EFFECTS OF LASER EXPOSURE ON AVIAN FORAGING BEHAVIOR

by

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A Thesis

Submitted to the Faculty of Purdue University

In Partial Fulfillment of the Requirements for the degree of

Master of Science

Department of Biological Sciences

West Lafayette, Indiana

May 2020

THE PURDUE UNIVERSITY GRADUATE SCHOOL
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To my family for their unwavering support.

ACKNOWLEDGMENTS

There are numerous people who have made this research possible. First, I would like to thank my advisor, Dr. Esteban Fernadnez-Juricic for allowing me to pursue a Master's degree in his lab. I would also like to thank my committee members, Dr. Ximena Bernal and Dr. Jeffrey Lucas for their incredible patience, feedback, and support.

Thank you to members of the Biology department who have helped me along the way. Thank you especially to Deona Harris who has been instrumental in the completion of my degree. I'd like to express my gratitude to Benny Goller who has been not only an inspiring colleague and helpful lab-mate, but an excellent friend. A special thank you goes to Gina Rupp who has guided me through this process under somewhat strange circumstances.

I would like to thank a few people who have been exceptional in their contributions to this project. Thank you, Bruce Stuck for answering my questions with patience and enthusiasm. Thank you, Matt Tang and all of Purdue REM for their cooperation and assistance in creating a safe environment to conduct our research. Thank you, Ed Melvin for the guidance and support. I am extremely grateful to Henrik Singmann who went above and beyond to help with the statistical analysis.

Lastly, I would like to thank the Packard Foundation and the National Fish and Wildlife Foundation for supporting this research.

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ABSTRACT

To prevent human-bird conflict, lasers have been developed as nonlethal control methods despite being known to cause eye injury and visual function deficits in humans under certain conditions. Determining the extent to which laser exposure is also an ocular hazard for birds is important because birds rely heavily on vision for activities critical to their survival, like foraging. The purpose of this study was to assess how laser exposure and the energy of exposure affects avian visual exploratory behavior for the purpose of foraging, as well as food consumption. We recorded the food visual exploratory behavior and food consumption of 40 house sparrows using foraging trials where they were tasked with finding millet seeds against a high contrast (easy task) and low contrast (difficult task) background according to their contrast sensitivity. After a baseline assessment of behavior, each bird was exposed to a unique laser energy and participated in the foraging trials again within week 1 after exposure and within week 2 after exposure. We found that house sparrows arrived at the food patch quicker and decreased their use of binocular vision within week 1 after exposure compared to before exposure. Within week 1 and within week 2 after exposure, birds changed their rates of scanning depending on the difficulty of the foraging task. They also developed laterality by increasing foveal vision rate using the left eye compared to the right. This laterality was even more pronounced in birds exposed to higher energy levels. Although laser exposure did not affect the overall amount of food birds consumed, they increased pecking rates and seed consumption rates both within week 1 and within week 2 after exposure. This study was the first controlled experiment examining the effects of laser exposure and laser energy on avian behavior. The evidence suggests that laser exposure can alter visual exploratory behavior in the context of foraging and influence foraging effort and food consumption rates. These results have important implications for the use of lasers as wild bird deterrents.

INTRODUCTION

Negative interactions between humans and wildlife can cause property damage and destroy crops, leading to monetary loss (De Grazio 1978, Allan 2000, Messmer 2000, Fagerstone et al. 2020). The United States Department of Agriculture, Wildlife Services estimated in 2001 the annual cost of wildlife damage to U.S. agriculture was US $944 million. The direct annual costs of collisions between aircraft and birds is estimated to be US $204 million (Dolbeer and Wright 2014, Anderson et al. 2015). These wildlife conflicts can also cause wildlife mortality (Erickson et al. 2002). For example, between 140,000 and 328,000 avian mortalities are caused by wind turbines (Loss et al. 2013) and between 89 and 340 million birds die from vehicle collisions each year in the US (Loss et al. 2014). This scenario has led to the development of different types of wildlife deterrents to manage populations of different species.

Traditional methods for wildlife management include the use of lethal techniques such as egg and nest destruction, shooting, and avicides as well nonlethal control methods like explosives, flags and kites, acoustics, dogs or raptors, and chemical repellents (Clark 1998, Bishop et al. 2003, Booth 2016, Rivadeneira et al. 2018). Lethal control methods have been declining in popularity as they've been increasingly shown to be controversial with the public and even non-effective for long-term management (Dolbeer 1998, Cook et al. 2008, Treves and Naughton-Treves 2009, Linz et al. 2015). Non-lethal deterrents, which employ an aversive stimulus in one of the sensory modalities be it visual, auditory, or olfactory, are preferred (Rivadeneira et al. 2018). Another popular non-lethal wildlife deterrent is the laser (light amplification by stimulated emission of radiation). Lasers have some advantages: they do not make noise, can target a specific area over a long distance, can be made in various colors, and can be used around various man-made structures (Blackwell et al. 2002, Gilsdorf et al. 2002, Cassidy 2013). At airport runways and flyways, lasers are used to repel nesting, feeding or flocking birds such as gulls, raptors, blackbirds, European starlings, waterfowl, doves, and wading birds (Blackwell et al. 2002, Briot 2005, Baxter 2007). Laser have also been used to successfully repel raptors, gulls, seabirds, migratory passerines, ducks, geese, and shorebirds from other anthropogenic structures such as windmills, shipping vessels, and oil sands (Cassidy 2013, Dredge 2014, Marques et al. 2014).

Classes of lasers and laser safety standards have been developed from the large body of mammalian and non-human primate literature. Due to the similarity between non-human primate

eyes and human eyes, results from these studies have been used to make inferences about laser injury thresholds for human eyes, determine safe viewing conditions, and predict damage to human eyes from a given exposure (Zwick 1984, Schmeisser 1996). The degree of damage depends on the energy delivered to the eye (Campbell et al. 1966, Peppers and Hammond 1969, Hudson 1998, Barkana and Belkin 2000) which is determined by the power output of the laser (Powell et al. 1971, William T. Ham et al. 1979), size of the laser beam on the retina (Robbins and Zwick 1999, ICNIRP 2000, American National Standards Institute 2014, Lund et al. 2014, Wang et al. 2014), length of exposure to the laser (Peppers and Hammond 1969, W T Ham et al. 1979), and wavelength of laser light (Ham et al. 1976, W T Ham et al. 1979, William T. Ham et al. 1979, Chen et al. 2011). The energy density of the laser exposure on an eye increases with increasing laser power, longer exposure time, and smaller beam diameter per a given power (ICNIRP 2000, Ziegelberger 2013a, b, American National Standards Institute 2014). Based on mammalian studies, we know laser-eye exposure has the potential to result in ocular injury. For example, it has been well documented that laser eye exposure can cause retinal lesions characterized by cell death, disruption of cellular layers, hypopigmentation, hemorrhage, or even retinal detachment (Birngruber et al. 1983, Leibu et al. 1999, Belokopytov et al. 2005, Lee et al. 2014, Xu et al. 2016). We also know that laser-eye exposure can cause functional loss of vision such as temporary or permanent loss of visual acuity (Weiskrantz and Cowey 1967, Zwick 1984, Glickman et al. 1996, Zwick et al. 1997, 1999, Robbins and Zwick 1999, Lee et al. 2014), decrease in the ability to distinguish objects of similar luminance, or decreased contrast sensitivity (i.e. ability to distinguish an object from the background based on luminance) (Gunduz and Arden 1989, Glickman et al. 1996, Zwick et al. 1999), decreased color discrimination (Robbins et al. 1980, Robbins and Zwick 1996), and impaired ability to track objects (Stuck et al. 1996).

Although the avian eye differs anatomically from the mammalian eye, they both share multiple common features to all vertebrates (Cronin 2014). Therefore, we should expect avian eyes, just like mammalian eyes, to be potentially vulnerable to the damage from monochromatic and minimally divergent laser light (Sliney 1995, Barkana and Belkin 2000). How laser light specifically affects avian eyes is for the most part unknown (Glahn and Dorr 2000). The differences between avian and mammalian eyes could influence how laser light is absorbed, reflected, and transmitted and may affect the energy levels that can cause retinal injury (Gabel and Birngruber 1981, Chen et al. 2011, Tsukahara et al. 2014), making it challenging to extrapolate

current knowledge about the threshold energy at which they would sustain a retinal injury (Geeraets and Berry 1968). For example, birds generally have smaller eyes and shorter focal lengths than non-human primates (Walls 1963, Ross and Kirk 2007, Hall and Heesy 2011). Smaller eyes with shorter focal lengths focus light onto smaller areas of the retina, resulting in potentially higher energy densities impacting the retina. This is exemplified in a study that found the threshold energy needed to produce a lesion in rabbit eyes (axial length approximately 15 mm (Bozkir et al. 1980)) was four times lower than that needed to create a lesion in humans (axial length approximately 25 mm (Norman et al. 2010, Read et al. 2010)) (Gabel and Birngruber 1981). Birds have four classes of single cones and one double cone compared to the three kinds of cones humans have. Additionally, avian cones contain photopigments which have spectral sensitivities that are different from the peak spectral sensitivities of the photopigments in human cones (Wald 1964, Hart 2001, Hart and Hunt 2007). Because of these slightly varying spectral ranges in avian cones, the laser light damage mediated by photopigments may have different effects on select avian photoreceptor types (Wu et al. 2006).

Given the degree to which birds rely on vision to find and consume food (Fernández-Juricic et al. 2004, Gill 2007, Cazetta et al. 2009) and detect predators (Fernández-Juricic 2012, Moore et al. 2013), eye injury or ocular diseases that harm visual function can have a negative impact on a bird's health and wellbeing (Newton 2009). Compensation by other senses may not be sufficient to enable birds to thrive in the conditions (Collin 1999, Martin 1999) or participate in activities such as flying that are crucial to their survival (Cousquer 2005, Korbel 2011). In the case of birds that are referred to wildlife rehabilitation centers after ocular trauma, individuals with monocular damage position themselves so that the unaffected eye is directed towards objects of interest and may make critical flight errors by missing perches or flying into walls (Pauli et al. 2007). Similarly, birds with cataracts may be reluctant to fly or crash into objects when they do (Slatter et al. 1983), and exhibit weight loss and lethargy (Moore et al. 1985). Foraging behavior and movement were both affected in birds with the ocular virus, conjunctivitis. Infected birds stayed at food patches for longer periods of time and had decreased feeding efficiency compared to non-infected birds (Hotchkiss et al. 2005).

Due to the emergence of lasers as established avian deterrents, it is essential that we understand how laser eye exposure can affect the ability of animals to seek and consume food. Our goal was to assess how exposure to the laser as well as the energy level of that exposure would

affect avian visual exploratory behavior for the purpose of foraging as well as food consumption. This study is the first to assess the effects of laser on avian behavior under controlled conditions, allowing us to establish cause-effect relationships. Our overall a-priori prediction was that laser exposure could impair vision (see above) and consequently modify the way birds seek visually and consume food. However, we did not have directional predictions for the different behavioral dimensions studied (see Methods) and consequently our study should be considered exploratory rather than confirmatory.

METHODS

We captured a total of 40 House sparrows (Passer domesticus) in West Lafayette and Lafayette, Indiana using potter traps from August 2017 to February 2018. We transferred all birds using soft bags to the indoor Purdue University animal care facility within 12 h of capture. There, we banded them, recorded sex and age, and randomly assigned them a laser exposure energy. Of the 40 house sparrows, 7 were adult females, 10 were juvenile females, 13 were adult males, and 10 were juvenile males. We housed up to six birds in 61 × 61 × 76 cm mesh-wired enclosures under a 14-h light/10-h dark light cycle. We made water (with vitamins) available to them ad libitum and gave each bird a standard Petri dishes (110 mm X 30 mm) with 80 g food mix per day. Food mix consisted of Purina game bird chow maintenance formula, black oils sunflower seeds, millet, and dried meal worms. All housing conditions and protocols were approved by the Purdue Animal Care and Use Committee (protocol number 1707001594)

The experiment consisted of five parts: 1) Training, 2) Before exposure trials, 3) Laser exposure, 4) Within week 1 after exposure trials, 5) Within week 2 after exposure trials. All trials used the same experimental paradigm. We designed a food patch by modifying a standard Petri dish (110 mm x 30 mm) with a transparent plastic barrier wrapped around 2/3 of the dish perimeter. The barrier was made by cutting the plastic into triangular points to encourage birds to land on the unobstructed portion of the dish. We filled the dish with 32 g of plastic beads so that the clear plastic bottom was not visible. Plastic beads were brand TOHO, could be bought in many different colors, were size 11/0, hole size 0.7 mm, and were approximately the size of a single white millet seed. We then evenly dispersed 15 white millet seeds on top of the bead substrate. By manipulating the color of the plastic bead substrate, we changed the contrast between the background substrate and the millet food items according to house sparrow contrast sensitivity calculated in a previous study (Ensminger and Fernández-Juricic 2014). We chose to manipulate chromatic contrast due to the importance of chromatic cues versus achromatic cues during avian foraging (Stuart-Fox et al. 2004, Cazetta et al. 2009, Lind et al. 2013). We used this paradigm to evaluate birds' visual behavior as they searched for food under different contrast conditions.

Training

We trained birds how to forage for millet seed from a background substrate to prepare them for the behavioral trails. Six randomly chosen birds were housed in one cage for two consecutive days before the pre-exposure trials. When the lights went off at 21:00, we removed the six food patches containing food mix from the cage and weighed them. Lights turned back on at 7:00. We returned the six food patches to the cage at 11 AM with 32 g highly contrasting black TOHO seed beads (size 11/0, hole size 0.7 mm) and between 10 and 30 millet seeds to acclimate birds to finding food on plastic substrate. There were 39 JNDs contrast difference between the black TOHO seed beads and the millet seeds according to the contrast sensitivity of house sparrows. (See Appendix A) We then left the room for 15 min to allow them to forage. When we returned to the room, we evaluated the success of the birds by noting if the millet seeds were eaten or remained untouched. If 50% or more of millet seeds were untouched, we considered this a failure and immediately gave birds a second chance. After the second try, we weighed each bird and replaced the beads with 80 g of food mix. We repeated this process the following day. After the second day of training for all bird groups, all food patches had at least 50% or more millet seeds eaten, and birds were considered ready to proceed to pre-exposure trials.

Before exposure trials

In order to assess baseline foraging behavior, birds completed two pre-exposure trials. After two days of training, we transferred the six birds to individual cages in an experimental room. This room contained six 0.61 x 0.61 x 0.76 m mesh-wired enclosures designed specifically for our experimental procedure. One side of the enclosure consisted of a 3.175 mm thick piece of acrylic, UV transparent Plexiglas. This Plexiglas wall allowed for us to video tape the bird using a camera (JVC GZ-E10BUS high definition camcorder) secured on the other side of the Plexiglas. The camera was secured at 8 cm from the bottom of the cage and flush with the Plexiglas. Food patches were placed in the cage so that birds could land on the smooth portion of the dish and face the Plexiglas wall and camera. On top of the cage was a full spectrum light (BluemaxTM Prolumne T8 fluorescent tubes, Model #109212, Full Spectrum Solutions, Inc., Jackson, MI). The wire side of the enclosure opposite the camera was covered by a black curtain to create a contrasting backdrop. The remainder of the enclosure was covered with white curtain to limit visual and

audible distractions for the birds. (See Appendix B for experimental cage setup) We placed all lights on a 12 hr light / 12 hr dark cycle from 0830 to 2030.

Birds were food deprived overnight by removing the food patches from the cages at 20:30 and weighing the food. Lights turned back on at 8:30 and we began experimental trials at 9:00. The birds were tasked with finding 15 millet seeds on a substrate of TOHO seed beads of either "high" or "low" chromatic contrast and exhibited similar achromatic contrasts. The high contrast treatment was the "silver" substrate (TOHO gold lustered grey seed bead, size 11/0, hole size 0.7 mm) which was 34 JNDs contrast between the millet seed. The low contrast treatment was the "gold" substrate (TOHO frosted gold-lined crystal seed bead, size 11/0, hole size 0.7 mm) and was 6 JNDs contrast between the millet seed. Each bird was randomly assigned either the high or low ("silver" or "gold") seed visual contrast and completed one trial per day. (See Appendix A) We left the room and video recorded the trial for 15 minutes, then retrieved the food patches and recorded the number of seeds eaten by the bird. We continued this process for each bird. If birds did not participate (i.e. 0 seeds eaten), we allowed them to make another attempt. If birds did not participate in the trial by 13:00 they were removed from the experiment. After all willing birds completed their trial, we weighed each bird and returned the food patches to the cages with 80g of food mix. We repeated these procedures for a second night/day but presented individuals with the substrate (either high seed visual contrast or low seed visual contrast) they were not given in the first trial. By holding the second trial the next day as opposed to later the same day, we were able to keep the hunger level and motivational conditions of both trials consistent.

Laser Exposure

After the second pre-exposure trial, we weighed and transferred them individually to another room in the Purdue animal care facility. We administered 20 µL of refrigerated rocuronium bromide to each eye to dilate the bird's pupils. This dosage was recommended by Dr. Townsend of Purdue University Veterinary Hospital. It took approximately 30 min for pupils to fully dilate. Birds were then anesthetized to eliminate small ocular movements which could alter the amount of laser light entering the eye (Lund 2019) and to reduce stress. We readied a syringe with a previously prepared anesthesia solution containing midazolam, ketamine, and xylazine. We initially based our dosage off (Velez et al. 2015), but adjusted it to 4 mg/kg midazolam, 8 mg/kg ketamine and 2 mg/kg xylazine. Using an aseptic technique and training from Purdue animal care and use committee, we

injected this dose into the bird's breast muscle. We gently transferred anesthetized birds to a different room inside a bag on a microwaved heating pad and several layers of towels.

The room was set up with the help and approval of Purdue REM and all persons in the room followed proper safety protocol by donning safety eyewear appropriate for the laser we were using. Multiple laser models are currently available to scare birds a safe distance away from potentially hazardous structures or undesirable areas such as Bird-X laser (https://bird-x.com/bird-products/lasers), Agrilaser Handheld (https://www.birdbgone.com/agrilaser-handheld-laser-bird-deterrent/), Fly Away Laser (https://birdbarrier.com/fly-away-laser.html), Desman rifle (http://www.desman.fr/products.htm), and Seabird Saver (https://www.seabirdsaver.com/). All emit wavelengths that we perceive as either red or green light and are continuous wave lasers, which means they deliver a constant energy. Class II lasers emit powers below 1mW and are not considered a hazard when viewed for 0.25 seconds (the human aversion response) or less (ICNIRP 2000, Ziegelberger 2013b, American National Standards Institute 2014). Class IIIA lasers include any devices that emit between 1 and 5 mW power. Class IIIB lasers are those that range from 5-500mW power and can be hazardous if viewed directly for any period of time. However, there are lasers available that exceed 500 mW, such as the laser prototype used in our study. Lasers operating over 500 mW are labelled as class IV and are considered by OSHA to be hazardous under any viewing condition, including diffuse viewing and viewing of reflections (OSHA Technical Manual (OTM) | Section III: Chapter 6 - Laser Hazards | Occupational Safety and Health Administration n.d., ICNIRP 2000, American National Standards Institute 2014). The laser, a prototype of the Seabird Saver (https://www.seabirdsaver.com/), had adjustable wattage(0-1000mW), had a beam diameter of 4cm at the aperture, beam divergence of 0.5mrad, gaussian beam shape, and 532 nm wavelength. The laser was taped securely on a table and fitted with a "Thor labs 1-inch optical beam shutter" and shutter controller attached so the new laser aperture was 1 in or 2.54 cm. Exactly one m from the laser aperture, we placed a power sensor (Ophir 30A-BB-18 power sensor). We visually aligned the center of the power sensor with the laser beam by adjusting the height of the meter and moving the meter either left or right. When the reading from the power meter (Ophir Vega laser power meter) was the power desired for exposure, we marked the location of center of the meter then moved the power meter approximately six cm directly backward. (see Appendix C laser exposure setup)

We strapped each bird into a foam cradle using Velcro straps and secured their feet. We placed the restrained bird on the marked location in front of the power meter and exactly one m from the laser aperture such that one eye of the bird was centered with both the power sensor and laser beam. The eye facing the beam was temporarily secured open. We exposed the bird to the appropriate power level and duration three times. We chose three exposures in order to replicate the likely conditions birds would experience in the field (Ed Melvin personal communication). We waited three seconds between exposures (recommended by Bruce Stuck Director of the Ocular Trauma Research Division at the U.S. Army Institute of Surgical Research in San Antonio, Texas until 2013) in order to prevent possible additive effects (Thomsen 1991, Lund and Sliney 2014) and repeated this on the opposite eye. After both eyes were exposed, we removed the bird from the cradle and placed it back in the bag over a warmed pad to maintain its body temperature. We monitored birds until they were awake (between 30 min and 3 h) and returned them to their individual cages with 80 g food and water.

We used an experimental regression (Lovell 2016, Briner and Kirwan 2017) design that would allow us to see potential non-linear affects in laser damage (Gerstman et al. 1996, Schulmeister et al. 2008). Each bird was exposed to a single energy. Under both time and resource constrictions, we limited our sample size to a total of 40 birds, each exposed to an incrementally different laser energy. Because no previous studies have determined laser injury thresholds in birds, we based our range of energies on the accepted human laser safety guidelines which are based on threshold data from controlled experiments mostly in non-human primates. In these experiments, the eye is exposed to incremental dosages and evaluated directly for signs of damage. The threshold for laser damage is the dose at which an individual has a 50% probability of having damage. This median dose is also known as the ED50, is the basis of other safety guidelines such as the Maximum Permissible Exposure (MPE) which is one tenth of the ED50. Detailed guidelines on the safe exposure to lasers have been published by both the American Nations Standard for Safe Use of Lasers and the International Commission on Non-Ionizing Radiation Protection. According to these guidelines, the MPE of continuous wave lasers which are 400-700nm for exposure times between 5μs and 10s can be calculated by the following formula:

$$MPE = 1.8 * t^{0.75} \frac{mJ}{cm^2}$$

According to this formula, the MPE of the laser we tested will depend on the time of exposure. We used 7 different durations of exposure (0.1, 0.25, 0.4, 0.55, 0.7, 0.85, 1.0 s) to reflect common exposure durations found in the literature, and the realistic exposure durations to birds in the field (personal communication Ed Melvin). We calculated an MPE for exposure times of 0.1s and 1 s to understand what the maximum range of corneal irradiances in mJ/cm2 would be. However, these values represent the range of MPEs for a human eye with a pupil size of 7mm. We corrected the MPEs for a house sparrow pupil size of 4mm by multiplying by the ratio of the human pupil area to the house sparrow pupil area. This gave us the maximum permissible exposure of laser irradiance to a house sparrow eye for exposures ranging from 0.1 to 1 second. We wanted to know where the threshold of laser eye injury was for birds, so we converted MPE, a safety guide, to ED50, the injury threshold. As stated previously, MPE is estimated to be about 10 times lower than the threshold energy, so we multiplied our estimated MPE irradiances by 10. Lastly, we divided these irradiances by three because we wanted to expose house sparrows three consecutive times. Based on these calculations, we estimated threshold of laser eye injury for house sparrows to three laser exposures of 0.1 to 1 second to be 3.27-18.38 mJ/cm2. This predicted range of ED50s gave us a guide to which irradiances to expose birds to in order to find the actual threshold of eye injury in birds. To clearly see where the threshold was, we decided to expose birds to irradiances that were both approximately 3 times below the lowest predicted ED50 and 3 times higher than the highest predicted ED50.

We calculated the corneal irradiances using the formula below:

$$\left(\frac{\text{Power } mW}{\text{Beam Area at Cornea } cm^2}\right) * \text{Time } s = \text{Corneal Irradiance} \frac{mJ}{cm^2}$$

This formula was modified from those in the ICNIRP and ANSI guidelines (Protection 2013). It is important to note that laser prototype diameter was 4 cm, but we used a shutter with smaller diameter of 2.54 cm and therefore 2.54 cm was used to calculate the beam area at the cornea. We assumed beam size did not change from the aperture to the cornea due to the low beam divergence (0.5 mrad). Using this formula, we substituted 7 different power levels (60, 90, 130, 165, 200, 235, 270 mW) and to calculate 49 different irradiances ranging from 1.18-53.3 mJ/cm^2. In order to compare threshold values to thresholds in the literature, we also converted the corneal irradiances to total intraocular energies (TIEs) by multiplying the irradiance by the area of the house sparrow pupil. Predicted ED50s adjusted for the house sparrow pupil ranged from 1.26-7.07

mJ/cm^2 and the TIEs we planned to expose birds to spanned from 0.15 to 6.71 mJ/cm^2 (0.15, 0.24, 0.32, 0.37, 0.41, 0.50, 0.58, 0.59, 0.60, 0.67, 0.81, 0.82, 0.94, 1.02, 1.04, 1.24, 1.27, 1.29, 1.30, 1.46, 1.49, 1.64, 1.65, 1.67, 1.77, 1.98, 2.00, 2.25, 2.26, 2.33, 2.36, 2.68, 2.73, 2.74, 2.86, 3.21, 3.22, 3.47, 3.48, 3.68, 4.08, 4.09, 4.22, 4.69, 4.95, 4.96, 5.69, 5.83, 6.70 mJ/cm^2). However, due to logistical and time constraints our sample size was only 40 birds and each bird was randomly assigned to a laser energy. The energy range the birds were exposed to was actually 0.15 to 5.7 mJ/cm^2 (0.15, 0.24, 0.32, 0.37, 0.41, 0.58, 0.59, 0.60, 0.67, 0.82, 0.94, 1.02, 1.04, 1.27, 1.29, 1.30, 1.46, 1.49, 1.64, 1.65, 1.67, 1.77, 1.98, 2.00, 2.25, 2.26, 2.33, 2.36, 2.68, 2.74, 2.86, 3.22, 3.47, 3.68, 4.08, 4.22, 4.69, 4.95, 4.96, 5.69 mJ/cm^2).

After Exposure Trials

The birds participated in the after-exposure trial following the same procedure as the before-exposure trials approximately 24 h after laser exposure, and again the day after that, approximately 48 h after exposure. We called these two trials "within week 1" trials. Seven days after the laser exposure the birds participated in another after-exposure trial. On the eighth day after-exposure, the birds completed the last trial. Three of the 40 birds participated in second after-exposure trail on the tenth day after-exposure due to errors in planning. We called these two trials "within week 2" trials. Afterward we weighed each bird and humanely euthanized. Birds were sacrificed by flooding a chamber with CO2 and placing the them in chamber until breathing has ceased. To ensure death we performed a cervical dislocation.

We compiled the 15 min videos from the six foraging trials all birds participated in: foraging trials at both high and low seed visual contrast before exposure, within week 1, and within week 2 after exposure. Using the program BORIS (Friard and Gamba 2016), we developed an ethogram to analyze bird behavior and used the frame by frame function to record behavior every 0.033 s for 30 s (see full list of behaviors coded in Table 1: Appendix D). This 30 s started from the moment the bird arrived at the food patch (both feet contact platform or dish) and only included time the bird remained at the food patch. During the 30 s, we recorded pecks (beak moves toward and makes contact with substrate), seeds eaten (seed seen in bird's beak, chewing, and possibly husk flying), changes in head position, and when the bird left the food patch (both feet no longer in contact with platform or dish). We recorded the bird's head position at the first clear frame after a bird had changed head position and classified the position as either binocular vision, binocular-

foveal vision, foveal vision, or scanning based on previous work done describing the visual field and foraging behavior of house sparrows (Fernández-Juricic et al. 2008, Dolan and Fernández-Juricic 2010, Ensminger and Fernández-Juricic 2014). We considered scanning (Fig 1a) as a combination of two separately coded head positions: 1. the bird's beak was below horizontal plane but not projecting into the food patch and 2. the bird's beak was above the horizontal plane. The other visual behaviors were chosen in order to interpret how birds were visually exploring the food patch. Foraging head positions included binocular vision, binocular-foveal vision, and foveal vision. We defined foveal vision as the fovea of one eye projecting into the food patch (Fig. 1b), binocular-foveal vision as the fovea of one eye and the binocular field projecting into the food patch (Fig. 1c), and binocular vision as the binocular field projecting into the food patch with the bird's head not tilted (Fig. 1d). To be clear, binocular-foveal vision is not the combination of binocular and foveal vision, but rather its own head position based on the projection of both a fovea and the binocular field into the food patch. If the bird was using foveal or binocular-foveal vision, we coded which eye the bird was using due to the body of evidence that birds use left and right eyes differently depending on the task (Franklin and Lima 2001, Templeton and Gonzalez 2004, Martinho III et al. 2014, Beauchamp 2015a, Butler et al. 2018).

After we scored the videos, we used Boris' "time budget" analysis tool to export the data to Microsoft Excel in individual files, one per trial per bird. Each data file contained the number of times a behavior occurred and the duration of each behavior. From this, we calculated the rates of pecking (pecks per min), seed consumption (seeds eaten per min), scanning (scans per min), binocular-foveal vision including left and right eye (times using binocular-foveal vision per min), and foveal vision including left and right eye (times using foveal vision per min). We were also able to calculate the percent of time birds spent using binocular vision and binocular-foveal vision (left and right eye) during the 30 sec we recorded them participating. In addition to the exported data, we recorded the total number of seeds birds consumed after the 15 min trial to calculate giving-up density. Giving-up density was the number of seeds eaten after the total 15 min trial. Lastly, we recorded the time each trial began and time the bird first arrived at the food patch to calculate latency. Latency was calculated by subtracting the time the bird arrived at the food patch from the time of the start of the trial.

Statistical analysis

We divided our statistical analyses in two sections: laser exposure effects and laser energy effects. In the laser exposure effects section, we focused on how different behavioral responses of house sparrows varied after laser exposure and between two time points after laser exposure (within week 1, within week 2) compared to before laser exposure (considering as well the effects of seed visual contrast and visual field when appropriate). In this section we did not consider the effects of different laser energy levels because in the before laser exposure treatment, individuals had not exposed to any laser energy level by design. In the laser energy effects section, we were interested in assessing the effects of energy levels relative to the other factors studied (considering seed visual contrast and visual field when appropriate) by leaving out the before laser exposure treatment and only including both after laser exposure treatments (within week 1, within week 2).

In both sections, we used general linear mixed models ran with the R package afex (Singmann et al. 2019). We analyzed the following dependent variables: latency to visit food patch (sec), percent of time using binocular vision, percent of time using binocular-foveal vision, binocular-foveal vision rate (events per min), foveal vision rate (events per min), pecking rate (events per min), seed consumption rate (events per min), seed giving-up density (i.e., number of seeds left at the end of the trial), scanning rate (events per min). We checked for the homogeneity of variance and normality of the error assumptions; the majority of the models met these assumptions, but a couple of them had minor deviations. We decided not to transform the data to facilitate the detection of interaction effects, which may be masked with some transformations (Gotelli & Ellison 2012). In all models, individual was included as a random factor. In the laser exposure effects section, for most of the dependent variables, we considered two within-subject factors: laser exposure (before, within week 1 after, within week 2 after) and seed visual contrast (low, high) and their interaction. For percent of time using binocular-foveal vision, binocular-foveal vision rate, and foveal vision rate, we considered a third within-subject factor (visual field; right, left), and all interactions between factors, to assess potential visual laterality effects when inspecting the food patch. Following (Singmann and Kellen 2019), we assessed random structures with different level of complexity (from more to less complex) until the models would converge. From this process, we chose the following random structures for models with two and three within-subject factors: (within-subject factor a + within-subject factor b || bird id; indicating by bird id random intercepts and by bird id random slopes for within-subject factor a plus within subject-

factor b without correlations between the intercepts and slopes) and (within-subject factor a + within-subject factor b + within-subject factor c || bird id; indicating by bird id random intercepts and by bird id random slopes for within-subject factor a plus within subject-factor b plus within subject-factor c without correlations between the intercepts and slopes), respectively.

In the laser energy effects section, for most of the dependent variables, we considered two within-subject factors (laser exposure (within week 1 after, within week 2 after) and seed visual contrast (low, high)) along with laser energy (continuous) and their interactions. We chose the two within-subject factor random structured described above. For percent of time using binocular-foveal vision, binocular-foveal vision rate, and foveal vision rate, considering a third within-subject factor (visual field; right, left) along with the continuous factor energy level and all the interactions prevented these complex models from converging. Therefore, for these three behavioral responses, we only included the within-subject factors that turned out to be significant in the laser exposure effects section, laser energy, and their interactions. Two of these models had a single within-subject factor, leading to the following random structure: (within-subject factor a || bird id; indicating by bird id random intercepts and by bird id random slopes for within-subject factor a without correlations between the intercept and slope). Laser energy was centered around 0 before running the general linear mixed models following Zuur et al. (2015).

We used R package emmeans (Lenth et al. 2019) to estimate the means and SEs for different treatment values. We also used R package afex (Singmann et al. 2019) to plot the effects of one or two within-subject factors using the function afex_plot, which considers the random bird id effects for the estimation of the means and SEs. We used the R package interactions (Long 2019) to plot the interactions between categorical and continuous factors using the function interact_plot, which portrays the predicted lines with 95% confidence bands. To make all these statistical analyses and figures reproducible, we included the R code in Appendix E.

RESULTS

Laser exposure effects

The latency of house sparrows to visit the food patch right after the trials began was significantly affected by laser exposure (Table 1; Fig. 2a), but we did not detect a significant effect of seed visual contrast or its interaction with laser exposure and trial order (Table 1). Individuals approached the food patch faster within week 1 after exposure than they did before laser exposure (z ratio = 2.89, P = 0.011; Fig. 2a) and faster than within week 2 after exposure (z ratio = -2.83, P = 0.013; Fig. 2a). There was no significant difference in latency between before and within week 2 after laser exposure (z ratio = -0.06, P = 0.998; Fig. 2a).

House sparrows changed the percentage of time using binocular vision when exploring the food patch relative to laser exposure (Table 1, Fig. 2b). The percentage of time allocated to binocular vision decreased significantly within week 1 after laser exposure compared to before exposure (z ratio = 1.94, P = 0.016; Fig. 2b); however, no significant differences were detected between within week 2 after exposure compared to before exposure (z ratio = 1.06, P = 0.323; Fig. 2b). Furthermore, we did not detect significant differences in the use of binocular vision between within week 1 and within week 2 after exposure (z ratio = -0.88, P = 0.422). Seed visual contrast and its interaction with laser exposure, along with trail order, were not significant (Table 1).

Both the percent of time house sparrows allocated to looking at the food patch with binocular-foveal vision and the rate of at which they used binocular-foveal vision when looking at the food patch were both influenced significantly by the independent factor, visual field (i.e. right or left eye) (Table 1). Individuals spent more time (right visual field, 4.95 ± 0.50 % of total time by food patch; left visual field, 7.33 ± 0.50 % of total time by food patch) and looked more often (right visual field, 10.20 ± 0.95 events/min; left visual field, 15.50 ± 0.95 events/min) with the left than the right visual field, irrespective of laser exposure and seed visual contrast (Table 1). Additionally, trial order significantly affected the percent of time using binocular-foveal vision (Table 1), which was higher in the first (6.65 ± 0.37 %) than in the second (5.63 ± 0.37 %) trial within a given laser exposure treatment (before, within week 1, within week 2).

The rate at which house sparrows looked at the food patch with foveal vision was significantly affected by the visual field as well as the interaction between laser exposure and

visual field (Table 1). Individuals used left foveal vision (13.69 ± 0.88 events/min) more often than right foveal vision (7.69 ± 0.88 events/min). Interestingly, this visual field effect was a function of laser exposure (Fig. 3a); such that before laser exposure there was not significant difference in foveal vision rate between visual fields (z ratio = -1.82, P = 0.070), but the increase in left relative to right foveal vision rate took place within week 1 (z ratio = -4.92, P < 0.001) and within week 2 (z ratio = -5.03, P < 0.001) after laser exposure (Fig. 3a).

The rate at which house sparrows pecked at seeds was affected significantly by laser exposure (Table 1; Fig. 2c), but we did not detect a significant effect of seed visual contrast or its interaction with laser exposure (Table 1). Individuals had higher peck rates within week 1 after than before laser exposure (z ratio = -2.97, P = 0.008) as well as within week 2 after than before laser exposure (z ratio = -2.35, P = 0.049; Fig. 2c). We did not find a significant difference in peck rate between within week 1 and within week 2 after laser exposure (z ratio = 0.15, P = 0.988; Fig. 2c).

The rate at which house sparrows consumed seeds at the beginning of the trial was significantly affected by both laser exposure and seed visual contrast, but not by their interaction (Table 1). House sparrows consumed more seeds per min within week 1 after than before laser exposure (z ratio = -3.40, P = 0.002) and within week 2 after than before laser exposure (z ratio = -2.69, P = 0.020; Fig. 2d). We did not find a significant difference in seed consumption rate between within week 1 and within week 2 after laser exposure (z ratio = 0.20, P = 0.978; Fig. 2d). Additionally, house sparrows consumed more seeds per min in the high (20.2 ± 1.0 events/min) than in the low (22.4 ± 1.0 events/min) seed visual contrast treatment (Table 1). Despite this variation in seed consumption rate, seed giving-up densities did not vary with any of the studied factors (Table 1)

House sparrows scanning rate was affected significantly by both seed visual contrast and the interaction between laser exposure and seed visual contrast (Table 1). Individuals scanned at a lower rate when seeds were more visually challenging to perceive (i.e., low visual contrast, 45.30 ± 1.60 events/min) than when they were more easily distinguished from the visual background (i.e., high visual contrast, 50.0 ± 1.6 events/min). However, this effect was a function of laser treatment due to the significant interaction effect (Fig. 3b). There was no significant difference in scanning rate between seed visual contrast treatments before laser exposure (z ratio = 0.33, P = 0.742), but the higher scanning rate in high compared to low seed visual contrast conditions

occurred within week 1 (z ratio = -2.82, P = 0.005) and within week 2 (z ratio = -3.11, P = 0.002) after laser exposure (Fig. 3b).

Laser energy effects

After house sparrows were exposed to the laser, their latency to visit the food patch was significantly affected by laser exposure (higher within week 2 after, 186 ± 32 secs, than within week 1 after exposure, 101 ± 32 sec; Table 2), but also by the 3-way interaction among laser exposure, contrast, and laser energy (Table 2, Fig. 4a). Within week 1 after laser exposure, the latency to visit the food patch did not seem to vary with energy at high seed visual contrast, but at low seed visual contrast (i.e., seeds were more difficult to detect) animals that had been exposed to higher laser energies tended to arrive sooner to the food patches (Fig. 4a). However, this pattern changed within week 2 after laser exposure, such that at low seed visual contrast, latency to visit the food patch increased with higher laser energy exposure, whereas at high seed visual contrast, latency decreased with higher laser energy exposure (Fig. 4a).

After laser exposure, the percentage of time house sparrows spent looking at the food patch with their binocular vision was not affected significantly by laser energy or any of the other factors considered (Table 2). Additionally, as reported in the previous section, the percent of time, as well as the rate, individuals allocated to looking at the food patch with binocular- foveal vision was significantly influenced by visual field (Table 2), but we did not detect a significant effect of laser energy (Table 2). House sparrows spent more time (right visual field, 4.67 ± 0.58 % of total time by food patch; left visual field, 7.32 ± 0.58 % of total time by food patch) and looked more often (right visual field, 9.99 ± 1.18 events/min; left visual field, 16.24 ± 1.18 events/min) with the left than the right visual field.

After house sparrows had been exposed to the laser, the rate they looked at the food patch with foveal vision was significantly affected by the visual field as well as the interaction between visual field and laser energy (Table 2). As reported in the previous section, left foveal vision (14.58 ± 0.99 events/min) was used at a higher rate than right foveal vision (6.96 ± 0.99 events/min). However, this effect was a function of the laser energy animals had been exposed to, such that the degree of difference in the use of left relative to right foveal vision increased with the energy of the laser exposure (Fig. 4b).

Seed pecking rate, after laser exposure, was affected significantly by seed visual contrast as well as the interaction among laser exposure, seed visual contrast, and laser energy (Table 2). Individuals had higher pecking rates when the seeds were more visually contrasting (i.e., high seed visual contrast, 31.10 ± 2.03 events/min) than when they were less visually contrasting (i.e., low seed visual contrast, 27.80 ± 2.03 events/min). However, this effect was a function of the timing of laser exposure and its energy levels (Fig. 5a). Within week 1 after exposure, the bias towards higher pecking rates in the high seed visual contrast treatment was more pronounced for those individuals that had been exposed to higher laser energy levels (Fig. 5a). Within week 2 after exposure, the bias towards higher pecking rates in the high seed visual contrast treatment occurred for those individuals exposed to lower laser energy levels, but at higher energy levels, the bias flipped towards increased pecking rates in the low seed visual contrast treatment (Fig. 5a).

Furthermore, seed consumption rate after laser exposure was affected significantly by seed visual contrast as well as the interaction among laser exposure, seed visual contrast, and laser energy (Table 2). House sparrows had higher seed consumption rates when the seeds were more visually contrasting (i.e., high seed visual contrast, 22.10 ± 1.23 events/min) than when they were less visually contrasting (i.e., low seed visual contrast, 19.10 ± 1.23 events/min). However, this effect was a function of the timing of laser exposure and its energy levels (Fig. 5b). Within week 1 after exposure, the bias towards higher seed consumption rates in the high seed visual contrast treatment was more pronounced for those individuals that had been exposed to higher laser energy levels (Fig. 5b). Within week 2 after exposure, the bias towards higher seed consumption rates in the high seed visual contrast treatment occurred for those individuals exposed to lower laser energy levels, but at higher energy levels, the bias flipped towards increased seed consumption rates in the low seed visual contrast treatment (Fig. 5b). Notwithstanding the variation in seed consumption rates, seed giving-up densities did not vary significantly with any of the studied factors (Table 2).

After animals were exposed to the laser, their scanning rates were only significantly affected by seed visual contrast (Table 1), as reported before, but not by laser energy. House sparrows scanned more under the high seed visual contrast (52.2 ± 1.9 events/min) than the low seed visual contrast (44.9 ± 1.89 events/min) treatments.

DISCUSSION

As the use of lasers for deterring birds becomes more widespread (Bishop et al. 2003, Vantassel and Groepper 2015, Atzeni et al. 2016), it is critical to understand their effects on avian behaviors that can indirectly affect their survival. While previous studies have documented bird avoidance and movement in response to laser exposure (Glahn and Dorr 2000, Werner and Clark 2003, Cassidy 2013, Atzeni et al. 2016, Gorenzel et al. 2016), our study is the first to investigate the direct effects of laser exposure on bird visual and foraging behavior through a manipulative approach in a controlled environment. After being exposed to the laser, house sparrows approached the food patch quicker, reduced their use of binocular vision, developed a bias for using the left eye when visually exploring the food patch, increased pecking rate, and changed scanning rates depending on how conspicuous seeds were. These behavioral modifications after laser exposure are consistent with the idea that lasers could damage the eye, resulting in changes in visual function while foraging.

In studies that exposed mammalian eyes to lasers, behavioral tests show a loss of visual function due to eye injury that may or not be detected (Zwick 1989, Zwick et al. 1994, Robbins and Zwick 1996). How long an injury takes to develop after laser exposure depends on the damage mechanism: thermal or photochemical (Barkana and Belkin 2000, Glickman 2002). Thermal damage occurs when energy from a particular wavelength is absorbed by a chromophore in a cell and temperature in the cell increases faster than it can be dissipated (Thomsen 1991, Barkana and Belkin 2000). Temperatures rising in the cell causes protein denaturation and coagulation and leads to loss of cell structure or cell death (Birngruber et al. 1985, Thomsen 1991). Photochemical damage is caused by long exposures of shorter wavelengths at low energy levels that do not increase cell temperature. Instead, these exposures induce chemical reactions that break down nucleic acids and lead to cell death over time (Barkana and Belkin 2000, Glickman 2002, Wu et al. 2006). Due to the complex nature of tissue and energy interaction, there is no clear boundary between the energies at which thermal and photochemical damage mechanisms operate, and instead there is thought to be exposure conditions where both damage mechanisms are operating (Zwick 1984, Robbins 1992, Glickman 2002, Denton et al. 2007, Pocock et al. 2014). Subsequent morphological and structural injury due to both thermal and photochemical laser damage develops over hours to days (Moon et al. 1978, Matylevitch et al. 1998, Glickman et al. 2007), and functional

changes in the eye could manifest as changes in visual behavior over longer periods of time(Zwick 1989, Zwick et al. 1997, DiCarlo et al. 2006). For instance, Robbins, 1997 noted an increase erratic behavior and variability in visual acuity for days and even weeks after laser exposure in rhesus monkeys.

In our study, we found changes in foraging and visual behavior that are contingent on the time since the laser exposure. House sparrows change how quickly they arrive to the food patch after laser exposure depending on the time since exposure. Birds arrived quicker to the food patch within week 1 after laser exposure. One explanation for this is that laser exposure could have affected house sparrow visual acuity. House sparrow visual acuity is 4.88 cycles/degree (Dolan and Fernández-Juricic 2010), meaning individuals can see a 2 mm millet seed from over 1 m. The food patch was placed approximately 0.60 m away from the perch, well within their range of visual acuity. Acute damage to the retina like retinal edema or swelling of the retinal tissue (Powell et al. 1971, Tso 1973, Robbins 1997, Barkana and Belkin 2000, Paulus et al. 2008) could cause functional deficits (Randolph et al. 1983, Schmeisser 1990) like visual acuity (Zwick 1984, Robbins 1997). A systematic review of case studies in which 111 patients were evaluated for laser-eye injury from continuous wave laser pointers revealed that of these 111 patients, 55% had visual acuity deficits of 50-95% at initial presentation (Birtel et al. 2017). A similar reduction in visual acuity would have consequences for a house sparrow's ability to visually explore the food patch. A 50% reduction in visual acuity would result in a house sparrow only being able to see a 2 mm millet seed from 0.56 m and a 95% reduction in visual acuity would result in a house sparrow only being able to see 2 mm millet seed from 5.6 cm. A reduction in visual acuity may have decreased latency if birds had to get closer to the food patch to resolve visually the presence of seeds compared to unexposed birds who should have been able to resolve the seeds from the perch.

Within week 2 after laser exposure, the time it took birds to approach the food patch returned to normal. This behavioral change after 7-10 days could be a result of functional improvements in visual acuity after injury to the eye begins to heal. In a study of the recovery of laser eye injury in rats, injuries were at their worst 24-48 hours after exposure and the healing process began 72 hours after exposure (Belokopytov et al. 2005). Another study reports that intense lesions in rabbits were reduced to 54% of their original size 1 full week after laser exposure (Paulus et al. 2008). Morphological change to photoreceptors correlates with some functional measures like acuity (Weiskrantz and Cowey 1967, Zwick et al. 1982), and improvements in visual

acuity following laser exposure have been well documented (Zwick 1984). Therefore, house sparrows may have sustained a retinal injury that depressed visual acuity within week 1 following exposure, but improved within week 2 after exposure, when the injury started healing.

Alternatively, reduced latency within week 1 after laser exposure could be due to stress after laser exposure and anesthesia (i.e., birds were anesthetized for laser exposure). Anesthesia is known to create oxidative stress (Kotzampassi et al. 2009) and increase stress hormones (Zahl et al. 2010). Acute stressors, like the handling house sparrows experienced during laser exposure, can elicit a release of the stress hormone corticosterone. Elevated corticosterone could have impacts on activity patterns such as increased exploration and perch hopping (Haller et al. 1997, Breuner et al. 1998, Wingfield and Kitaysky 2002). However, the activation of an acute stress response usually lasts only minutes after an event like capture (Romero et al. 1997, Rich and Romero 2005), and although a study on Japanese quail found that birds had elevated stress hormones 24 hrs after handling (Malisch et al. 2010), it was the first one to do so for an avian species.

While birds arrived at the food patch quicker within week 1 after exposure, how quickly a bird approached the food patch was also affected by the interaction among laser exposure, seed visual contrast, and laser energy. We posit that latency to visit the food patch decreases after laser exposure because birds may not be able to see the seeds in the food patch from the perch and therefore need to approach the food patch sooner to confirm the presence of seeds. This is in alignment with what we see within week 1 after exposure where birds tended to arrive quicker to food patches with low seed visual contrast (i.e. the more difficult task) as laser energy increased. As birds are exposed to higher energies, we assume the physical damage to their retinas increases (Barkana and Belkin 2000). As damage to the retina increases, we assume functional deficits in vision, such as visual acuity, increase as well (Weiskrantz and Cowey 1967, Zwick et al. 1982, Robbins 1997, Ben-shlomo et al. 2006, DiCarlo et al. 2006). Following this logic, birds exposed to higher energies potentially have more severe retinal injuries that could make visual acuity deficits larger. Lower visual acuity combined with a more difficult foraging task could reduce birds' ability to see individual seeds from the perch and explain why, as energy increases, they arrive quicker to the food patch.

Within week 2 after laser exposure, although latency returned to normal, there are greater differences in latency between the seed visual contrast treatments as laser energy increases. At

low seed visual contrast, latency to arrive to the food patch increased with increasing energy whereas at high seed visual contrast, latency decreased. The latency trends at high and low contrast within week 2 after exposure may differ from the those within week 1 after exposure because of complex development and healing of retinal injury. We predicted that edema and retinal swelling may subside, and visual acuity may be improving. However, studies on humans and non-human primates support the idea that laser exposure can change chromatic sensitivity and chromatic acuity (D.O. Robbins, Zwick, & Haenlein, 1980; Harry Zwick, Lund, Brown, Jr., Stuck, & Loveday, 2003), even if acuity is normal (Glickman et al., 1996). Reduced contrast sensitivity despite normal acuity may be a result of altered cell composition in the retina. Laser exposure can cause damage to or even death of photoreceptors and leave lesions or areas unpopulated by cells in the retina (Powell et al. 1971, Busch et al. 1999, Zwick et al. 2008). Some studies have reported the shrinking of lesions as well as functional improvements over time (Young et al. 2010, Zwick et al 1992, Tso 1973), and other studies have established that photoreceptors appear in spots that consisted only of dead photoreceptors. (Busch et al. 1999, Paulus et al. 2008, Zwick et al. 2008, Sher et al. 2013). There is no evidence of photoreceptors regenerating in mammals (Sher et al. 2013) or adult birds (Goldman 2015); therefore, photoreceptors could be actively or passively migrating to these empty spots from other parts of the retina (Tso 1973, Zwick et al. 1999, 2003, 2008), which could fundamentally change the way birds are both using their centers of acute vision, as well as how they perceive color. Because the difference between the millet seeds and the background is only 6 JNDs in the low seed visual contrast task, birds may have trouble discriminating them as they are exposed to higher energies, whereas the millet seeds and the high seed visual contrast task would still be distinguishable. Birds who have trouble distinguishing the millet seeds in the low seed visual contrast might perceive the food patch as containing only the low contrast beads and therefore take longer to approach the food patch.

Impaired contrast sensitivity after-exposure could also explain why scanning rates change depending on the seed visual contrast of the foraging trial. We found that after-exposure, birds scanned significantly more when they could more easily distinguish seeds from the visual background (i.e. high seed visual contrast) than when seeds were more challenging to detect (i.e., low seed visual contrast). If laser exposure decreases contrast sensitivity, low contrast foraging trials may become more difficult and birds might reduce scanning rate in order to allocate more time to other foraging behaviors that help discriminate food from the background. For example,

Lawrence 1985 showed that when blackbirds fed on cryptic prey, twice as much time elapsed between scans, and Dukas and Kamil 2000 showed that blue jays have lower visual detection ability when their attention is focused on a complex foraging task.

We also found that house sparrows changed foraging specific visual search behaviors after laser exposure. After exposure, house sparrows preferred to use the binocular-foveal and foveal vision of their left eye over their right eye despite being exposed to the laser in both eyes and no difference in cone type densities between the eyes (Ensminger and Fernández-Juricic 2014). Preference for one eye over the other is well documented in birds (Franklin and Lima 2001, Rogers 2008, Templeton and Christensen-Dykema 2008, Martinho III et al. 2014) such as chickens (Vallortigara et al. 1996, 2001), pigeons (Güntürkün and Kesch 1987), European starlings (Templeton and Gonzalez 2004), and quail (Zucca and Sovrano 2008). Birds exhibit preferences in one eye over the other in multiple contexts including courtship (George et al. 2006), tool use (Martinho III et al. 2014), predator detection (Randier 2005, Koboroff et al. 2008, Beauchamp 2015b), and conspecific recognition (Zucca and Sovrano 2008). There is evidence that Passerines may use their left eye preferentially for interpreting spatial cues (Clayton and Krebs 1994). Specifically, there's evdience that house sparrows may have lateralization of copulatory behavior where males preferrentially make cloacal contact with females on the left (Nyland et al. 2003). Lateralization in vision has been well documented in the context of foraging as well (Mench and Andrew 1986, Valenti et al. 2003, Beauchamp 2015a). It is thought that birds with visual asymmetry have increased foraging success (Güntürkün et al. 2000) possibly because of the specialization of brain hemispheres for certain visual tasks (Güntürkün and Kesch 1987, Parsons and Rogers 1993). For example, birds may use either the right or left eye preferentially to aid in differentiating a stimulus from its surroundings (Andrew 1988, Rashid and Andrew 1989) or color discrimination (Vallortigara 1989, Vallortigara et al. 1996, Skiba et al. 2000). Pigeons, for example, are left-hemisphere, right-eye dominant when visually processing objects (e.g. discriminating grain from grit) (Güntürkün and Kesch 1987, Güntürkün 1997). Following this logic, reduced quality of visual input in both eyes after laser exposure could increase the difficulty of the foraging trials and cause house sparrows to use the brain hemisphere that is specialized for interpreting cues important to foraging. If we assume eye injury and thus quality of visual input gets worse as the energy of exposure increases, birds may be compensating by increasing the use of the specialized brain hemisphere as the energy of exposure increases.

Increased differences between the function of the left and right eyes may influence how birds use their eyes together and have consequences for foraging in the wild. Our study shows that house sparrows decrease their use of binocular vision after laser exposure despite the fact that binocular vision is thought to be used for close range, visually guided foraging (Fernández-Juricic et al. 2011, Tyrrell and Fernández-Juricic 2017) like that of the house sparrow (Fernández-Juricic et al. 2008) in order to enhance prey detection and food handling (Martin 2014, Moore et al. 2017). One reason binocular vision is proposed to be used to find prey items before pecking is due to a phenomenon called binocular summation which is the visual advantage of binocular versus monocular viewing through enhanced acuity, contrast sensitivity, flicker detection, form recognition, and visuomotor coordination (Blake et al. 1981, Kambanarou 2005). Indeed, this is demonstrated by Templeton and Christensen-Dykema 2008 who showed starlings are able to use binocular vision are better able to find inconspicuous prey and by Watanabe et al. 1984 who showed pigeons perform better in visual-discrimination tasks when allowed to use binocular vision. There is evidence, however, that binocular summation only exists when there is symmetry between the eyes (Marmor and Gawande 1988, Pardhan and Gilchrist 1992, Jiménez Cuesta et al. 2003, Castro et al. 2009, Pineles et al. 2013, Arba Mosquera and Verma 2016). Furthermore, asymmetrical eye performance can even cause binocular inhibition, which is the binocular performance is worse than monocular vision (Pardhan and Gilchristt 1990, Pardhan 1993) A lack of binocular summation or binocular inhibition due to asymmetrical function of the right and left eye could explain why house sparrows decrease the use of binocular vision after laser exposure, as shown here, and could result in reduced ability for individuals to find inconspicuous prey in the wild.

In alignment with the reduction in binocular vision and increased left-eye bias, we also found changes in pecking behavior after laser exposure. Preceding pecking, bird species like house sparrows with laterally placed eyes commonly inspect food items using their binocular vision (Bischof 1988, Hodos 1993). If house sparrows use less binocular vision after laser exposure, their ability to accurately locate a food item may be inhibited which could cause them to peck at higher rates in order to successfully capture and consume a seed. However, birds do not use binocular vision significantly less within week 2 after exposure, yet still have increased rates of pecking. Additionally, birds have higher rates of seed consumption along with higher pecking rates within week 1 and within week 2 after laser exposure. More likely than changes in binocular vision being

solely responsible for changes in pecking and seed consumption rates, the cumulative changes in how birds are visually exploring the food patch, including which eye they prefer to use, could increase pecking and seed consumption rates as birds try to counteract visual deficits.

It is important to note that, in general, birds increase pecking rate despite our finding that there is no significant difference in the total number of seeds birds eat in the 15 min trial before laser exposure versus after laser exposure. This means that birds are spending more effort (i.e., pecking) in the first 30 s they participated in the foraging trail to obtain the same amount of food over the full 15 min. However, we did not collect data on the number of inaccurate pecks within the first 30 s or the number of successful or non-successful pecks after the first 30 s. Therefore, we cannot assert what, if any changes birds experienced in foraging efficiency over the length of the 15 min trial.

The rates at which birds pecked and consumed seeds were also affected by the interaction among laser exposure, seed visual contrast, and laser energy. Within week 1 after exposure, birds pecked at higher rates in the high seed visual contrast as laser energy increased. One possible explanation for this is the complex interplay between the time birds spend using other visual behaviors and the functional effects of laser exposure. The same pattern was seen in seed consumption rate. Birds use binocular vision less within week 1 after laser exposure, but they also spend more time scanning only in the high seed visual contrast trials. This means birds could be spending less time visually searching for food, specifically in high contrast conditions. Reduced time searching for food and reduced visual function with increasing energy could lead to birds increasing pecking rate to make up for the uncertainty a peck will be successful. Within week 2 after laser exposure, birds pecked at lower rates in the high seed visual contrast as energy increased and additionally, birds pecked at increasing rates in the low seed visual contrast as energy increased. Again, seed consumption rate followed the same pattern. Although birds continued to scan at higher rates in the high seed visual contrast within week 2 after exposure, there was no significant difference in how much time birds spent using binocular vision before laser exposure compared to within week 2 after laser exposure. The shift in pecking and seed consumption rates could possibly be explained by circumstances similar to those posited to affect latency. Decreased contrast sensitivity as laser energy increases could develop several days after exposure and cause the low seed visual contrast task to become considerably more difficult than the high seed visual contrast. Increased difficulty discerning seeds from the background in the low seed visual contrast task

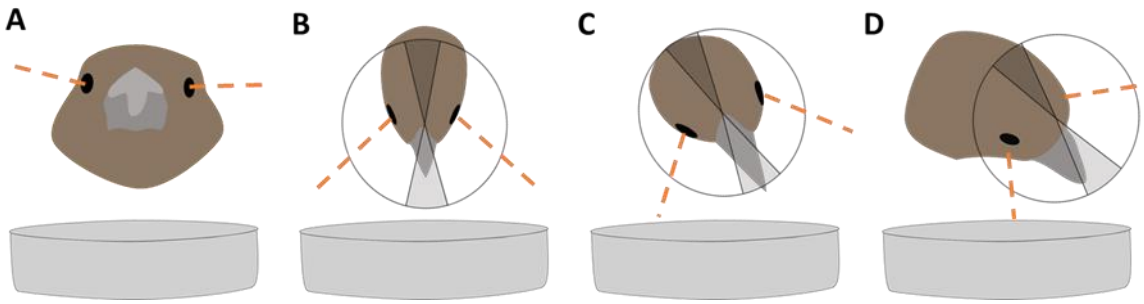
could cause birds to increase rates of pecking in an attempt to counteract difficult foraging conditions as energy of exposure increases.

Together, the results of our study have important implications for the health and survival of wild birds that have been exposed to lasers. Our study shows that laser eye exposure, including exposure at energy levels three times below those we predicted to cause a retinal lesion, affects how birds forage, how quickly they arrive to a food patch, and the rate at which they scan for predators. These behavioral modifications could feasibly have real fitness consequences. Birds exposed to laser light may move from patches earlier than a bird not exposed to a laser due to decreased ability to recognize inconspicuous prey, which may also lead birds to modify scanning rates. These behavioral changes could increase energy expenditure and vulnerability to predators (O'Brien et al. 1990, Dukas and Kamil 2000, Fernández-Juricic and Tran 2007). However, because this was the first study of its kind, we do not yet know the long-term consequences of laser exposure. There is evidence that repeated exposure can have an additive effect on visual function and lead to permanent, long-term, as opposed to temporary, short-term, visual deficits (Griess and Blankenstein 1981, Robbins and Zwick 1996).

This study lays the groundwork for future research that should investigate short- and long-term effects of lasers on avian eyes before using them as deterrents worldwide. Specifically, future work should investigate evidence of physical injury to avian eyes effects on the complex energy-tissue interactions that take place in avian eyes to more thoroughly understand the mechanisms underlying the behavioral findings we document here. Although these interactions are well studied in mammalian eyes, more research is needed to understand how various wavelengths, energies, spot sizes, and length of exposures affect avian eyes in particular. Lasers used for bird deterrence come in many different wavelengths, which can have dramatically different effects of avian behavior and physiology (Lustick 1973, Alaasam et al. 2018). Finally, our study looked exclusively at the foraging behavior of a seed eating passerine. Laser bird deterrents can be used to disperse birds that are much larger, have different feeding strategies, and have drastically different visual systems (Glahn and Dorr 2000, Werner and Clark 2003, Sherman and Barras 2004, Gorenzel et al. 2016). More research is needed to understand the physical and behavioral effects of laser exposure on commonly repelled birds such as water birds and seabirds.

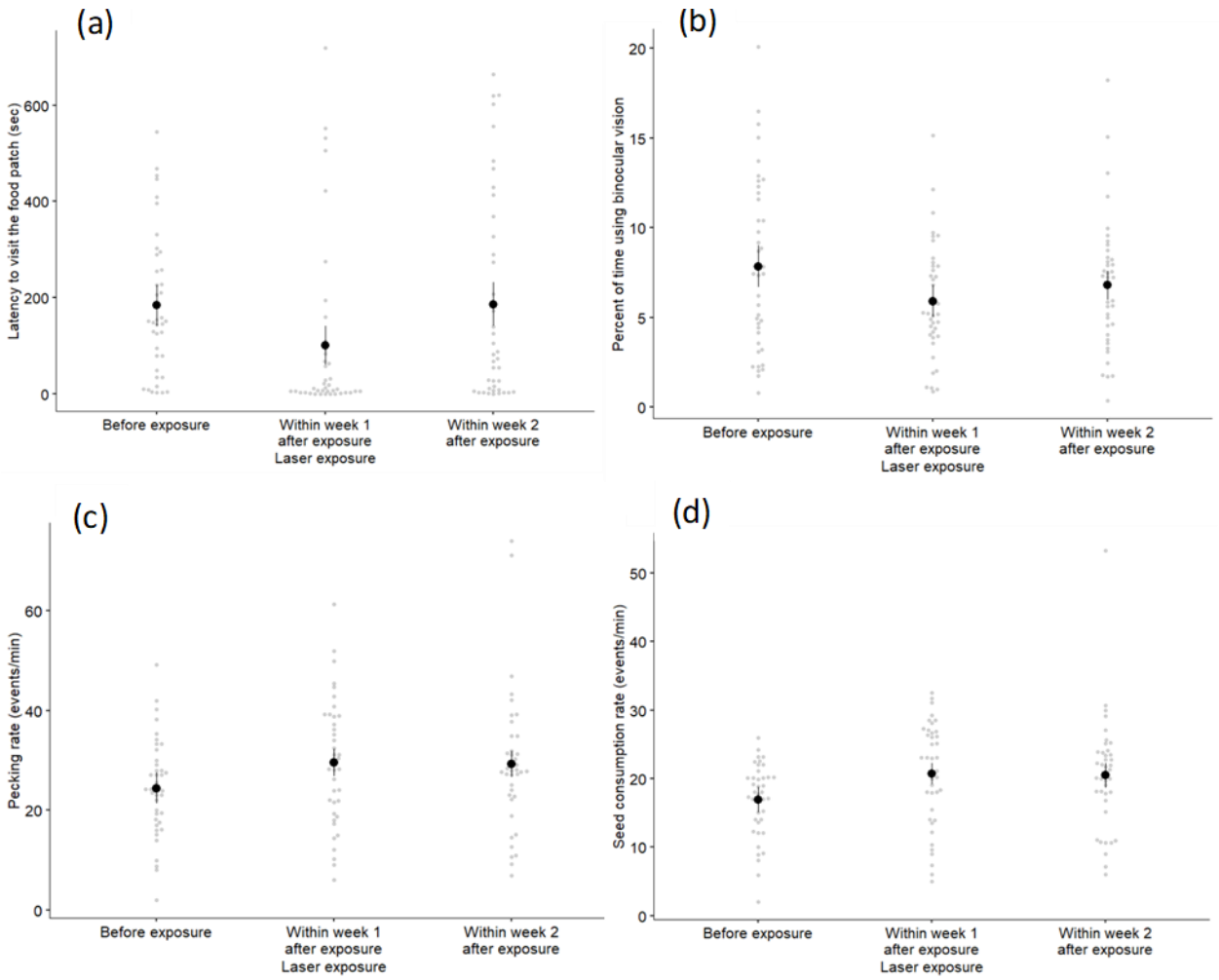
FIGURES

Figure 1



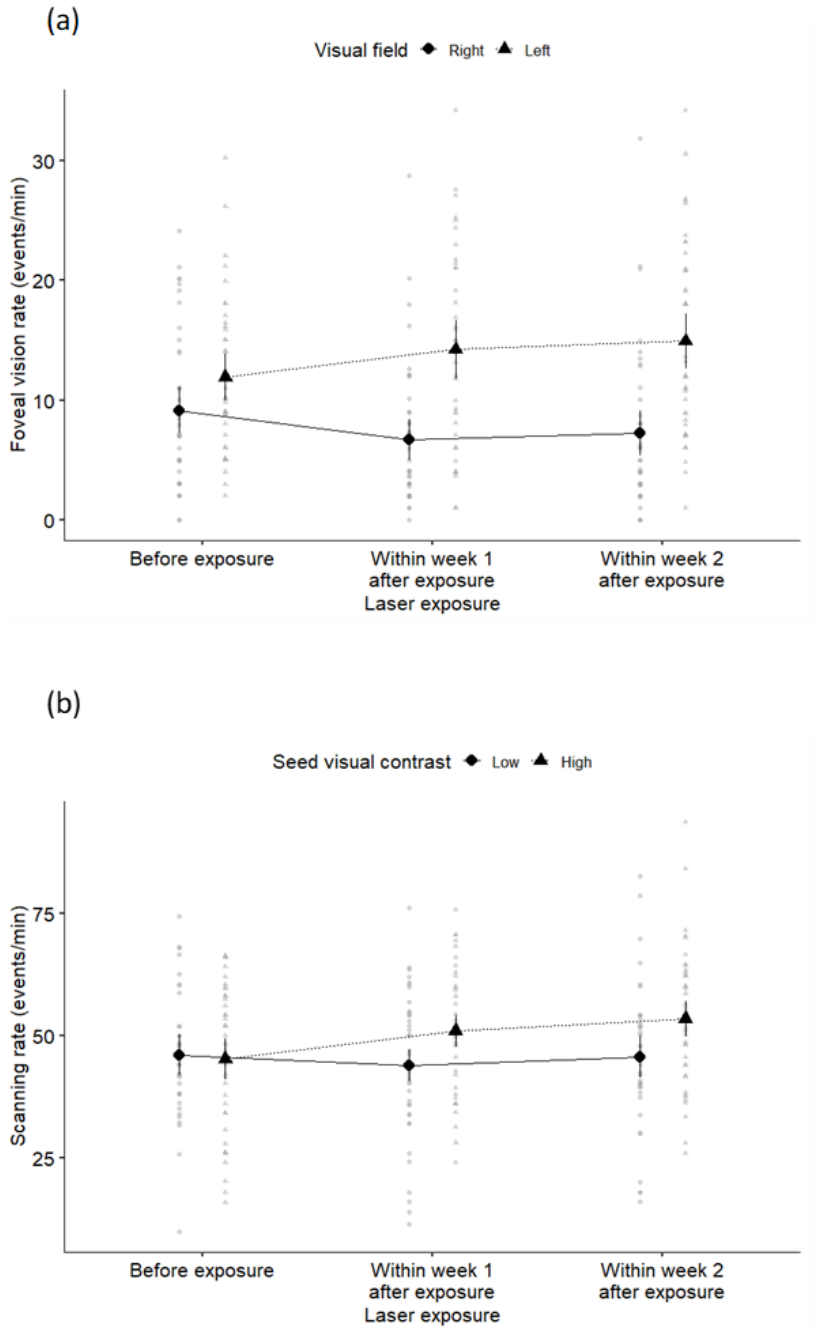
Head positions recorded during the behavioral trials. Dashed lines indicate the foveal projections for the right and left eyes and the gray portions of the visual field in front of the bill individual the average binocular field of house sparrows. (a) Scanning position with the bill above or slightly below the horizontal plane but not projecting into the food patch. (b) Individual exploring the food patch with binocular vision, with the bill projecting into the patch and the head not tilted. (c) Individual using a combination of binocular-foveal vision, with the bill and one fovea (either right or left) projecting into the food patch. (d) Individual using foveal vision, with one fovea (either right or left) but not the bill projecting into the food patch.

Figure 2



Effects of laser exposure on house sparrow behavior. (a) Latency to visit the food patch, (b) percentage of time using binocular vision looking at the food patch, (c) pecking rate, and (d) seed consumption rate relative to the timing of laser exposure (before, within week 1 after, within week 2 after). Shown are means, SEs, and raw data points.

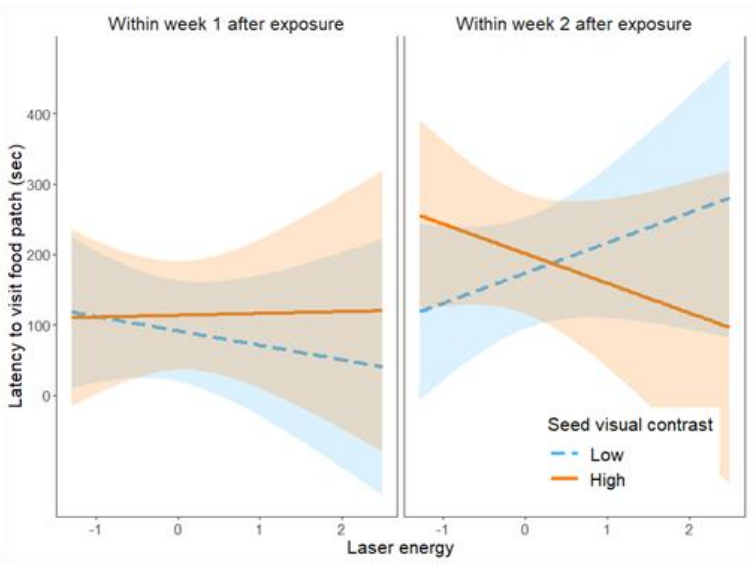
Figure 3



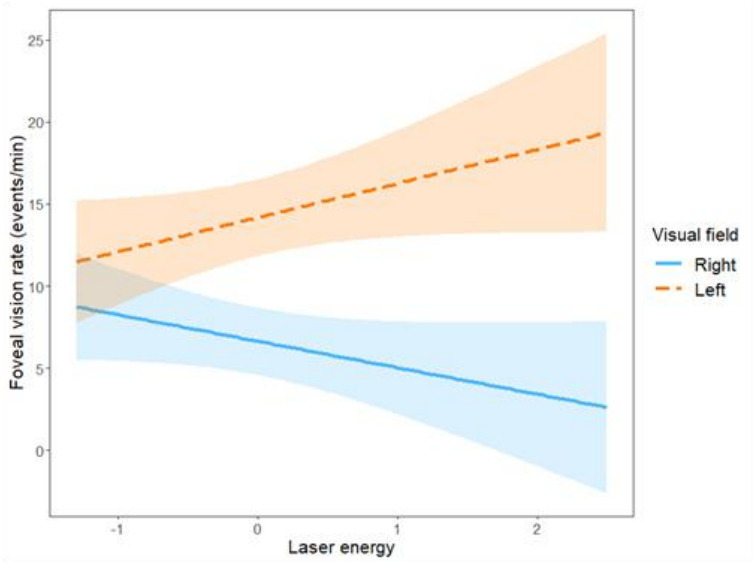
Effects of laser exposure on house sparrow behavior. (a) Rate of use of foveal vision towards the food patch relative to the timing of laser exposure (before, within week 1 after, within week 2 after) and the visual field (right, left). (b) Rate of scanning the environment relative to the timing of laser exposure and the visual contrasts of seeds (low, high).

Figure 4

(a)

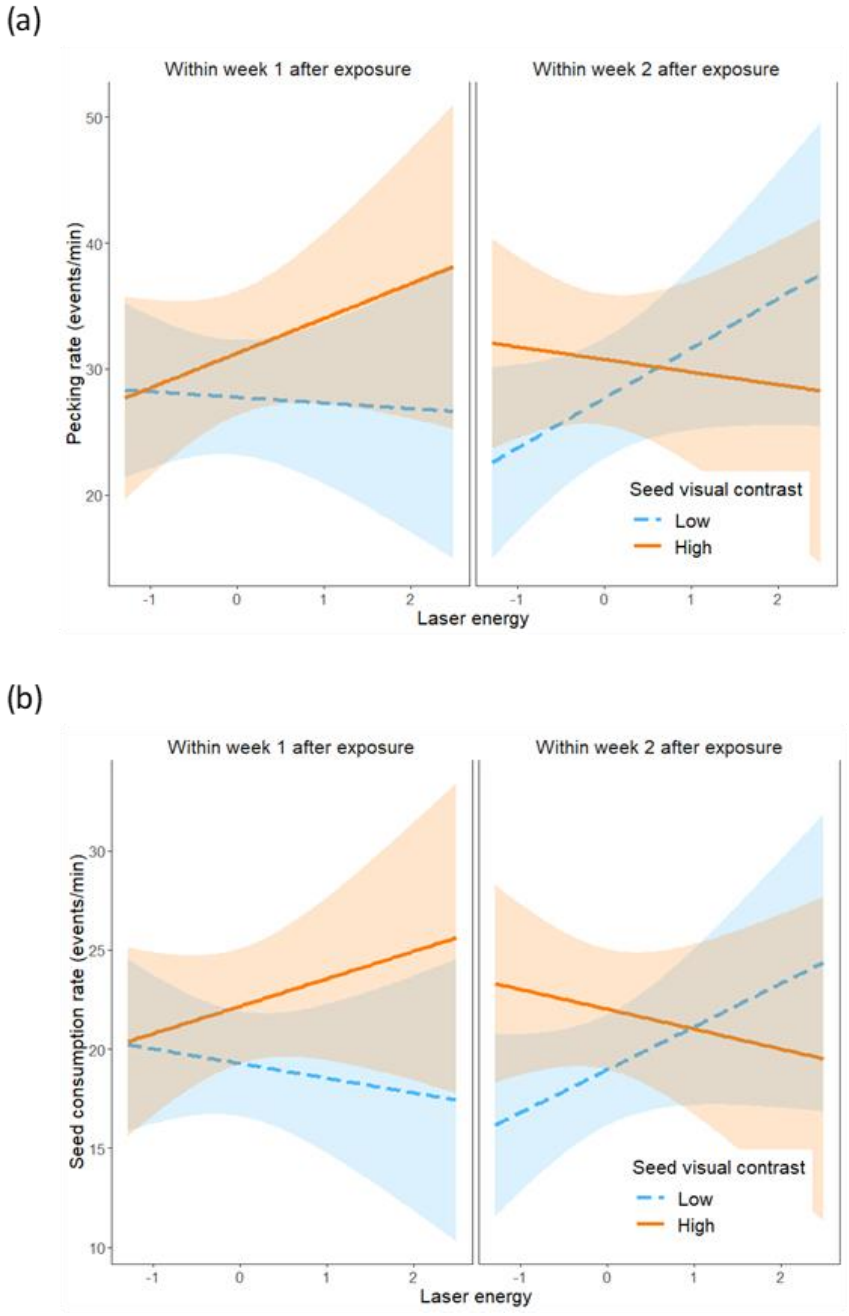


(b)



Effects of laser energy on house sparrow behavior considering the treatments after laser exposure. (a) Latency to visit the food patch relative to laser exposure (within week 1 after, within week 2 after), seed visual contrast (low, high), and laser energy level. (b) Rate of use of foveal vision towards the food patch relative to the visual field (right, left) and laser energy level.

Figure 5



Effects of laser energy on house sparrow behavior considering the treatments after laser exposure. (a) Seed pecking rate and (b) seed consumption rate relative to laser exposure (within week 1 after, within week 2 after), seed visual contrast (low, high), and laser energy level. Shown are predicted trends by the model with 95% confidence bands.

TABLES

Table 1 Effects of laser exposure (before, within week 1 after, within week 2 after), seed visual contrast (high, low), visual field (right, left) and their interactions on different house sparrow behavioral responses related to using different areas their visual system relative to the food patch (binocular vision, foveal vision), pecking, scanning, and the latency to visit the food patch. Results from general linear mixed models (significant values are bolded).

	F	***d.f***	***p***
Latency to visit food patch (sec)			
Laser exposure	5.69	2, 51.1	**0.006**
Seed visual contrast	0.33	1, 38.64	0.569
Trial order	2.94	1, 127.3	0.089
Laser exposure X Seed visual contrast	0.06	2, 89.7	0.940
Percent of time using binocular vision			
Laser exposure	3.78	2, 51.1	**0.030**
Seed visual contrast	0.00	1, 38.7	0.980
Trial order	0.06	1, 130.2	0.815
Laser exposure X Seed visual contrast	0.43	2, 91.9	0.651
Percent of time using binocular-foveal vision			
Laser exposure	0.44	2, 52.4	0.644
Seed visual contrast	0.06	1, 38.6	0.802
Visual field	10.13	1, 39	**0.003**
Trial order	8.09	1, 194.5	**0.004**
Laser exposure X Seed visual contrast	0.74	2, 281.2	0.479
Laser exposure X Visual field	0.68	2, 279.6	0.507
Seed visual contrast X Visual field	0.07	2, 279.6	0.792
Laser exposure X Seed visual contrast X Visual field	0.13	2, 279.6	0.874
Binocular-foveal vision rate (events per min)			
Laser exposure	0.65	2, 52.3	0.526
Seed visual contrast	0.23	1, 38.6	0.636
Visual field	13.02	1, 39.00	**0.001**
Trial order	1.05	1, 194.4	0.308
Laser exposure X Seed visual contrast	0.83	2, 280.5	0.437
Laser exposure X Visual field	2.11	2, 278.8	0.122
Seed visual contrast X Visual field	0.55	1, 278.8	0.457
Laser exposure X Seed visual contrast X Visual field	1.55	2, 278.8	0.214
Foveal vision rate (events per min)			
Laser exposure	0.28	2, 52.9	0.757
Seed visual contrast	0.73	1, 38.6	0.400

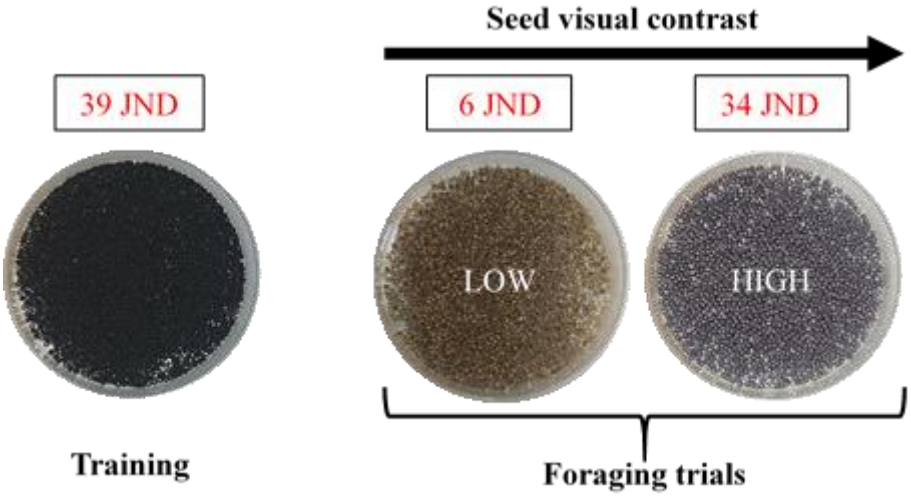
Visual field	22.57	1, 39.0	**< 0.001**
Trial order	0.61	1, 223.2	0.434
Laser exposure X Seed visual contrast	0.08	2, 284.1	0.919
Laser exposure X Visual field	6.96	2, 283.1	**0.001**
Seed visual contrast X Visual field	0.53	1, 283.1	0.469
Laser exposure X Seed visual contrast X Visual field	0.16	2, 283.1	0.851
Pecking rate (events per min)			
Laser exposure	4.77	2, 51.2	**0.013**
Seed visual contrast	1.57	1, 38.6	0.218
Trial order	0.11	1, 122.2	0.742
Laser exposure X Seed visual contrast	1.79	2, 86.9	0.172
Seed consumption rate (events per min)			
Laser exposure	6.07	2, 51.1	**0.004**
Seed visual contrast	6.77	1, 38.6	**0.013**
Trial order	0.98	1, 123.5	0.325
Laser exposure X Seed visual contrast	1.08	2, 88.6	0.343
Seed giving-up density			
Laser exposure	2.14	2, 51.2	0.128
Seed visual contrast	2.68	1, 38.6	0.109
Trial order	1.19	1, 123.6	0.278
Laser exposure X Seed visual contrast	2.13	2, 88.8	0.124
Scanning rate (events per min)			
Laser exposure	1.35	2, 51.2	0.269
Seed visual contrast	8.52	1, 38.7	**0.006**
Trial order	0.16	1, 124.8	0.689
Laser exposure X Seed visual contrast	4.07	2, 86.3	**0.020**

Table 2 Effects of laser exposure (before, within week 1 after, within week 2 after), seed visual contrast (high, low), laser energy, visual field (right, left) and their interactions on different house sparrow behavioral responses related to using different areas their visual system relative to the food patch (binocular vision, foveal vision), pecking, scanning, and the latency to visit the food patch. Results from general linear mixed models (significant values are bolded)

	F	***d.f***	***p***
Latency to visit food patch (sec)			
Laser exposure	7.81	1, 38.0	**0.008**
Seed visual contrast	0.61	1, 38.2	0.440
Laser energy	0.02	1, 38.0	0.882
Trial order	0.04	1, 68/2	0.852
Laser exposure X Seed visual contrast	0.02	1, 37.2	0.898
Laser exposure X Laser energy	0.09	1, 38.0	0.762
Seed visual contrast X Laser energy	0.99	1, 37.8	0.324
Laser exposure X Seed visual contrast X Laser energy	5.49	1, 39.3	**0.024**
Percent of time using binocular vision			
Laser exposure	2.89	1, 38.0	0.097
Seed visual contrast	0.31	1, 38.2	0.583
Laser energy	0.17	1, 38.0	0.682
Trial order	0.00	1, 74.9	0.950
Laser exposure X Seed visual contrast	0.49	1, 37.3	0.487
Laser exposure X Laser energy	0.14	1, 38.0	0.708
Seed visual contrast X Laser energy	0.02	1, 37.6	0.896
Laser exposure X Seed visual contrast X Laser energy	0.04	1, 39.7	0.850
Percent of time using binocular-foveal vision			
Visual field	9.72	1, 38	**0.003**
Laser energy	0.13	1, 38	0.717
Trial order	0.76	1, 239	0.385
Visual field X Laser energy	0.26	1, 38	0.616
Binocular-foveal vision rate (events per min)			
Visual field	12.80	1, 38	**< 0.001**
Laser energy	0.10	1, 38	0.76
Trial order	0.09	1, 239	0.758
Visual field X Laser energy	0.59	1, 38	0.447
Foveal vision rate (events per min)			
Laser exposure	0.73	1, 38	0.398
Visual field	29.95	1, 38	**< 0.001**
Laser energy	1.15	1, 38	0.290
Trial order	0.03	1, 197	0.875
Laser exposure X Visual field	0.02	1, 197	0.900

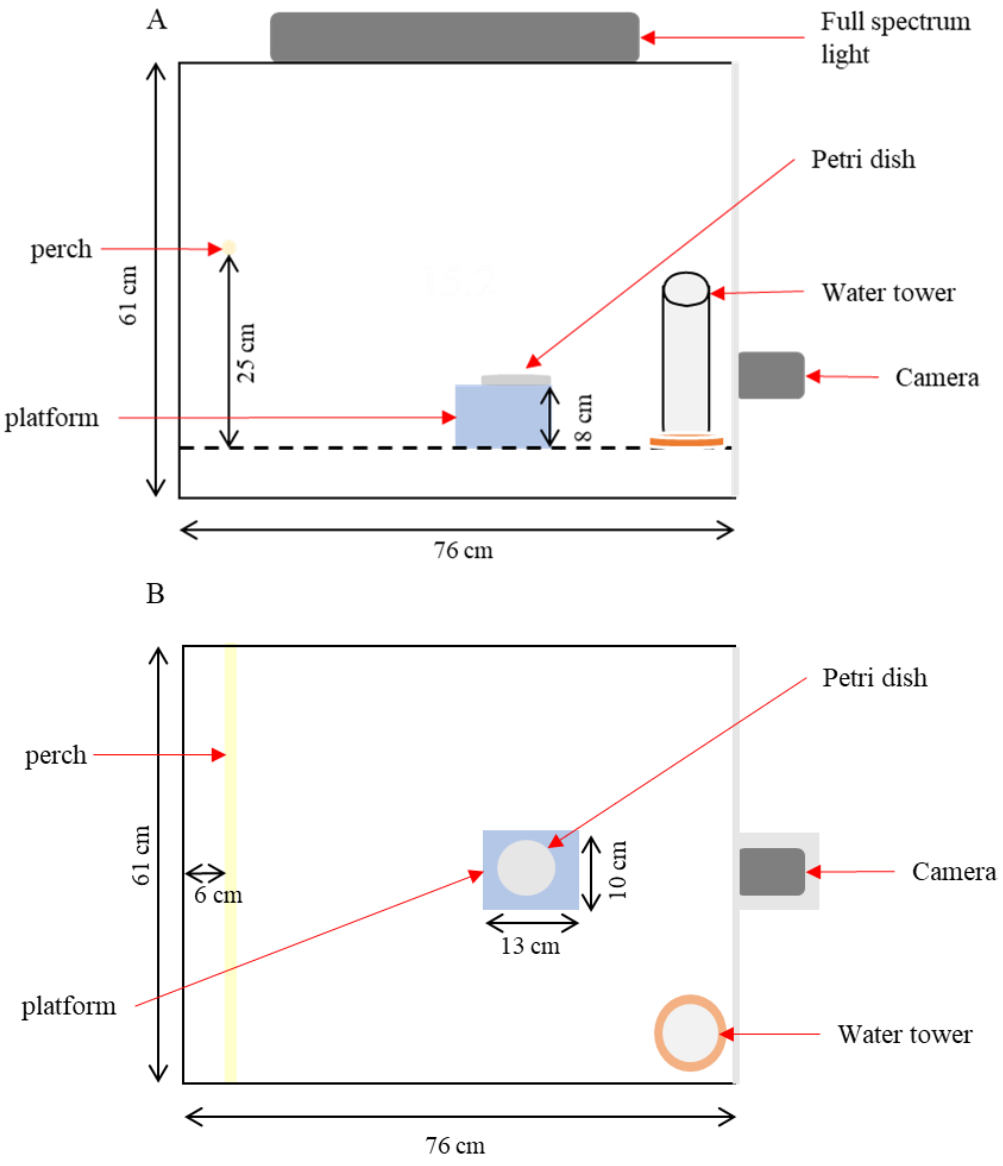
Laser exposure X Laser energy	2.18	1, 38	0.148
Visual field X Laser energy	9.30	1, 38	**0.004**
Laser exposure X Visual field X Laser energy	0.62	1, 197	0.430
Peck rate (events per min)			
Laser exposure	0.02	1, 38.0	0.876
Seed visual contrast	4.74	1, 38.1	**0.036**
Laser energy	0.48	1, 38.0	0.492
Trial order	0.03	1, 74.9	0.872
Laser exposure X Seed visual contrast	0.03	1, 37.3	0.872
Laser exposure X Laser energy	0.03	1, 38.0	0.859
Seed visual contrast X Laser energy	0.33	1, 37.6	0.570
Laser exposure X Seed visual contrast X Laser energy	6.98	1, 39.7	**0.011**
Seed consumption rate (events per min)			
Laser exposure	0.04	1, 38.0	0.842
Seed visual contrast	8.99	1, 38.1	**0.005**
Laser energy	0.16	1, 38.0	0.687
Trial order	0.40	1, 74.9	0.528
Laser exposure X Seed visual contrast	0.00	1, 37.3	0.974
Laser exposure X Laser energy	0.05	38.0	0.822
Seed visual contrast X Laser energy	0.20	1, 37.6	0.658
Laser exposure X Seed visual contrast X Laser energy	7.20	1, 39.7	**0.011**
Seed giving-up density			
Laser exposure	2.64	1, 38	0.113
Seed visual contrast	0.93	1, 38.1	0.342
Laser energy	0.17	1, 38	0.685
Trial order	3.89	1, 74.9	0.052
Laser exposure X Seed visual contrast	2.92	1, 37.3	0.095
Laser exposure X Laser energy	1.89	1, 38	0.177
Seed visual contrast X Laser energy	1.45	1, 37.6	0.237
Laser exposure X Seed visual contrast X Laser energy	0.32	1, 39.7	0.573
Scanning rate (events per min)			
Laser exposure	1.28	1, 38.0	0.265
Seed visual contrast	18.07	1, 38.1	**< 0.001**
Laser energy	0.01	1, 38.0	0.914
Trial order	0.11	1, 74.9	0.744
Laser exposure X Seed visual contrast	0.06	1, 37.4	0.809
Laser exposure X Laser energy	0.90	1, 38.0	0.348
Seed visual contrast X Laser energy	0.39	1, 37.6	0.534
Laser exposure X Seed visual contrast X Laser energy	0.17	1, 39.7	0.680

APPENDIX A. FORAGING TRIALS



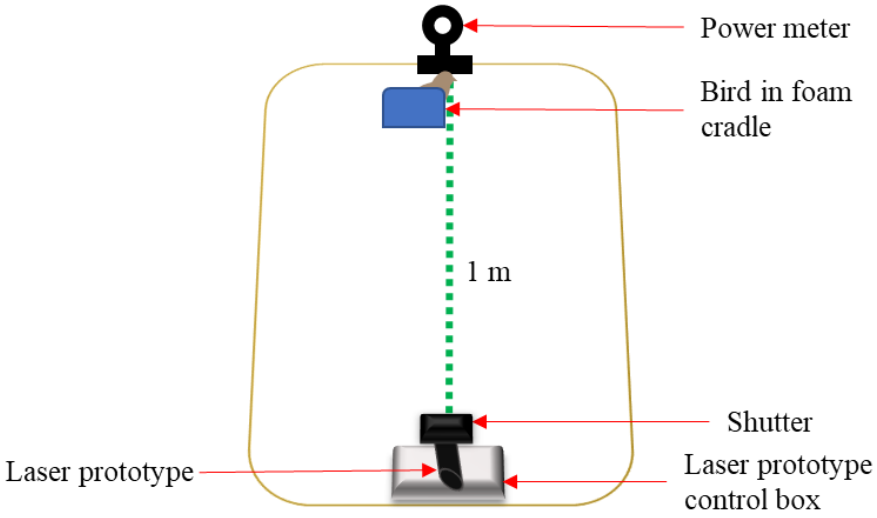
Food patches were constructed from standard Petri dishes (110 mm x 30 mm) and filled with 32 g of TOHO brand seed beads as substrate (bead size 11/0, hole size 0.7 mm). Birds learned how to forage for 15 millet seeds in the modified food patches with the Matt Opaque Black Toho Seed beads which had a chromatic contrast of 39 JND with the millet seeds. Birds participated in a high seed visual contrast trial with the Gold Lustered Grey TOHO seed bead as substrate (chromatic contrast 34 JND) and a low seed visual contrast trial with the Frosted Gold-lined Crystal seed bead as substrate (chromatic contrast 6 JND). Chromatic contrasts between millet seeds and substrate were determined from the visual perspective of house sparrows.

APPENDIX B. EXPERIMENTAL CAGE SET-UP



(A) side view (B) top view of experimental cage setup

APPENDIX C. LASER EXPOSURE SET-UP



Each bird was placed in a foam cradle exactly 1 m from the aperture of the laser which was secured on a table and fitted with a Thor labs beam shutter 2.54 cm diameter and 15.24 cm behind the bird was an Ophir power sensor which was aligned to the center of the laser beam.

APPENDIX D. LIST OF BEHAVIORS CODED FOR IN BORIS USING FRAME BY FRAME FUNCTION

Behavior Coded	Definition of behavior
Start	Trial begins when the experimental cage door closes
End	Trial ends when the bird has been participating (at the food patch) for 30 seconds
Arrive	Both feet make contact with the dish or platform
Leave	Both feet are no longer in contact with the dish or platform
Peck	Bird makes head movement toward dish and beak makes contact with substrate or seed
Seed consumption	Bird successfully captures seed. Seed seen in beak accompanied by chewing or husk flying
Scan 1	Beak is above the horizontal and head is not tilted or head is turned away from the dish so that the beak is not projecting into the food patch
Scan 2	Beak is below horizontal but does not project into the food patch and head is not tilted
Binocular vision	Beak projects into the food patch and head is not tilted
Binocular-foveal vision	Beak projects into the food patch and head is tilted so that both eyes can still see into the food patch
Foveal vision	Beak does not project into dish and head is tilted so that only one eye can see the food patch
Can't tell	Bird's head and/or beak is blocked or cannot be determined

APPENDIX E. R CODE USED FOR THE STATISTICAL ANALYSES AND FIGURES

```
# R packages

library(devtools)
library(tidyverse)
library(psych)
library(ggfortify)
library(Rmisc)
library(sjstats)
library(car)
library(outliers)
library(afex)
library(knitr)
library(emmeans)
library(lme4)
library(nlme)
library(ggbeeswarm)
library(summarytools)
library(effsize)
library(corrr)
library(ggpubr)
library(pwr)
library(bbmle)
library(plotly)
library(rgl)
library(interactions)
library(sandwich)
library(jtools)
library(cowplot)
library(multcomp)



# LASER EXPOSURE EFFECTS: BEFORE vs within week 1 vs within week 2

setwd("C:/ECOSTATS") # sets folder

rm(list = ls ()) # clears R’s memory

energy <- read.csv("laserexposure_wo_laterality_final.csv", na.strings =
c("","NA"), header=TRUE) # opens file

set_sum_contrasts() # criterion for running the contrasts in afex

View(energy) # view dataset

str(energy) # summary of the types of variables and their values

energy$id <- as.factor(energy$id) # changes variable from an integer to a factor
```

```
energy$trialorder2 <- as.factor(energy$trialorder2) # changes variable from an
integer to a factor

str(energy) # summary of the types of variables and their values

energy$contrast <- relevel(energy$contrast, "L") # changing the order of the levels
within the factor contrast


###### latency

Mlatency <- mixed(latency ~ treatment + contrast + treatment*contrast + trialorder2
+ (treatment + contrast||id), data = energy, method = "KR",
                  control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(Mlatency) # requesting the model output


# defining the lme4 model to check for assumptions

Mlatency.assump <-lmer(latency ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy)

anova(Mlatency.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Mlatency.assump)

#way 2:
boxplot(residuals(Mlatency.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(Mlatency.assump))


# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_treatment <- emmeans(Mlatency, "treatment", model = "multivariate")
emm_treatment

# testing for pairwise post-hoc comparisons
pairs(emm_treatment)


# plotting treatment effects
afex_plot(Mlatency, x = "treatment", id = "id", error = "within", dodge = 0.4,
point_arg = list(size = 4), factor_levels = list(treatment = c("Before exposure",
"Within week 1\nafter exposure", "Within week 2\nafter exposure"))) + labs(y =
"Latency to visit the food patch (sec)", x = "Laser exposure") + theme_pubr(16)
```

```
###### % time using binocular vision

Mdownperc <- mixed(downperc ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy, method = "KR",
control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re = TRUE)

anova(Mdownperc) # requesting the model output


# defining the lme4 model to check for assumptions

Mdownperc.assump <-lmer(downperc ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy)

anova(Mdownperc.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Mdownperc.assump)

#way 2:
boxplot(residuals(Mdownperc.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(Mdownperc.assump))


# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_treatment <- emmeans(Mdownperc, "treatment", model = "multivariate")
emm_treatment

# checking for pairwise post-hoc comparisons
pairs(emm_treatment)

# plotting treatment effects
afex_plot(Mdownperc, x = "treatment", id = "id", error = "within", dodge = 0.4,
point_arg = list(size = 4), factor_levels = list(treatment = c("Before exposure",
"Within week 1\nafter exposure", "Within week 2\nafter exposure"))) + labs(y =
"Percent of time using binocular vision", x = "Laser exposure") + theme_pubr(16)



###### pecking rate

Mpeckrate <- mixed(peckrate ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy, method = "KR",
control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re = TRUE)

anova(Mpeckrate) # requesting the model output
```

```
# defining the lme4 model to check for assumptions

Mpeckrate.assump <-lmer(peckrate ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy)

anova(Mpeckrate.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Mpeckrate.assump)

#way 2:
boxplot(residuals(Mpeckrate.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(Mpeckrate.assump))


# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_treatment <- emmeans(Mpeckrate, "treatment", model = "multivariate")
emm_treatment

# post-hoc pairwise comparisons
pairs(emm_treatment)


# plotting treatment effects
afex_plot(Mpeckrate, x = "treatment", id = "id", error = "within", dodge = 0.4,
point_arg = list(size = 4), factor_levels = list(treatment = c("Before exposure",
"Within week 1\nafter exposure", "Within week 2\nafter exposure"))) + labs(y =
"Pecking rate (events/min)", x = "Laser exposure") + theme_pubr(16)



###### scan rate

Mscanrate <- mixed(vigilancerate ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy, method = "KR",
                   control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(Mscanrate) # requesting the model output


# defining the lme4 model to check for assumptions

Mscanrate.assump <-lmer(vigilancerate ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy)
```

```
anova(Mscanrate.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Mscanrate.assump)

#way 2:
boxplot(residuals(Mscanrate.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(Mscanrate.assump))


# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(Mscanrate, "contrast", model = "multivariate")
emm_contrast

# post-hoc pairwise comparisons
pairs(emm_contrast)

#calculating means for interaction
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_int <- emmeans(Mscanrate, "contrast", by = c("treatment"), model =
"multivariate")
emm_int

# post-hoc pairwise comparisons
pairs(emm_int)


# plotting the interaction
afex_plot(Mscanrate, x = "treatment", trace = "contrast", id = "id", error =
"within", dodge = 0.4, point_arg = list(size = 4), factor_levels = list(treatment =
c("Before exposure", "Within week 1\nafter exposure", "Within week 2\nafter
exposure"), contrast = c("Low", "High")), legend_title = "Seed visual contrast") +
labs(y = "Scanning rate (events/min)", x = "Laser exposure") + theme_pubr(16)




# LASER EXPOSURE EFFECTS: BEFORE vs within week 1 vs within week 2 - ASSESSING
LATERALITY EFFECTS

setwd("C:/ECOSTATS")  # sets folder

rm(list = ls ()) # clears R’s memory

energy <- read.csv("laserexposure_w_laterality_final.csv", na.strings = c("","NA"),
header=TRUE) # opens file
```

```
set_sum_contrasts() # criterion for running the contrasts in afex

View(energy) # view dataset

str(energy) # summary of the types of variables and their values

energy$id <- as.factor(energy$id) # changes variable from an integer to a factor

energy$trialorder2 <- as.factor(energy$trialorder2) # changes variable from an
integer to a factor

str(energy) # summary of the types of variables and their values

energy$eye <- relevel(energy$eye, "R") # changing the order of the levels within
the factor eye


###### Percent of time using binocular + foveal vision
Medgeperc <- mixed(edgeperc ~ treatment + contrast + eye + treatment*contrast +
treatment*eye + contrast*eye + treatment*contrast*eye + trialorder2 + (treatment +
contrast + eye||id), data = energy, method = "KR",
                   control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(Medgeperc)


# defining the lme4 model to check for assumptions

Medgeperc.assump <-lmer(edgeperc ~ treatment + contrast + eye + treatment*contrast
+ treatment*eye + contrast*eye + treatment*contrast*eye + trialorder2 + (treatment
+ contrast + eye||id), data = energy)

anova(Medgeperc.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Medgeperc.assump)

#way 2:
boxplot(residuals(Medgeperc.assump) ~ energy$treatment + energy$contrast +
energy$eye)


# this is for testing the normality of the residuals
qqnorm(residuals(Medgeperc.assump))


# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(Medgeperc, "eye", model = "multivariate")
emm_contrast
```

```
# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(Medgeperc, "trialorder2", model = "multivariate")
emm_contrast



###### Binocular + foveal vision rate (events per min)
Medgerate <- mixed(edgerate ~ treatment + contrast + eye + treatment*contrast +
treatment*eye + contrast*eye + treatment*contrast*eye + trialorder2 + (treatment +
contrast + eye||id), data = energy, method = "KR",
                   control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(Medgerate)


# defining the lme4 model to check for assumptions

Medgerate.assump <-lmer(edgeperc ~ treatment + contrast + eye + treatment*contrast
+ treatment*eye + contrast*eye + treatment*contrast*eye + trialorder2 + (treatment
+ contrast + eye||id), data = energy)

anova(Medgerate.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Medgerate.assump)

#way 2:
boxplot(residuals(Medgerate.assump) ~ energy$treatment + energy$contrast +
energy$eye)


# this is for testing the normality of the residuals
qqnorm(residuals(Medgerate.assump))


# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(Medgerate, "eye", model = "multivariate")
emm_contrast



######### Foveal vision rate (events per min)

Mfovearate <- mixed(fovearate ~ treatment + contrast + eye + treatment*contrast +
treatment*eye + contrast*eye + treatment*contrast*eye + trialorder2 + (treatment +
contrast + eye||id), data = energy, method = "KR",
                    control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re
```

```
= TRUE)

anova(Mfovearate)


# defining the lme4 model to check for assumptions

Mfovearate.assump <-lmer(fovearate ~ treatment + contrast + eye +
treatment*contrast + treatment*eye + contrast*eye + treatment*contrast*eye +
trialorder2 + (treatment + contrast + eye||id), data = energy)

anova(Mfovearate.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Mfovearate.assump)

#way 2:
boxplot(residuals(Mfovearate.assump) ~ energy$treatment + energy$contrast +
energy$eye)


# this is for testing the normality of the residuals
qqnorm(residuals(Mfovearate.assump))

# calculating means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_eye <- emmeans(Mfovearate, "eye", model = "multivariate")
emm_eye


#calculating means for interaction

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_int <- emmeans(Mfovearate, "eye", by = c("treatment"), model = "multivariate")
emm_int

# estimating post-hoc pairwise comparisons per level of treatment
pairs(emm_int)

# plotting the interaction
afex_plot(Mfovearate, x = "treatment", trace = "eye", id = "id", error = "within",
dodge = 0.4, point_arg = list(size = 4), factor_levels = list(treatment = c("Before
exposure", "Within week 1\nafter exposure", "Within week 2\nafter exposure"), eye =
c("Right", "Left")), legend_title = "Visual field") + labs(y = "Foveal vision rate
(events/min)", x = "Laser exposure") + theme_pubr(16)




# LASER ENERGY EFFECTS: (without the before treatment)
```

```
setwd("C:/ECOSTATS")  # sets folder

rm(list = ls ()) # clears R’s memory

energy <- read.csv("laserenergy_wo_laterality_final.csv", na.strings = c("","NA"),
header=TRUE) # opens file

set_sum_contrasts() # criterion for running the contrasts in afex

View(energy) # view dataset

str(energy) # summary of the types of variables and their values

energy$id <- as.factor(energy$id) # changes variable from an integer to a factor

energy$trialorder2 <- as.factor(energy$trialorder2) # changes variable from an
integer to a factor

str(energy) # summary of the types of variables and their values

#Centering continuous variables - a very recommended practice for MIXED models
MyNorm <- function(x){ (x-mean(x))/sd(x)}
#Add na.rm = TRUE to deal with NAs
energy$energyc <- MyNorm(energy$energy)


str(energy) #checking that centering worked

energy$contrast <- relevel(energy$contrast, "L") #changing the order of levels
within the factor contrast


###### latency

MElatency <- mixed(latency ~ treatment + contrast + energyc + treatment*contrast +
treatment*energyc + contrast*energyc + treatment*contrast*energyc + trialorder2 +
(treatment+contrast||id), data = energy, method = "KR",
                   control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(MElatency)


# defining the lme4 model to check for assumptions

MElatency.assump <-lmer(latency ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + trialorder2 + (treatment+contrast||id), data = energy)

anova(MElatency.assump)


# we can check the homogeneity of variances in two ways
# way 1:
```

```
plot(MElatency.assump)

#way 2:
boxplot(residuals(MElatency.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(MElatency.assump))


# treatment means

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_treatment <- emmeans(MElatency, "treatment", model = "multivariate")
emm_treatment


#plotting the 3-way interaction between 2 categorical and 1 continuous
interact_plot(MElatency.assump, pred = energyc, modx = contrast, mod2 = treatment,
interval = TRUE, int.width = 0.95,
              line.thickness = 1.5, x.label = "Laser energy",
              y.label = "Latency to visit food patch (sec)", modx.labels = c("Low",
"High"),
              mod2.labels = c("Within week 1 after exposure", "Within week 2 after
exposure"), legend.main = "Seed visual contrast") +
  theme_apa(facet.title.size = 16, legend.pos = "bottomright") +
  theme (axis.title.y = element_text(size=16), axis.text.y = element_text(size=13),
         axis.title.x = element_text(size=16), axis.text.x = element_text(size=13),
         legend.title = element_text(size=16), legend.text = element_text(size=16))
+
  scale_y_continuous(breaks = c(0, 100, 200, 300, 400))


####### Percent of time using binocular vision

MEpercbino <- mixed(downperc ~ treatment + contrast + energyc + treatment*contrast
+ treatment*energyc + contrast*energyc + treatment*contrast*energyc + trialorder2 +
(treatment+contrast||id), data = energy, method = "KR",
                    control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re
= TRUE)

anova(MEpercbino)


# defining the lme4 model to check for assumptions

MEpercbino.assump <-lmer(downperc ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + trialorder2 + (treatment+contrast||id), data = energy)

anova(MEpercbino.assump)


# we can check the homogeneity of variances in two ways
```

```
# way 1:
plot(MEpercbino.assump)

#way 2:
boxplot(residuals(MEpercbino.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(MEpercbino.assump))



#### Pecking rate

MEpeckrate <- mixed(peckrate ~ treatment + contrast + energyc + treatment*contrast
+ treatment*energyc + contrast*energyc + treatment*contrast*energyc + trialorder2 +
(treatment+contrast||id), data = energy, method = "KR",
                    control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re
= TRUE)

anova(MEpeckrate)


# defining the lme4 model to check for assumptions

MEpeckrate.assump <-lmer(peckrate ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + trialorder2 + (treatment+contrast||id), data = energy)

anova(MEpeckrate.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(MEpeckrate.assump)

#way 2:
boxplot(residuals(MEpeckrate.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(MEpeckrate.assump))


# contrast means

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(MEpeckrate, "contrast", model = "multivariate")
emm_contrast


#plotting the 3-way interaction between 2 categorical and 1 continuous factor
interact_plot(MEpeckrate.assump, pred = energyc, modx = contrast, mod2 = treatment,
interval = TRUE, int.width = 0.95,
```

```
              line.thickness = 1.5, x.label = "Laser energy",
              y.label = "Pecking rate (events/min)", modx.labels = c("Low",
"High"),
              mod2.labels = c("Within week 1 after exposure", "Within week 2 after
exposure"), legend.main = "Seed visual contrast") +
  theme_apa(facet.title.size = 16, legend.pos = "bottomright") +
  theme (axis.title.y = element_text(size=16), axis.text.y = element_text(size=13),
         axis.title.x = element_text(size=16), axis.text.x = element_text(size=13),
         legend.title = element_text(size=16), legend.text = element_text(size=16))
+
  scale_y_continuous(breaks = c(20, 30, 40, 50))



##### Vigilance rate

MEvigilancerate <- mixed(vigilancerate ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + trialorder2 + (treatment+contrast||id), data = energy,
method = "KR",
                         control = lmerControl(optCtrl = list(maxfun = 1e6)),
expand_re = TRUE)

anova(MEvigilancerate)


# defining the lme4 model to check for assumptions

MEvigilancerate.assump <-lmer(peckrate ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + trialorder2 + (treatment+contrast||id), data = energy)

anova(MEvigilancerate)


# we can check the homogeneity of variances in two ways
# way 1:
plot(MEvigilancerate)

#way 2:
boxplot(residuals(MEvigilancerate) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(MEvigilancerate))


# contrast means

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(MEvigilancerate, "contrast", model = "multivariate")
emm_contrast
```

```
# LASER ENERGY EFFECTS: (without the before treatment) CONSIDERING LATERALITY

setwd("C:/ECOSTATS") # sets folder

rm(list = ls ()) # clears R's memory

energy <- read.csv("laserenergy_w_laterality_final.csv", na.strings = c("","NA"),
header=TRUE) # opens file

set_sum_contrasts() # criterion for running the contrasts in afex

View(energy)  # views dataset

str(energy) # summary of the types of variables and their values

energy$id <- as.factor(energy$id) # changes variable from an integer to a factor

energy$trialorder2 <- as.factor(energy$trialorder2) # changes variable from an
integer to a factor

str(energy) # summary of the types of variables and their values

#Centering continuous variables - a very recommended practice for MIXED models
MyNorm <- function(x){ (x-mean(x))/sd(x)}
#Add na.rm = TRUE to deal with NAs
energy$energyc <- MyNorm(energy$energy)

str(energy) #checking that centering worked

energy$eye <- relevel(energy$eye, "R") #changing the order of levels within the
factor contrast


####### Percent of time using binocular + foveal vision

MEedgeperc <- mixed(edgeperc ~  eye + energyc + eye*energyc + trialorder2 +
(eye||id), data = energy, method = "KR",
                    control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re
= TRUE)

anova(MEedgeperc)


# defining the lme4 model to check for assumptions

MEedgeperc.assump <-lmer(edgeperc ~ eye + energyc + eye*energyc + trialorder2 +
(eye||id), data = energy)

anova(MEedgeperc.assump)


# we can check the homogeneity of variances in two ways
# way 1:
```

```
plot(MEedgeperc.assump)

#way 2:
boxplot(residuals(MEedgeperc.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(MEedgeperc.assump))


# eye means

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_eye <- emmeans(MEedgeperc, "eye", model = "multivariate")
emm_eye



##### Binocular + foveal vision rate (events per min)

MEedgerate <- mixed(edgerate ~  eye + energyc + eye*energyc + trialorder2 +
(eye||id), data = energy, method = "KR",
                    control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re
= TRUE)

anova(MEedgerate)


# defining the lme4 model to check for assumptions

MEedgerate.assump <-lmer(edgerate ~ eye + energyc + eye*energyc + trialorder2 +
(eye||id), data = energy)

anova(MEedgerate.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(MEedgerate.assump)

#way 2:
boxplot(residuals(MEedgerate.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(MEedgerate.assump))


# eye means

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_eye <- emmeans(MEedgerate, "eye", model = "multivariate")
emm_eye
```

```
####### foveal vision rate

MEfovea <- mixed(fovearate ~  treatment + eye + energyc + treatment*eye +
treatment*energyc + eye*energyc + treatment*eye*energyc + trialorder2 + (treatment
+ eye||id), data = energy, method = "KR",
                 control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(MEfovea)


# defining the lme4 model to check for assumptions

MEfovea.assump <-lmer(fovearate ~ treatment + eye + energyc + treatment*eye +
treatment*energyc + eye*energyc + treatment*eye*energyc + trialorder2 + (treatment
+ eye||id), data = energy)

anova(MEfovea.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(MEfovea.assump)

#way 2:
boxplot(residuals(MEfovea.assump) ~ energy$eye)


# this is for testing the normality of the residuals
qqnorm(residuals(MEfovea.assump))


# eye means

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_eye <- emmeans(MEfovea, "eye", model = "multivariate")
emm_eye


# plotting interaction effect between 1 categorical and 1 continuous factor
interact_plot(MEfovea.assump, pred = energyc, modx = eye, interval = TRUE,
int.width = 0.95,
              line.thickness = 1.5, x.label = "Laser energy",
              y.label = "Foveal vision rate (events/min)", modx.labels = c("Right",
"Left"), legend.main = "Visual field") +
  theme_apa() +
  theme (axis.title.y = element_text(size=16), axis.text.y = element_text(size=13),
         axis.title.x = element_text(size=16), axis.text.x = element_text(size=13),
         legend.title = element_text(size=16), legend.text = element_text(size=16))
+
  scale_y_continuous(breaks = c(0, 5, 10, 15, 20, 25))
```

```
# FORAGING EFFICIENCY: BEFORE vs after1d vs after1w (all variables)

setwd("C:/ECOSTATS") # sets folder

rm(list = ls ()) # clears R’s memory

energy <- read.csv("laserexposure_seeds_final.csv", na.strings = c("","NA"),
header=TRUE) # opens file

set_sum_contrasts() # criterion for running the contrasts in afex

View(energy) # view dataset

str(energy) # summary of the types of variables and their values

energy$id <- as.factor(energy$id) # changes variable from an integer to a factor

energy$trialorder2 <- as.factor(energy$trialorder2) # changes variable from an
integer to a factor

str(energy) # summary of the types of variables and their values

energy$contrast <- relevel(energy$contrast, "L") # changing the order of the levels
within the factor contrast


# all models have the following random structure: (treatment + contrast||id), which
indicates two within-subject factors (treatment and contrast) and bird id as a
random factor


###### seedspermin (seeds consumed per unit time during the approx first 30 seconds
in the food tray)

Mseedspermin <- mixed(seedspermin ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy, method = "KR",
                      control = lmerControl(optCtrl = list(maxfun = 1e6)),
expand_re = TRUE)

anova(Mseedspermin) # requesting the model output


# defining the lme4 model to check for assumptions

Mseedspermin.assump <-lmer(seedspermin ~ treatment + contrast + treatment*contrast
+ trialorder2 + (treatment + contrast||id), data = energy)

anova(Mseedspermin.assump)


# we can check the homogeneity of variances in two ways
```

```
# way 1:
plot(Mseedspermin.assump)

#way 2:
boxplot(residuals(Mseedspermin.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(Mseedspermin.assump))


# calculating means per treatment
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_treatment <- emmeans(Mseedspermin, "treatment", model = "multivariate")
emm_treatment

# testing for pairwise post-hoc comparisons
pairs(emm_treatment)


# plotting treatment effects
afex_plot(Mseedspermin, x = "treatment", id = "id", error = "within", dodge = 0.4,
point_arg = list(size = 4), factor_levels = list(treatment = c("Before exposure",
"Within week 1\nafter exposure", "Within week 2\nafter exposure"))) + labs(y =
"Seed consumption rate (events/min)", x = "Laser exposure") + theme_pubr(16)


# calculating means per contrast
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(Mseedspermin, "contrast", model = "multivariate")
emm_contrast



###### giving up seed densities (seeds consumed at the end of the 15 min trials)

# define new variable

energy <- mutate(energy, givingup = (seeds0min - seeds15min))

str(energy)


#running model with new variable

Mgivingup <- mixed(givingup ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy, method = "KR",
                   control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(Mgivingup) # requesting the model output
```

```
# defining the lme4 model to check for assumptions

MMgivingup.assump <-lmer(givingup ~ treatment + contrast + treatment*contrast +
trialorder2 + (treatment + contrast||id), data = energy)

anova(MMgivingup.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(MMgivingup.assump)

#way 2:
boxplot(residuals(MMgivingup.assump) ~ energy$treatment + energy$contrast)

# this is for testing the normality of the residuals
qqnorm(residuals(MMgivingup.assump))



# FORAGING EFFICIENCY: ENERGY EFFECTS (including after1d  and after1w, but removing
before)

setwd("C:/ECOSTATS") # sets folder

rm(list = ls ()) # clears R's memory

energy <- read.csv("laserenergy_seeds_final.csv", na.strings = c("","NA"),
header=TRUE) # opens file

set_sum_contrasts() # criterion for running the contrasts in afex

View(energy) # view dataset

str(energy) # summary of the types of variables and their values

energy$id <- as.factor(energy$id) # changes variable from an integer to a factor

energy$trialorder2 <- as.factor(energy$trialorder2) # changes variable from an
integer to a factor

str(energy) # summary of the types of variables and their values

energy$contrast <- relevel(energy$contrast, "L") # changing the order of the levels
within the factor contrast

#Centering continuous variables - a very recommended practice for MIXED models
MyNorm <- function(x){ (x-mean(x))/sd(x)}
#Add na.rm = TRUE to deal with NAs
energy$energyc <- MyNorm(energy$energy)

str(energy) #checking that centering worked

# all models have the following random structure: (treatment + contrast||id), which
indicates two within-subject factors (treatment and contrast) and bird id as a
```

```
random factor


###### seedspermin (seeds consumed per unit time during the approx first 30 seconds
in the food tray)

Mseedspermin <- mixed(seedspermin ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + trialorder2 + (treatment+contrast||id), data = energy,
method = "KR",
                      control = lmerControl(optCtrl = list(maxfun = 1e6)),
expand_re = TRUE)

anova(Mseedspermin) # requesting the model output


# defining the lme4 model to check for assumptions

Mseedspermin.assump <-lmer(seedspermin ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + (treatment+contrast||id), data = energy)

anova(Mseedspermin.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Mseedspermin.assump)

#way 2:
boxplot(residuals(Mseedspermin.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(Mseedspermin.assump))


# contrast means

emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(Mseedspermin, "contrast", model = "multivariate")
emm_contrast


# plotting interaction effect

interact_plot(Mseedspermin.assump, pred = energyc, modx = contrast, mod2 =
treatment, interval = TRUE, int.width = 0.95,
              line.thickness = 1.5, x.label = "Laser energy",
              y.label = "Seed consumption rate (events/min)", modx.labels =
c("Low", "High"),
              mod2.labels = c("Within week 1 after exposure", "Within week 2 after
exposure"), legend.main = "Seed visual contrast") +
  theme_apa(facet.title.size = 16, legend.pos = "bottomright") +
```

```
  theme (axis.title.y = element_text(size=16), axis.text.y = element_text(size=13),
         axis.title.x = element_text(size=16), axis.text.x = element_text(size=13),
         legend.title = element_text(size=16), legend.text = element_text(size=16))
+
  scale_y_continuous(breaks = c(10, 15, 20, 25, 30))


###### giving up seed densities (seeds consumed at the end of the 15 min trials)

# define new variable

energy <- mutate(energy, givingup = (seeds0min - seeds15min))

str(energy)


#running model with new variable

Mgivingup <- mixed(givingup ~ treatment + contrast + energyc + treatment*contrast +
treatment*energyc + contrast*energyc + treatment*contrast*energyc + trialorder2 +
(treatment+contrast||id), data = energy, method = "KR",
                   control = lmerControl(optCtrl = list(maxfun = 1e6)), expand_re =
TRUE)

anova(Mgivingup) # requesting the model output


# defining the lme4 model to check for assumptions

Mgivingup.assump <-lmer(givingup ~ treatment + contrast + energyc +
treatment*contrast + treatment*energyc + contrast*energyc +
treatment*contrast*energyc + trialorder2 + (treatment+contrast||id), data = energy)

anova(Mgivingup.assump)


# we can check the homogeneity of variances in two ways
# way 1:
plot(Mgivingup.assump)

#way 2:
boxplot(residuals(Mgivingup.assump) ~ energy$treatment + energy$contrast)


# this is for testing the normality of the residuals
qqnorm(residuals(Mgivingup.assump))

# trial order means
emm_options(lmer.df = "asymptotic") # also possible: 'satterthwaite', 'kenward-
roger'
emm_contrast <- emmeans(Mgivingup, "trialorder2", model = "multivariate")
emm_contrast
```

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