Received: 28 April 2017 | Revised: 30 June 2017 | Accepted: 7 July 2017

DOI: 10.1111/eth.12658

RESEARCH PAPER

WILEY ethology

Does artificial light pollution impair problem-solving success in peafowl?

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Funding information
College of Agriculture and Life Sciences at Texas A&M University; Texas A&M AgriLife Research

Editor: L. Ebensperger

Abstract

Behavioral innovations allow animals to adjust their behavior to solve novel problems. While innovative behavior can be important for animals living in new environments, anthropogenic pollution may limit their ability to adapt by impairing cognition or motivation. In particular, exposure to light pollution at night can cause sleep deprivation and may, therefore, hinder innovative behavior. To test this hypothesis, we examined experimentally whether exposure to acute light pollution impacts problem-solving success in peafowl (*Pavo cristatus*). After peafowl were exposed to artificial light pollution for one night, they were presented with a problem-solving task in which they could extract food by piercing the lid of an unfamiliar food bowl. Their problem-solving success was unrelated to short-term light pollution exposure. Other factors, including persistence, sex of the bird, and moon illumination, influenced their success in solving the task. The results suggest that short-term exposure to light pollution does not limit behavioral innovation, but long-term studies are necessary to further probe this question.

KEYWORDS
artificial light at night, cognition, motivation, sensory ecology, sensory pollution, urbanization

1 | INTRODUCTION

Innovation is an important behavior for animals that are adapting to novel environments. It allows them to exhibit new behaviors or modify existing ones to address new challenges (Reader & Laland, 2003). Behavioral innovation has been documented in a range of different taxonomic families (e.g., Overington, Cauchard, Côté, & Lefebvre, 2011; Reader & Laland, 2001; Sargeant, Mann, Berggren, & Krutzen, 2005). These innovations occur in a variety of contexts such as foraging, agonism, and courtship (Reader & Laland, 2001). A classic example is British titmice gaining access to an additional resource when living in an urban environment by opening milk bottles (Fisher & Hinde, 1949).

While innovative behavior can be critical for animals adapting to changing environments, the environment could limit this behavior. Animals exposed to different types of environmental pollution can suffer cognitive and motivational deficits that could impact their innovative behaviors. Noise pollution frequently has negative impacts on cognition and motivation (Naguib, 2013): When mice are exposed to noise pollution, their ability to solve a water maze is impaired (Cheng, Wang, Chen, & Liao, 2011). Their latency to find a platform in the water maze is longer when they are exposed to noise compared to when they are not exposed. Furthermore, mice exposed to the noise pollution suffer oxidative damage in brain regions associated with learning and audition. In addition, explicit memory in humans declines when they experience noise pollution (Benfield, Bell, Troup, & Soderstrom, 2010) and they become less motivated to complete tasks (Cohen, Evans, Krantz, & Stokols, 1980). Chemical pollution also has detrimental effects on cognition and motivation (Zala & Penn, 2004). With exposure to lead, herring gull recognition and learning abilities suffer (Burger & Gochfeld, 1993, 2005). Rhesus macaques' spatial memory declines with perinatal chemical exposure (polychlorinated biphenyl (PCB)), potentially because of damage to the prefrontal cortex (Schantz, Levin, & Bowman, 1991). Furthermore, rats are less motivated to drink when exposed to pesticides (carbaryl; Sideroff & Santolucito, 1972).

We know less about cognitive and motivational deficits resulting from light pollution and whether this impacts innovative behavior. Light pollution can disrupt circadian rhythms and lead to sleep loss (Cho, Joo, Koo, & Hong, 2013; Raap, Pinxten, & Eens, 2015; Tapia-Osorio, Salgado-Delgado, Angeles-Castellanos, & Escobar, 2013; Yorzinski et al., 2015). In turn, sleep loss (both short term and long term) can lead to cognitive and motivational deficits (reviewed in Alkadhi, Zagaar, Alhaider, Salim, & Aleisa, 2013; Engle-Friedman, 2014; Vorster & Born, 2015) in a wide range of species, including birds (Jackson et al., 2008), humans (Drummond et al., 2005; Thomas et al., 2000), insects (Beyaert, Greggers, & Menzel, 2012), mice (Linden, Bern, & Fishbein, 1974), and rats (McDermott et al., 2003). It is, therefore, possible that light pollution negatively influences innovation, by impairing cognition, motivation, or both (Griffin & Guez, 2014; van Horik & Madden, 2016).

Due to street lighting, lighted buildings, security lights, and other anthropogenic light sources, light pollution affects nearly 20% of land on earth (Cinzano, Falchi, & Elvidge, 2001). This light pollution has significant effects on animals (Rich & Longcore, 2006): It can alter their movement patterns (Avery, Springer, & Cassel, 1976; Tuxbury & Salmon, 2005), courtship behavior (Kempenaers, Borgström, Loës, Schlicht, & Valcu, 2010; Miller, 2006), foraging success (Yurk & Trites, 2000), and antipredator behavior (Yorzinski et al., 2015). We are unaware of any studies directly examining the impact of light pollution on innovation.

We, therefore, investigated whether artificial light pollution impacts innovation. We addressed this topic in peafowl (*Pavo cristatus*), a species that is increasingly exposed to light pollution as it expands into new habitats due to habitat loss (Ramesh & McGowan, 2009). Previous work demonstrated that peafowl increase their nocturnal vigilance rates when exposed to artificial light pollution and therefore spend less time sleeping at night (Yorzinski et al., 2015). Because sleep deprivation can lead to cognitive and motivational deficits (Alkadhi et al., 2013; Engle-Friedman, 2014; Vorster & Born, 2015), we expected that peafowl exposed to light pollution would be less successful in solving a problem-solving task. After either being exposed to artificial light pollution at night or not being exposed, the peafowl were presented with a problem-solving task. Problem-solving tasks are considered valid assays of innovation because innovation in the wild is strongly correlated with problem-solving success (Griffin & Guez, 2014; Lefebvre, Reader, & Sol, 2004; Lefebvre & Sol, 2008; Webster & Lefebvre, 2001). We investigated whether acute exposure to light pollution impacted the birds' success in solving the problem-solving task. We also examined whether other factors, including sex of the bird, persistence, and environmental variables impacted problem-solving success.

2 | METHODS

2.1 | Animal subjects and study site

We tested the problem-solving success of 42 adult Indian peafowl (15 females and six males were exposed to light pollution; 14 females and seven males were not exposed to light pollution; and all of the birds in the flock were tested) from a captive population in West Lafayette, Indiana (40.450327°N, −87.052574°E) between June 2015 and September 2015 (see Yorzinski, Patricelli, Babcock, Pearson, & Platt, 2013; for further details on the population). The birds were captured as adults (exact ages were unknown) from feral populations between 2008 and 2010; they were captured from rural and suburban populations and therefore likely had some exposure to light pollution prior to being held in captivity. While in captivity, they were not exposed to light pollution (they were housed in rural areas) except in 2–4 nights during a previous study (Yorzinski et al., 2015). The birds were accustomed to humans entering their enclosure to provide daily care. They had never been tested on a problem-solving task prior to this study. The peafowl were individually marked with plastic or metal leg bands and housed in an outdoor enclosure (24.4 m × 18.3 m × 1.8 m). They were given food (corn and maintainer pellets) once a day and water ad libitum. This study was approved by Purdue University's Animal Care and Use Committee (#1504001232).

2.2 | Experimental procedure

For each trial, a bird was randomly selected from our captive population and released into a testing room at least 4 hours before sunset (8.56 ± 0.31 hr; range: 4.2–12.2 hr). The testing room was a section (9 m × 4.5 m) within the outdoor enclosure which was surrounded by black plastic so that the bird being tested could not see the rest of the flock. The testing room had a wooden roost that was 4.5 m from an LED flood light (Philips 17-Watt Outdoor and Security Bright White; model: PAR38). This flood light had a flicker rate of 38 kHz, and the spectral radiance had two peaks: 4 mW/nm at 450 nm and 8.4 mW/nm at 600 nm (see Philips technical application guides for complete graph of spectral radiance). The light was suspended from the roof (1.8 m from the ground). The light was turned on in half of the trials and turned off in the other half of the trials (trials were randomly assigned to this treatment). During trials in which the light was on, the light was turned on immediately before the bird was put inside the testing room and remained on until after the trial ended the next day; given variation in day length across the study period, the birds were exposed to light pollution at night for at least 8 hr (amount of time between sunset the previous day and sunrise on the trial day: 9.72 ± 0.13 hr; range: 8.92–11.97 hr). At night, when the light was turned on, the light intensity was 1,260 lux below the light (light meter on ground facing up at light) and 0.75 lux at the roost (light meter facing toward the light); when the light was turned off, the light intensity was 0.04 lux below the light and 0.01 lux at the roost (Extech EasyView 31 light meter; resolution: 0.01 lux for readings below 20 lux and 1 lux for readings above 999; measurements taken during a night with clear skies and 69.5% moon illumination). The setup in the testing room was identical to that used in a related study investigating artificial light pollution (Yorzinski et al., 2015) except there was only water and no food available; while we did not provide food, the trial birds may still have been able to eat insects that passed through the testing room or vegetation that fell inside.

An experimenter entered the testing room the following morning within four hours after sunrise, placed the problem-solving task on the ground and 1 m from the roost, and then left the testing room. The problem-solving task was similar to that used in another problem-solving study (feeder two in Bókony et al., 2014). The problem-solving task consisted of two clear bowls (diameter: 0.12 m; height: 0.06 m; black paper lined the bottom of the bowls) separated by 0.19 m that were glued to a wooden board (0.15 m × 0.60 m; Figure 1). One of the bowls ("non-puzzle bowl") had no lid and five mealworms (*Tenebrio molitor*) inside. The other bowl ("puzzle bowl") had ten mealworms inside but had a lid made of bakery paper. The problem-solving task was novel to the birds in that they had never encountered these particular bowls before but they did regularly see wooden boards (as their roosts were made of wooden boards). The peafowl are not regularly fed mealworms but they are a preferred food item (pers. obs.). Sticks were placed around the problem-solving task to delineate an area that extended 1 m in front of the problem-solving task (the problem-solving task was placed 0.35 m from the edge of the testing room). A trial ended when the bird solved the problem-solving task (broke through the bakery paper of the puzzle bowl and ate the first mealworm). If the bird did not solve the task within three hours, the trial was ended. The experiment was recorded using three cameras (Bolide IR Bullet Camera) multiplexed to a DVR (Swann DVR4-2600). The experimenter remained concealed during the trials but observed them through a monitor that was connected to the DVR. The bird was returned to the main enclosure after the trial ended.

FIGURE 1 A peahen is within the rectangle in front of the problem-solving task. The non-puzzle bowl is on the right side of the board, and the puzzle bowl is on the left side. The problem-solving task has not yet been solved (the baking paper lid of the puzzle bowl has not been pierced)

2.3 | Measurements and statistical analysis

The behavior of the birds was analyzed using the video recordings (InqScribe software). The latency to solve the puzzle was the amount of time between solving the puzzle and when the bird first contacted the puzzle bowl. We calculated the contact rate by counting the number of times that each bird contacted (pecked or scratched) the puzzle bowl and dividing by the contact trial duration (amount of time between solving puzzle or trial end [if the bird did not solve the puzzle] and when the bird first contacted the puzzle bowl). We calculated the percentage of time near the task by summing the amount of time that each bird was within the 1-m rectangle around the problem-solving task (including the area immediately between the puzzle and edge of the testing room) and dividing by the time trial duration (amount of time between solving puzzle or trial end [if the bird did not solve the puzzle] and when the bird first entered the 1-m rectangle).

We performed a survival analysis using Cox proportional hazards model with stepwise selection (PROC PHREG; Cox, 1972). We report the full model as well as the reduced model (treatment + significant variables from the selection procedure). We also reran the reduced model without contact rate and time spent near the task; the effect of treatment was qualitatively the same as in the reduced model with those behavioral variables included. This survival analysis is appropriate for our dataset because it includes censored values (not solving the puzzle within the experimental time limit) instead of treating them as missing data in the analyses. If the bird solved the puzzle, the dependent variable was the latency to solve the puzzle. If the bird did not solve the puzzle, the dependent variable was the censored value (3 hr; total time that the trials lasted). The independent variables were whether the birds were exposed to artificial light during the preceding night (treatment), sex of the bird, nighttime length (amount of time between sunset the previous day and sunrise on the trial day), amount of time the birds spent in the testing room prior to the start of the trial (amount of time between the start of the trial and when the bird was put inside the testing room the previous day), their latency to initially contact the problem-solving task, contact rate, percentage of time near the task, whether they scratched at the problem-solving task or not (all of the birds pecked at the task but only some of them also scratched at it), and environmental variables (temperature and wind speed at the start of each trial as well as moon illumination and mean cloud cover during the preceding night). The temperature, wind speed, moon illumination (fraction of the moon's surface that was illuminated), and cloud cover (percentage of the sky covered in clouds on a scale from 1 to 5) were obtained from nearby sources (temperature and wind speed: http://iclimate.org, ACRE- West Lafayette, 40.4749°N, -86.9915°E; moon: http://www.timeanddate.com, Lafayette, IN, 40.25°N, -86.54°E; cloud cover: https://mesonet.agron.iastate.edu, 40.4148°N, -86.9333°E).

We also performed general linear models (PROC GLM) to examine whether behaviors (contact rate, percentage of time near the task, and latency to initially contact the problem-solving task) were impacted by the light treatment or sex of the bird; separate models were run for each analysis. All statistics were performed with SAS (Version 9.4; SAS Institute). Means ± standard errors are provided.

3 | RESULTS

With the exception of three females (two tested with light pollution and one tested without light pollution), all of the birds ate the mealworms in the non-puzzle bowl (mean latency to eat first mealworm in non-puzzle bowl after task presented: 1666 ± 371 s; range: 48–7891 s) and made contact with the puzzle bowl; we excluded these three females from the analyses because they did not eat the mealworms in the non-puzzle bowl and they never made contact with the problem-solving task. All of the birds that solved the problem-solving task (33%) ate the mealworms in the non-puzzle bowl before the mealworms in the puzzle bowl. The amount of time it took the birds to solve the problem-solving task varied widely (mean: 1567 ± 486 s; range: 166.2–5245.2 s).

The birds' success at the problem-solving task was unrelated to whether they were exposed to artificial light during the preceding night or not, the nighttime length, the amount of time they were in the testing room prior to the start of the trial, their latency to initially contact the problem-solving task, whether they scratched the problem-solving task or not, temperature, cloud cover, or wind speed (Table 1: reduced model). When birds were exposed to light pollution, 26.3% (95% CI using Wilson method [Brown, Cat, & DasGupta, 2001;]: 11.8–48.8%) of them solved the task; when the birds were not exposed to light pollution, 40.0% (95% CI using Wilson method: 21.9–61.3%) of them solved the task (Figure 2a). However, males were more likely to solve the task than females (hazard ratio: 0.059, 95% CI: 0.010–0.33; Figure 2b): 54% of males solved the task while only 23% of females solved the task. The birds were more likely to solve the problem-solving task if they exhibited a higher contact rate and spent a higher percentage of time near the task. Lastly, birds were more likely to solve the task when the moon illumination was high (Table 1: reduced model).

The light treatment did not impact contact rate ($F_{1,37}$=0.00, p = .97), percentage of time near the task ($F_{1,37}$=0.01, p = .91), nor the latency to initially contact the problem-solving task ($F_{1,37}$=0.57, p = .45). The sex of the bird also did not impact contact rate ($F_{1,37}$=1.4, p = .24), percentage of time spent near the task ($F_{1,37}$=0.54, p = .47), nor the latency to initially contact the problem-solving task ($F_{1,37}$=0.62, p = .44).

4 | DISCUSSION

The results of this study do not support the hypothesis that acute exposure to artificial light pollution (one night) impairs the problem-solving success of peafowl. Problem-solving success in peafowl was unrelated to whether they were exposed to artificial night lighting or not.

Light pollution can negatively impact the fitness of animals (Rich & Longcore, 2006). Previous research on peafowl found that they increase their nocturnal vigilance levels in response to light pollution and therefore spend less time sleeping at night (Yorzinski et al., 2015). Their nocturnal vigilance levels are significantly increased by even a single night of exposure to light pollution; this increase in nocturnal vigilance reduces the percentage of time they spend sleeping from approximately 50% of the night (without artificial light) to only 20% of the night (with artificial light; Yorzinski et al., 2015). Given that a single night of sleep deprivation can lead to cognitive and motivational deficits (Alkadhi et al., 2013; Engle-Friedman, 2014; Vorster & Born,

TABLE 1 The impact of behavioral and environmental variables on the latency of peafowl to solve the problem-solving task. DF is 1 for all variables. * indicates that the variable is a significant predictor of the latency of peafowl to solve the task

	Full Model			Reduced Model		
Variable	Parameter Estimate (SE)	X^2	*p*	Parameter Estimate (SE)	X^2	*p*
Treatment	5.34 (3.43)	2.42	.12	0.93 (0.77)	1.46	.23
Sex	16.03 (8.04)	3.98	.046*	2.84 (0.89)	10.25	.0014*
Nighttime length	3.36 (2.83)	1.41	.24	-	-	-
Amount of time spent in testing room prior to trial start	3.97 (2.16)	3.37	.066	-	-	-
Latency to initially contact the problem-solving task	0.12 (0.06)	3.61	.058	-	-	-
Contact rate	31.23 (17.96)	3.02	.082	6.85 (2.03)	11.43	.0007*
Percentage of time near the task	25.09 (13.16)	3.64	.057	2.98 (1.26)	5.62	.0178*
Scratch	5.82 (3.31)	3.10	.079	-	-	-
Temperature	-0.09 (0.20)	0.23	.63	-	-	-
Moon illumination	0.18 (0.09)	3.78	.052	0.034 (0.013)	6.74	.0094*
Cloud cover	4.30 (2.55)	2.86	.091	-	-	-
Wind speed	−0.80 (0.76)	1.10	.29	-	-	-

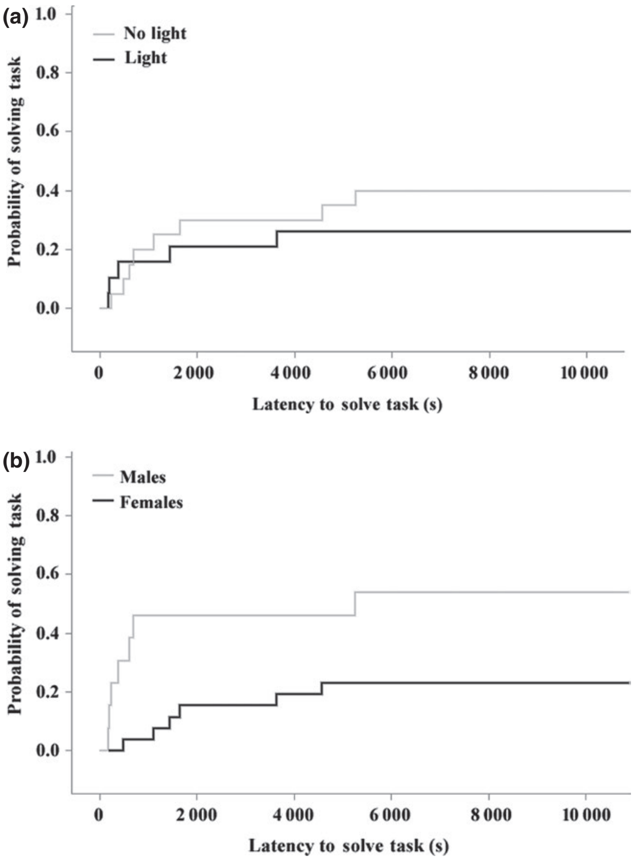

FIGURE 2 The probability of birds solving the task in relation to (a) treatment and (b) sex

2015), we expected that birds exposed to light pollution would have impaired cognitive or motivational functioning. However, problem-solving success in peafowl was unrelated to acute exposure to light pollution. Previous studies have found that urban birds exposed to light pollution (along with other pollutants associated with urbanization) are more successful in problem-solving tasks compared to their rural counterparts (Audet, Ducatez, & Lefebvre, 2016; Cook, Weaver, Hutton, & McGraw, 2017; Preiszner et al., 2017), further suggesting that birds can adapt to light pollution without negative consequences on their problem-solving success.

Animals could experience acute or chronic exposure to light pollution at night. Some animals do not sleep at the same location each night (Mendes-Pontes & Soares, 2005; Phoonjampa, Koenig, Borries, Gale, & Savini, 2010; and may, therefore, be exposed to light pollution one night but not another night. Even animals that sleep in the same area every night may be exposed to differing levels of light pollution if they alter their exact sleeping spot. In contrast, other animals may experience chronic exposure to light pollution if they sleep in the same area and at the same sleeping spot nightly. No studies have examined where individual peafowl sleep each night in the wild, but captive peahens will modify their sleep site to avoid light pollution (Yorzinski et al., 2015). Therefore, it is possible that peafowl experience acute exposure to light pollution if they are living in environments where they can alter their exact sleeping spot or have chronic exposure if they are living in environments where light pollution is unavoidable.

The peafowl were exposed to light pollution for one night in this study and it is, therefore, possible that their problem-solving success would have been impaired if they were exposed to light pollution for a longer period of time. Additional experiments in which birds experience light pollution over a longer time span are necessary to further understand the relationship between light pollution and problem-solving success. While acute exposure to light pollution did not impact the problem-solving success of peafowl, other factors did influence their problem-solving success.

Birds were more likely to solve the task when natural nocturnal lighting was greater (i.e., high levels of moon illumination). It is possible that lunar phase impacts sleep stages in the birds and influences their cognitive and motivational abilities. As has been found in humans (Cajochen et al., 2013), the phase of the moon can impact the amount of time spent in deep sleep. Additional research will be necessary to explore the link between lunar phase and innovation in birds.

Persistence, or task-directed motivation, is another factor that underlies problem-solving success (Griffin & Guez, 2014). Many studies have found that persistence is strongly linked to individuals' abilities to solve a task. For example, great tits and blue tits are more successful in a problem-solving task in the wild when they spend more time near the task (Morand-Ferron, Cole, Rawles, & Quinn, 2011). Likewise, Indian mynas and pheasant chicks are most successful in a task when they frequently peck at the task (van Horik & Madden, 2016; Sol, Griffin, & Barthomeus, 2012). Our results are consistent with this previous work in that peafowl were also more likely to solve the task when they spent more time near the task and contacted the task more often. The peafowl exhibited wide variation in their persistence behavior with some individuals spending nearly all of their time near the problem-solving task and others rarely visiting it. Given that the birds were deprived of their regular food for a limited period prior to trial onset (and could have also eaten some insects or vegetation), it would be interesting to see if their persistence behavior and problem-solving success would increase if they were deprived of food for more time. Guppies are more innovative when they are food-deprived compared to when they are regularly fed (Laland & Reader, 1999).

The problem-solving success of peafowl differed between the sexes. Peacocks were more likely to solve the problem-solving task than females. Because males are larger than females, their nutritional requirements are likely greater and being deprived of food could exert a stronger physiological demand on their bodies than it does in females. However, we did not find that motivation to solve the task differed between the sexes: males and females spent a similar amount of time near the task and pecked at the task a similar number of times. Peacocks are under extreme sexual selection as only a small proportion of males reproduce (Petrie, Halliday, & Sanders, 1991). Because of this intense competition among males, problem-solving success in males may be favored. In fact, male satin bowerbirds with superior problem-solving success secure the most matings (Keagy, Savard, & Borgia, 2009; but see Isden, Panayi, Dingle, & Madden, 2013). Future studies that examine the relationship between problem-solving success and mating success in peacocks would be informative. Problem-solving success also differs between the sexes in other species. Female guppies are more likely to solve a foraging task than males (Laland & Reader, 1999), and male meerkats are more likely to solve a foraging task than females (Thornton & Samson, 2012). Across different types of problem-solving tasks, males in many species of primates are more innovative than females (Reader & Laland, 2001). In many avian species, however, differences in problem-solving success between the sexes have not been found (Cole, Cram, & Quinn, 2011; Morand-Ferron et al., 2011; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Kozlovsky, Branch, & Pravosudov, 2015) except those reported here. Further studies examining the problem-solving success of species under intense sexual selection would be valuable.

ACKNOWLEDGEMENTS

We thank the Purdue Department of Forestry and Natural Resources for allowing us to house the birds on their property and providing logistical support. Barny Dunning also provided valuable logistical support. Edward Jones and Shiyuan He provided statistical advice. This research was funded by the College of Agriculture and Life Sciences at Texas A&M University and Texas A&M AgriLife Research.

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How to cite this article: Yorzinski JL, Ordonez KA, Chema KT. Does artificial light pollution impair problem-solving success in peafowl?. *Ethology*. 2017;00:1–7. https://doi.org/10.1111/eth.12658