Will T, Loss SS, Marra PP. 2014. Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability. *The Condor* **116**:8–23. Available from <https://academic.oup.com/condor/article/116/1/8/5153098> (accessed November 6, 2022).
- Martin GR, Osorio D. 2008. Vision in Birds. Pages 25–52 *The Senses: A Comprehensive Reference*. Elsevier. Available from <https://linkinghub.elsevier.com/retrieve/pii/B9780123708809004011> (accessed August 16, 2024).
- Melgar J, Lind O, Muheim R. 2015. No response to linear polarization cues in operant conditioning experiments with zebra finches. *Journal of Experimental Biology*:jeb.122309. Available from <https://journals.biologists.com/jeb/article/doi/10.1242/jeb.122309/262121/No-response-to-linear-polarization-cues-in-operant> (accessed April 9, 2023).
- Morrison M. 2002. Searcher bias and scavenging rates in bird/wind energy studies. Pages 1–5. NREL/SR-500-30876, 15000702. Available from <http://www.osti.gov/servlets/purl/15000702-YFxEp/native/> (accessed December 15, 2022).
- Muheim R, Moore FR, Phillips JB. 2006. Calibration of magnetic and celestial compass cues in migratory birds— a review of cue-conflict experiments. *The Journal of Experimental Biology* **209**:2–17. Available from <https://journals.biologists.com/jeb/article/209/10/2004/16060/Calibration-of-magnetic-and-celestial-compass-cues> (accessed December 15, 2022).
- Muheim R, Sjöberg S, Pinzon-Rodriguez A. 2016. Polarized light modulates light-dependent magnetic compass orientation in birds. *Proceedings of the National Academy of Sciences* **113**:1654–1659. *Proceedings of the National Academy of Sciences*. Available from <https://www.pnas.org/doi/10.1073/pnas.1513391113> (accessed April 16, 2023).
- Phillips JB, Waldvogel JA. 1988. Celestial polarized light patterns as a calibration reference for sun compass of homing pigeons. *Journal of Theoretical Biology* **131**:55–67. Available from <https://linkinghub.elsevier.com/retrieve/pii/S0022519388801206> (accessed March 5, 2023).
- Rosenzweig C, Parry ML. 1994. Potential impact of climate change on world food supply. *Nature* **367**:133–138. Nature Publishing Group. Available from <https://www.nature.com/articles/367133a0> (accessed July 20, 2024).

- Urone PP, Hinrichs R. 2012. Polarization. Page College Physics, 1st edition. OpenStax. Available from <https://courses.lumenlearning.com/suny-physics/chapter/27-8-polarization/> (accessed August 14, 2024).
- Visser E, Perold V, Ralston-Paton S, Cardenal AC, Ryan PG. 2019. Assessing the impacts of a utility-scale photovoltaic solar energy facility on birds in the Northern Cape, South Africa. *Renewable Energy* **133**:1285–1294. Available from <https://linkinghub.elsevier.com/retrieve/pii/S0960148118310565> (accessed November 6, 2022).
- Waterman TH, Forward RB. 1970. Field evidence for polarized light sensitivity in the fish *Zenarchopterus*. *Nature* **228**:85–87. Available from <https://www.nature.com/articles/228085a0> (accessed March 27, 2023).