



Evaluating potential effects of solar power facilities on wildlife from an animal behavior perspective

Rachel Y. Chock¹ | Barbara Clucas² | Elizabeth K. Peterson^{3,4} |
Bradley F. Blackwell⁵ | Daniel T. Blumstein⁶ | Kathleen Church⁷ |
Esteban Fernández-Juricic⁸ | Gabriel Francescoli⁹ | Alison L. Greggor¹ |
Paul Kemp¹⁰ | Gabriela M. Pinho⁶ | Peter M. Sanzenbacher¹¹ |
Bruce A. Schulte¹² | Pauline Toni¹³

¹Recovery Ecology, San Diego Zoo Institute for Conservation Research, Escondido, California

²Department of Wildlife, Humboldt State University, Arcata, California

³Communities to Build Active STEM Engagement, Colorado State University-Pueblo, Pueblo, Colorado

⁴Department of Biology, Colorado State University-Pueblo, Pueblo, Colorado

⁵U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Sandusky, Ohio

⁶Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, California

⁷Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario, Canada

⁸Department of Biological Sciences, Purdue University, West Lafayette, Indiana

⁹Sección Etología, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

¹⁰International Centre for Ecohydraulics Research, Faculty of Engineering and Physical Sciences, Department of Civil, Maritime and Environmental Engineering, University of Southampton, Southampton, UK

¹¹U.S. Fish and Wildlife Service, Palm Springs, California

¹²Department of Biology, Western Kentucky University, Bowling Green, Kentucky

¹³Department of Biology, Université de Sherbrooke, Québec, Canada

Correspondence

Rachel Y. Chock, Recovery Ecology, San Diego Zoo Institute for Conservation Research, Escondido, CA.
Email: rchock@sandiegozoo.org

Funding information

Animal Behavior Society

Abstract

Solar power is a renewable energy source with great potential to help meet increasing global energy demands and reduce our reliance on fossil fuels. However, research is scarce on how solar facilities affect wildlife. With input from professionals in ecology, conservation, and energy, we conducted a research-prioritization process and identified key questions needed to better understand impacts of solar facilities on wildlife. We focused on animal behavior, which can be used to identify population responses before mortality or other fitness consequences are documented. Behavioral studies can also offer approaches to understand the mechanisms leading to negative interactions (e.g., collision, singeing, avoidance) and provide insight into mitigating effects. Here, we review how behavioral responses to solar facilities,

Rachel Y. Chock, Barbara Clucas, and Elizabeth K. Peterson contributed equally to this study.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. Conservation Science and Practice published by Wiley Periodicals LLC on behalf of Society for Conservation Biology

including perception, movement, habitat use, and interspecific interactions are priority research areas. Addressing these themes will lead to a more comprehensive understanding of the effects of solar power on wildlife and guide future mitigation.

KEYWORDS

animal behavior, concentrating solar power (CSP), conservation, conservation behavior, photovoltaic (PV) cells, research prioritization process, solar power, utility-scale solar energy (USSE)

1 | INTRODUCTION

As the global human population continues to grow, energy demand increases (IEA, 2019; Pazheri, Othman, & Malik, 2014). Although fossil fuels still dominate energy production, renewable energy sources are a rapidly expanding sector of the global energy market (Islam, Huda, Abdullah, & Saidur, 2018; USEIA, 2019). Renewable resources can help combat climate change, and with falling production costs, serve as an economical alternative to fossil fuels (IRENA, 2019). Most U.S. states now have Renewable Portfolio Standards and other policies that further incentivize production of renewable energy (NCCETC, 2020; NREL, 2019).

The number and size of utility-scale (e.g., >20 MW) solar energy facilities (hereafter solar facilities) have dramatically increased during the past 20 years (Figure 1; Hernandez et al., 2014); for example, the average utility-scale photovoltaic (PV) system installation size increased over 80% from 2010 to 2019 in the United States (NREL, 2020). Solar energy technologies typically fall into two main categories: (a) PV cells that convert sunlight into electrical current (Figures 1a and 2) concentrating solar power (CSP) which uses mirrors to focus sunlight to heat fluids that power steam turbines or generators (Figure 1b,c).

Our current understanding of the impacts of solar facilities on wildlife is limited, despite the pace and scale of its development. Environmental effects, such as soil erosion, changes in water use, and increases in local temperature, are well documented (Barron-Gafford et al., 2016; Hernandez et al., 2014; Moore-O'Leary et al., 2017). A few studies suggest that solar facilities could affect wildlife through exclusionary fencing, habitat destruction or alteration, and direct mortality (Table 1; Northrup & Wittemyer, 2013; Walston, Rollins, LaGory, Smith, & Meyers, 2016), but their relative scarcity highlights the need for additional research (see also Agha, Lovich, Ennen, & Todd, 2020). In particular, studies of wildlife behavioral response to solar facilities have been called for, including by working groups focused on bird interactions

with solar facilities (ASCWG, 2020; ASWG, 2020); but such studies are largely still lacking from the literature (Lovich & Ennen, 2011; Northrup & Wittemyer, 2013).

Behavioral responses are often the most visible signs of detrimental effects, as behavioral shifts are usually an animal's first response to environmental change (Dimitri & Longland, 2018; Northrup & Wittemyer, 2013). Although direct mortality is the most obvious sign of negative impacts, large energy facilities may also impact individual fitness, as measured by survival and reproduction (hereafter "fitness"), resulting in population-level impacts that are harder to quantify without long-term demographic studies or using behavioral observations. For example, individuals could decrease mating behavior in response to increased disturbance (Holloran, Kaiser, & Hubert, 2010), stress levels (Lovich & Ennen, 2011), and pollution (Peterson et al., 2017). In addition, behavioral studies can offer approaches to understand the mechanisms leading to negative effects and to provide mitigative strategies. Animal behavior has been successfully utilized by wildlife and natural resource managers to mitigate problems and improve management strategies (Berger-Tal et al., 2011; Dimitri & Longland, 2018). For example, animal behavior has been used to understand and develop approaches to mitigate avian collisions at airports (Blackwell & Fernández-Juricic, 2013). It is imperative for the solar industry to incorporate behavioral research now, in a relatively early stage of the solar boom, to ensure solar power is sustainable for local wildlife populations and to avoid similar developmental and legal pitfalls that plagued the wind industry in its early boom (Brown & Escobar, 2007).

Using a multiphase research-prioritization process (see Supporting Information 1 for detailed methods) we implemented an online survey to ask professionals in the fields of ecology, conservation and energy to identify key behavioral research questions related to potential wildlife conservation issues at solar facilities (see Supporting Information 2 for full survey). We reduced and prioritized these questions at a 2019 workshop held

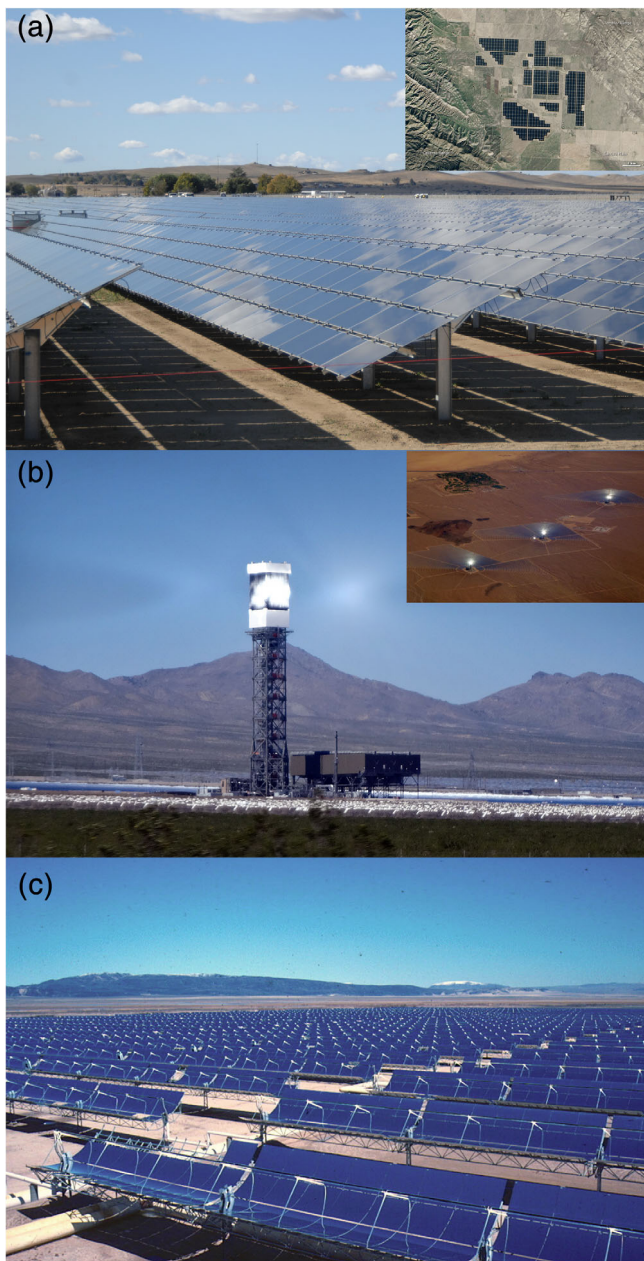


FIGURE 1 (a) An example of photovoltaic (PV) solar panels at topaz solar (550 MW; 4,700 acres). Photo by Pacific Southwest Region from Sacramento, U.S.—Solar Panels at topaz solar 1, Public Domain, <https://commons.wikimedia.org/w/index.php?curid=36895794>. Inset: aerial photo by Earth Observatory image by Jesse Allen, using EO-1 ALI data provided courtesy of the NASA EO-1 team. Public Domain, <https://commons.wikimedia.org/w/index.php?curid=38864327>. (b) An example of a concentrating solar power (CSP) tower at Ivanpah Solar Electric Generating System (377 MW; 3,500 acres). Photo by Craig Dietrich—Flickr: Ivanpah Solar Power Facility, CC BY 2.0, <https://commons.wikimedia.org/w/index.php?curid=28676343>. Inset: aerial photo by Jllm06—Own work, CC BY-SA 4.0, <https://commons.wikimedia.org/w/index.php?curid=42975801>. (c) An example of a CSP parabolic trough at Solar Energy Generating Systems (SEGS; 354 MW; 1,600 acres). Photo by USA.Gov—BLM—Public domain

by the Animal Behavior Society Conservation Committee (Supporting Information 1), and summarize here the emerging themes that resulted from this process (Table 2).

2 | WILDLIFE PERCEPTION OF SOLAR FACILITIES

Solar facilities have the potential to deter, attract, or be imperceptible to individuals, all of which can lead to negative consequences for a variety of species (Kagan et al., 2014; Smith & Dwyer, 2016). Avoidance of solar facilities may lead to use of lower quality habitat or population fragmentation (Hernandez et al., 2014; Saunders, Hobbs, & Margules, 1991) and species attracted to solar facilities might be victims of ecological traps (Robertson & Hutto, 2006). When species attracted to facilities experience low survival or reproduction onsite, regional population dynamics could follow a source-sink pattern, affecting populations beyond site boundaries (Delibes, Gaona, & Ferreras, 2001). Alternatively, solar facilities may attract and provide high quality habitat for non-native or urban adapted species (Hufbauer et al., 2011; Tuomainen & Candolin, 2011). High population density of a few species could have cascading effects, potentially reducing food web integrity (Jessop, Smissen, Scheelings, & Dempster, 2012) or altering species' interactions (see below). Species unable to detect or avoid structures (e.g., power lines, glass windows) are at risk of collision and direct mortality (Bevanger, 1994).

At the core of the problem, we do not fully understand the mechanisms involved in wildlife perception of solar facilities or all the factors that influence avoidance or attraction (but see work by Horváth et al. (2010) and others on aquatic insect attraction to polarized light and solar panels). Individuals deterred by noise pollution might avoid facilities during construction and operation (Halfwerk & Slabbekoorn, 2015) and could also be affected by road noise from traffic associated with them. Individuals might be attracted to these sites because of microclimatic conditions, cover, water availability (e.g., evaporative cooling ponds; Walston et al., 2016), enhanced prey density, lighting, confusion of visual cues, or other potential factors (Dominoni et al., 2020). We also need to know if there is variation in perception and response to solar facilities within and between species and at different temporal scales, both seasonal and daily.

We can identify key behavioral responses by studying how species perceive solar facility structures (Kagan et al., 2014) relative to surrounding landscape elements. Ultimately, this process can allow for manipulation of

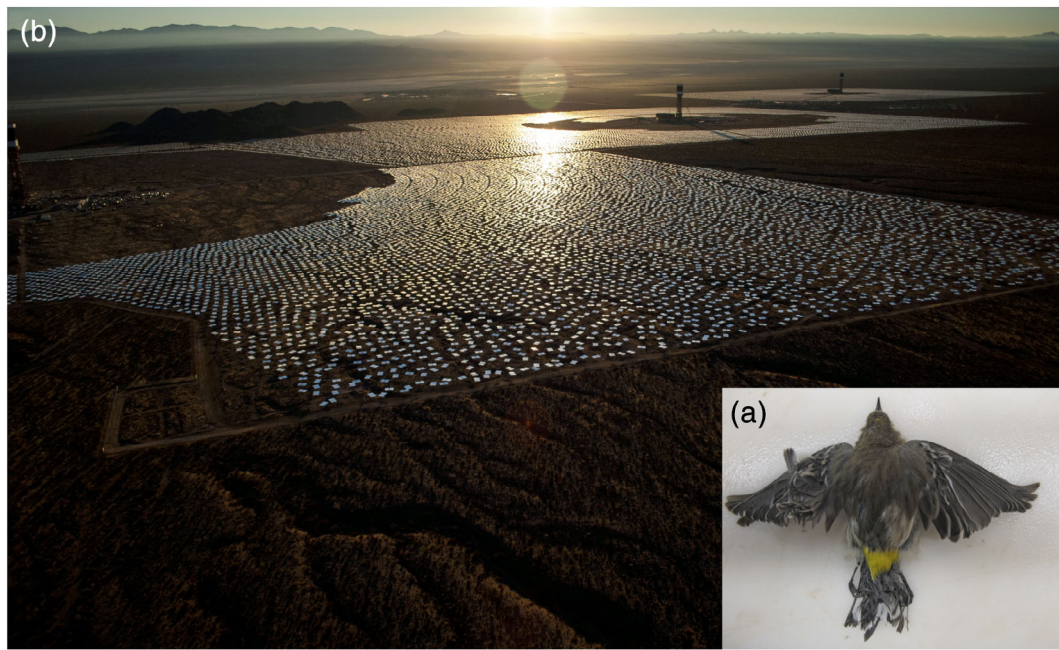


FIGURE 2 (a) Concentrating solar power (CSP) facilities can cause direct mortality to aerial species that fly into solar flare, such as this yellow-rumped warbler burned mid-air at Ivanpah (photograph by U.S. Fish and Wildlife Service, 2013, public domain). (b) CSP or PV facilities can create a “lake effect” (photograph by Kerry Holcomb, used with permission, Ivanpah Solar Electric Generating System, CA); water birds that mistakenly land on the hard surfaces can die on impact, become injured, or are unable to take off from terrestrial surfaces and ultimately die of exposure

TABLE 1 Examples of direct injury and mortality effects, as well as secondary mortality effects, on wildlife species that use the airspace and land covers at solar energy facilities. Noted effects are based on a select number of government and peer-reviewed literature sources, but not a complete survey or synthesis of the current literature

Effect		Taxa affected	Source ¹
Direct injury/ mortality	Solar flux	Birds, insects	2, 3, 4, 6, 7, 8, 9, 10
	Undefined trauma	Birds	8
	Impact trauma	Birds, bats	1, 2, 3, 5, 6, 8, 11
	Electrocution	Birds	6, 8, 11
	Entrapment/drowning in water in-take structures and evaporation ponds	Birds, mammals, insects	4, 6, 7
	Entrapment in soil ruts from vehicle passage	Amphibians, reptiles	10
Secondary mortality	Predation trauma	Amphibians, birds, reptiles	10, 8
	Light pollution	Amphibians, birds, bats, other mammals, insects, reptiles	4, 5, 10
	Electromagnetic field effects	Amphibians, bats, insects, reptiles	4, 10
	Other anthropogenic effects	Amphibians, birds, bats, other mammals, insects, reptiles	5, 7, 8, 10

Note: 1. Costantini, Gustin, Ferrarini, and Dell’Omo (2016); 2. Diehl, Valdez, Preston, Wellik, and Cryan (2016); 3. Ho (2016); 4. Horváth et al. (2010); 5. Huso, Dietsch, and Nicolai (2016); 6. Jeal, Perold, Ralston-Paton, and Ryan (2019); 7. Jeal, Perold, Seymour, Ralston-Paton, and Ryan (2019); 8. Kagan, Viner, Trail, and Espinoza (2014); 9. Loss, Dorning, and Diffendorfer (2019); 10. Lovich and Ennen (2011); 11. McCrary, McKernan, Schreiber, Wagner, and Sciarrotta (1986).

stimuli and associated behavior to reduce mortality (sensu Blackwell et al., 2009 and citations therein). Birds, for example, can experience risk of mortality due to

collision (i.e., direct contact with the solar facility), solar-flux (i.e., birds are either burned or singed by exposure to the solar facility; Figure 2a), or become stranded

TABLE 2 Key themes in animal behavior research that could improve our understanding of impacts of solar facilities on wildlife and potential solutions. These themes emerged from a multiphase research prioritization process (see Supporting Information 1) and the final list of priority research questions (Table S4)

Theme	Research areas	Research priority questions	Examples from the literature related to or applicable to solar power facilities
Perception of solar facilities: natural attraction or deterrence?	<ol style="list-style-type: none"> 1. Understand factors involved in wildlife perception of solar facilities 2. Quantify key sensory mechanisms of species with high mortality at facilities 3. Use information in perception models to quantify conspicuousness of facility elements 4. Modify facility elements to enhance or reduce conspicuousness and measure behavioral response 	<ul style="list-style-type: none"> • Do solar facilities attract or deter species? • What are the behavioral/sensory mechanisms involved in creating attraction or deterrence to solar facilities? • What characteristics of solar facilities are attracting and/or deterring certain species? What are the fitness consequences? • How can solar facilities be designed to reduce attraction and reduce negative fitness consequences? 	Blackwell, Fernández-Juricic, Seamans, and Dolans (2009), Horváth et al. (2010), Blackwell and Fernández-Juricic (2013), Arnett, Hein, Schirmacher, Huso, and Szewczak (2013), Kagan et al. (2014), Smith and Dwyer (2016), Fernández-Juricic (2016), Száz et al. (2016)
Habitat use in and around solar facilities in resident and migratory species	<ol style="list-style-type: none"> 1. Impacts on resident species <ol style="list-style-type: none"> a. Home range b. Habitat modification (e.g., fragmentation) 2. Impacts on migratory species <ol style="list-style-type: none"> a. Habitat connectivity b. Disruption of migratory behavior 	<ul style="list-style-type: none"> • What impact do solar facilities have on habitat use of resident species? • How far do the impacts on behavior extend into habitat? • How is migration behavior impacted by solar facilities? • How does solar facility type affect movement behavior? • Where should solar facilities be built to minimize impacts on behavior and fitness? 	Tsoutos, Frantzeskaki, and Gekas (2005), Arnett et al. (2008), Lovich and Ennen (2011), Turney and Fthenakis (2011), DeVault et al. (2014), Hernandez et al. (2014), Grippo, Hayse, and O'Connor (2015), Jeal et al. (2019,b)
Other impacts on fitness associated behavior	<ol style="list-style-type: none"> 1. Behavioral change before and after <ol style="list-style-type: none"> a. Impacts on foraging b. Impacts on species interactions <ol style="list-style-type: none"> i Antipredator behavior ii Predation iii Competition c. Impacts on reproduction 	<ul style="list-style-type: none"> • How does behavior (including activity patterns, foraging, predation, antipredator behavior, competition, habitat use, and movement) change before and after solar facility construction? • How do different types of solar facilities impact animal behavior of species directly and indirectly? 	Vistnes, Nellemann, Jordhoy, and Strand (2004); Epps et al. (2005); Reimers, Dahle, Eftestøl, Colman, and Gaare (2007); Sawyer, Kauffman, and Nelson (2009); Holloran et al. (2010); Cypher et al. (2019)

(i.e., water birds that cannot take off due to lack of water; ANL & NREL, 2015). It is therefore important to understand how birds and other wildlife perceive solar facilities and why they are attracted, deterred, or fail to detect them. In addition to individual responses to cues generated by solar facilities, vulnerability will vary according to species' ecology and behavior. We discuss below how animal movement, breeding, foraging behavior, and interspecific interactions may influence population level responses to solar facilities.

3 | MOVEMENT AND HABITAT USE IN AND AROUND SOLAR FACILITIES

Many animals, particularly those living in arid environments where solar facilities are more common, are living at their physiological limits; any added movement may thus be costly (Vale & Brito, 2015). Whether and how movements are influenced by a solar facility will be determined by: (a) the trade-off of associated benefits and

costs, (b) whether species are attracted or deterred by solar facilities, (c) whether a species is residential or migratory, and (d) the fitness impact of the responses.

3.1 | Resident species

Solar facility construction and operation directly and indirectly alter habitat use via functional habitat fragmentation, dispersal limitations, population isolation, and altered habitat quality (as previously reviewed in Lovich and Ennen (2011)). For example, vegetation at road edges appears to attract Agassiz's desert tortoises (*Gopherus agassizii*) to build burrows there, despite the apparent noise pollution and risk of vehicle collision (Lovich & Daniels, 2000; von Seckendorff Hoff & Marlow, 2002). CSP facilities can include evaporation ponds with chemically treated waters; these polluted waters can kill via drowning, poisoning, egg mortality, or biomagnification (Jeal, Perold, Ralston-Paton, & Ryan, 2019). Electromagnetic fields created by buried and aerial cables transporting energy can affect orientation of some organisms, impairing habitat use and likely causing additional physiological harm (Lovich & Ennen, 2011; Shepherd et al., 2019; Wyszowska, Shepherd, Sharkh, Jackson, & Newland, 2016). Also, changes in albedo from vegetation removal could cause local increases in temperature and evapotranspiration, which may influence movement patterns, reproductive success, and survival (Barron-Gafford et al., 2016). Although certain habitat modifications could benefit species, such as birds that can exploit solar facility structures for foraging, roosting or nesting (Jeal, Perold, Ralston-Paton, & Ryan, 2019) or prey species that experience reduced predation (Cypher et al., 2019), in most cases, modifications are likely to have negative impacts.

3.2 | Migratory species

Migratory animals are under escalating threat due to growth in human activity (Hardesty-Moore et al., 2018; Wilcove & Wikelski, 2008). Compared to other groups of species, migratory birds appear to suffer disproportionately higher mortality from solar facilities, particularly those located on migration routes and/or near breeding and wintering grounds (Walston et al., 2016). The greater abundance of insect prey attracted by the high structures and light (Diehl et al., 2016) likely attracts aerial insectivores, resulting in a higher risk to burning via solar flux from concentrated solar power (Figure 2a; McCrary et al., 1986; Kagan et al., 2014). Migratory water bird species are also susceptible because solar facilities may be

perceived as waterbodies (a hypothesized "lake effect"), attracting them to land and injuring, killing, or stranding them in the process (Figure 2b; Kagan et al., 2014).

3.3 | Facility siting

The effects of solar facilities on wildlife may be exacerbated or mitigated through decisions about where to build them. Models have been developed at regional scales to identify areas that have both high potential for solar energy development and suitability for species of special concern (Phillips & Cypher, 2019), or high species richness (Thomas et al., 2018), representing potential conflict areas that should be avoided. These and other studies also identify priority areas for facility siting that minimizes the loss of high quality habitat (DRECP, 2020; Stoms, Dashiell, & Davis, 2013). While these models provide greatest benefit to resident species, research on migratory routes for aerial and terrestrial wildlife is critical to improve siting recommendations (e.g., Ruegg et al., 2014). The infrastructure necessary to operate solar facilities often extends far into the habitat, and effects of these structures on migratory wildlife have been documented in other energy sectors. For instance, mule deer (*Odocoileus hemionus*) abandoned former migration corridors as a result of oil and gas exploration and moved into suboptimal habitat, resulting in migration bottlenecks with no observed acclimation over several years (Sawyer et al., 2009). Reindeer (*Rangifer tarandus*) actively avoid power lines (Reimers et al., 2007; Vistnes et al., 2004), a behavioral response that could similarly alter migration routes for other ungulates. Gene flow in populations of desert bighorn sheep (*Ovis canadensis nelsoni*) is impeded by the presence of barriers, including roadways and large mining operations, resulting in rapid declines in genetic diversity (Epps et al., 2005). Minimizing these off-site impacts by siting facilities closer to existing infrastructure is important for mitigating effects on wildlife (Stoms et al., 2013).

4 | OTHER FITNESS ASSOCIATED BEHAVIORS: FORAGING AND SPECIES INTERACTIONS

4.1 | Foraging

Foraging involves a complex suite of behaviors, including detection of food sources, perceiving temporal and spatial cues about food availability, and food searching, choice, retrieval, and processing. Solar facilities might alter cues and predation risk assessment or disrupt normal search

patterns via habitat change or construction of novel obstacles. Therefore, we must understand a species' trophic level (Fauvelle, Diepstraten, & Jessen, 2017; Moore-O'Leary et al., 2017) and the mechanisms underpinning its foraging decisions (e.g., olfactory cues; Schmitt, Shuttleworth, Ward, & Shrader, 2018) to estimate the impact of landscape alteration caused by solar facilities.

Spatial knowledge, which is critical in foraging behavior, increases individual fitness (Spencer, 2012), and changes in spatial distribution of resources may impact species depending on their capacity to update such information. Assessments on the plasticity of cognitive mapping and role of memory in animal foraging decisions would contribute to our understanding about the impact of solar facilities. For example, bison (*Bison bison*) remembered and used information about location and quality of meadows to make movement decisions, building individual cognitive maps of their environment (Merkle, Fortin, & Morales, 2014). Studies of species affected by solar facilities measuring the effect of changes in the distribution and availability of resources on animal behavior can help predict impacts of development at a population level.

4.2 | Predation, antipredator behavior, and competition

Habitat modification can affect predator-prey dynamics (Dorresteijn et al., 2015; Hawlena, Saltz, Abramsky, & Bouskila, 2010) and competitive interactions between species (Berger-Tal & Saltz, 2019). At solar facilities, reflective surfaces of buildings and PV panels create polarized light pollution that attracts polarotactic organisms, including many insects (Horváth, Kriska, Malik, & Robertson, 2009). Insectivorous species might benefit from the increased availability of prey but trade off potential danger from collisions with reflective surfaces and increased competition for food. In the Mojave Desert, the population of urban-associated common ravens (*Corvus corax*) has increased with development, and they exert high predation pressure on threatened desert tortoise (Kristan & Boarman, 2003), which also face other impacts due to solar development (Lovich & Ennen, 2011).

Alternatively, PV panels or mirrors could serve as shelter for some animals against predators, especially aerial ones, and solar facility buildings and fences can also provide shelter and escape routes for smaller prey by excluding larger terrestrial predators (Cypher et al., 2019). Increased vegetation near structures due to runoff (BLM & DOE, 2012) may be perceived as protective cover from predators (Jacob, 2008), but the vegetation may also make it more difficult to detect predators. Peripheral visibility

has been shown to be valued by both mammals (Bednekoff & Blumstein, 2009) and birds (Bednekoff & Lima, 1998); in areas with reduced peripheral visibility, animals perceive a greater risk of predation and may modify their behavior in potentially maladaptive ways, such as increasing time allocated to vigilance over foraging.

5 | FUTURE RESEARCH AND DESIGNING SOLUTIONS

As evidenced by our research and those of others (Agha et al., 2020; Conkling, Loss, Diffendorfer, Duerr, & Katzner, 2020), more studies about the potential impacts of solar facilities on wildlife are needed to develop solutions. Documented efforts to deter wildlife from solar power facilities and other human-made structures include acoustic (Arnett et al., 2013; May, Reitan, Bevanger, Lorentsen, & Nygård, 2015; Swaddle, Moseley, Hinders, & Smith, 2016), visual (Martin, 2011; Goller, Blackwell, DeVault, Baumhardt, & Fernández-Juricic, 2018; Hausberger, Boigné, Lesimple, Belin, & Henry, 2018), and tactile deterrents (Ho, 2016; Seamans, Martin, & Belant, 2013). Evaluation of the effectiveness of such deterrents, however, is often limited or inconclusive (e.g., Dorey, Dickey, & Walker, 2019), and may not address why individuals are attracted to the facilities or collide with facility structures in the first place. A more effective approach may be to understand wildlife perception of solar facilities and minimize features that attract them (e.g., Horváth et al., 2010), or modify features so that wildlife detect them and avoid collisions, burning and singeing. For instance, we can better understand how wildlife visually or otherwise perceive solar facilities by: (a) quantifying key properties of the sensory systems of species that experience high mortality, (b) use this information to quantify the degree of conspicuousness of solar panels and other structures from the species' sensory perspective, then (c) modify the properties of the solar panels to enhance or reduce their conspicuousness, and (d) measure behavioral responses to these modifications (Blackwell & Fernández-Juricic, 2013; Fernández-Juricic, 2016). For example, Horváth et al. (2010) tested the attraction of several aquatic insect species to PV solar panels with various modified features and found that white-framed and white-gridded panels were less attractive than black panels.

Our survey identified several research priorities for designing solutions focusing on where and how solar facilities can be built to minimize influences on behavior and fitness (Table 2 and Supporting Information 1). Another overarching question identified, while not specific to behavior, was whether facility designs should be exclusionary or permeable to wildlife. Some solar

facilities are currently evaluating how to co-manage wildlife and PV panels by making them more permeable (e.g., Cypher et al., 2019; Wilkening & Rautenstrauch, 2019). Nevertheless, the answer to this question is likely complex and specific to geography and species (see also Moore-O'Leary et al., 2017).

With regard to assessing and minimizing impacts of solar facilities on wildlife, our workshop identified the need for more purposeful study designs to begin addressing these priority questions (Table 2). Ideally, a before-after control-impact design is desirable; whereby, key behaviors are studied before and after the solar facility is developed, both at the facility location and at control sites (Conkling et al., 2020; Lovich & Ennen, 2011). While this rarely happens (see Agha et al., 2020), such design is the most powerful way to isolate the effects of a solar facility on behavior while controlling for other spatial and temporal variation. Experimental studies assessing impacts of different design features (such as panel height and spacing, corridor placement and size, and vegetation treatment), in addition to studying behavior at different distances from solar facilities, are also necessary to minimize detrimental effects on wildlife.

6 | CONCLUSIONS

Development of utility-scale solar facilities is expected to continue at a rapid pace (USEIA, 2019). There is an urgent need to address how to better locate, design, and operate solar facilities to mitigate potential negative effects on wildlife populations. We have highlighted major research themes addressing how approaches using animal behavior can be utilized to study wildlife-solar facilities interactions and how they could lead to solutions to reduce negative effects. Similar to how those in the wind energy industry have worked with animal behaviorists to reduce wildlife fatalities (e.g., Cryan et al., 2014), finding such solutions will need collaboration across industry, research, and management agencies. This can be achieved by forming working groups that can bring together entities from solar power facilities, wildlife agencies, and academia to determine shared research goals and to facilitate access to solar facilities, research permitting, and research funding opportunities (e.g., Bats and Wind Energy Cooperative, 2020).

ACKNOWLEDGMENTS

The authors thank the Animal Behavior Society for the opportunity and funding to organize a workshop (entitled "Conservation Behavior Workshop: Implications of Solar Power on Wildlife Conservation") at the Animal

Behavior Society Conference 2019 (Chicago, IL), and the funding to publish this manuscript. The authors thank everyone who responded to the online survey and participated in the workshop, especially Dr Thomas Dietsch and Peter Sanzenbacher (U.S. Fish and Wildlife Service). The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR' CONTRIBUTIONS

Rachel Y. Chock, Barbara Clucas, and Elizabeth K. Peterson: Organized the workshop that resulted in this study and coordinated the manuscript. All authors participated in the workshop and extensively contributed to the writing and revision of the manuscript.

DATA AVAILABILITY STATEMENT

Survey questionnaire and results from the workshop are freely available and included as Supporting Information.

ETHICS STATEMENT

The survey was approved by the Humboldt State University Institutional Review Board (IRB# 18-161).

ORCID

Rachel Y. Chock  <https://orcid.org/0000-0003-3954-5959>

REFERENCES

- Agha, M., Lovich, J. E., Ennen, J. R., & Todd, B. D. (2020). Wind, sun, and wildlife: Do wind and solar energy development "short-circuit" conservation in the western United States? *Environmental Research Letters*, *15*, 075004.
- Argonne National Laboratory & National Renewable Energy Laboratory (ANL & NREL). (2015). A review of avian monitoring and mitigation information at existing utility-scale solar facilities. Report prepared for US Department of Energy, SunShot Initiation and Office of Energy Efficiency & Renewable Energy.
- Arnett, E. B., Brown, W. K., Erickson, W. P., Fiedler, J. K., Hamilton, B. L., Henry, T. H., ... Tankersley, R. D. (2008). Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management*, *72*, 61–78.
- Arnett, E. B., Hein, C. D., Schirmacher, M. R., Huso, M. M. P., & Szwczak, J. M. (2013). Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing bat fatalities at wind turbines. *PLoS one*, *8*, e65794.
- Avian Solar Work Group (ASWG). (2020). Avian solar work group. Retrieved from <http://www.aviansolar.org/>.
- Avian-Solar Collaborative Working Group (ASCWG). (2020). Multiagency Avian-Solar Collaborative Working Group. Retrieved from <https://blmsolar.anl.gov/program/avian-solar/>.
- Barron-Gafford, G. A., Minor, R. L., Allen, N. A., Cronin, A. D., Brooks, A. E., & Pavao-Zuckerman, M. A. (2016). The

- photovoltaic heat island effect: Larger solar power plants increase local temperatures. *Scientific Report*, 6, 35070.
- Bats and Wind Energy Cooperative. (2020). Retrieved from <http://batsandwind.org/>.
- Bednekoff, P. A., & Blumstein, D. T. (2009). Peripheral obstructions influence marmot vigilance: Integrating observational and experimental results. *Behavioral Ecology*, 20, 1111–1117.
- Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology & Evolution*, 13, 284–287.
- Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B. P., & Saltz, D. (2011). Integrating animal behavior and conservation biology: A conceptual framework. *Behavioral Ecology*, 22, 236–239.
- Berger-Tal, O., & Saltz, D. (2019). Invisible barriers: Anthropogenic impacts on inter- and intra-specific interactions as drivers of landscape-independent fragmentation. *Philosophical Transactions of the Royal Society B*, 374, 20180049.
- Bevanger, K. (1994). Bird interactions with utility structures: Collision and electrocution, causes and mitigating measures. *Ibis*, 136, 412–425.
- Blackwell, B. F., & Fernández-Juricic, E. (2013). Behavior and physiology in the development and application of visual deterrents at airports. In T. L. DeVault, B. F. Blackwell, & J. L. Belant (Eds.), *Wildlife management in airport environments* (pp. 11–22). Baltimore, MD: The Johns Hopkins University Press.
- Blackwell, B. F., Fernández-Juricic, E., Seamans, T. W., & Dolans, T. (2009). Avian visual configuration and behavioural response to object approach. *Animal Behaviour*, 77, 673–684.
- Brown, B. T., & Escobar, B. A. (2007). Wind power: Generating electricity and lawsuits. *Energy Law Journal*, 28, 489–515.
- Bureau of Land Management & U.S. Department of Energy (BLM & DOE). (2012). Final programmatic environmental impact statement for solar energy development in six southwestern states, FES 12-24, DOE/EIS-0403.
- Conkling, T. J., Loss, S. R., Diffendorfer, J. E., Duerr, A., & Katzner, T. E. (2020). Limitations, lack of standardization, and recommended best practices in studies of renewable energy effects on birds and bats. *Conservation Biology*. <https://doi.org/10.1111/cobi.13457>
- Costantini, D., Gustin, M., Ferrarini, A., & Dell’Omo, G. (2016). Estimates of avian collision with power lines and carcass disappearance across differing environments. *Animal Conservation*, 20, 173–181.
- Cryan, P. M., Gorresen, P. M., Hein, C. D., Schirmacher, M. R., Diehl, R. H., Huso, M. M., ... Heist, K. (2014). Behavior of bats at wind turbines. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 15126–15131.
- Cypher, B. L., Westall, T. L., Spencer, K. A., Meade, D. E., Kelly, E. C., Dart, J., & van Horn Job, C. L. (2019). Response of San Joaquin kit foxes to topaz solar farms: Implications for conservation of kit foxes. Final Report prepared for: BHE Renewables Topaz Solar Farms.
- Delibes, M., Gaona, P., & Ferreras, P. (2001). Effects of an attractive sink leading into maladaptive habitat selection. *The American Naturalist*, 158, 277–285.
- Desert Renewable Energy Conservation Plan (DRECP). (2020). Retrieved from <https://www.energy.ca.gov/programs-and-topics/programs/desert-renewable-energy-conservation-plan/>.
- DeVault, T. L., Seamans, T. W., Schmidt, J. A., Belant, J. L., Blackwell, B. F., Mooers, N., ... van Pelt, L. (2014). Bird use of solar photovoltaic installations at US airports: Implications for aviation safety. *Landscape and Urban Planning*, 122, 122–128.
- Diehl, R. H., Valdez, E. W., Preston, T. M., Wellik, M. J., & Cryan, P. M. (2016). Evaluating the effectiveness of wildlife detection and observation technologies at a solar power tower facility. *PLoS one*, 11, e0158115.
- Dimitri, L. A., & Longland, W. S. (2018). The utility of animal behavior studies in natural resource management. *Rangelands*, 40, 9–16.
- Dominoni, D. M., Halfwerk, W., Baird, E., Buxton, R. T., Fernández-Juricic, E., Frstrup, K. M., ... Barber, J. R. (2020). Why conservation biology can benefit from sensory ecology. *Nature Ecology & Evolution*, 4, 502–511.
- Dorey, K., Dickey, S., & Walker, T. R. (2019). Testing efficacy of bird deterrents at wind turbine facilities: A pilot study in Nova Scotia, Canada. *Proceedings of the Nova Scotian Institute of Science (NSIS)*, 50, 91.
- Dorresteijn, I., Schultner, J., Nimmo, D. G., Fischer, J., Hanspach, J., Kuemmerle, T., ... Ritchie, E. G. (2015). Incorporating anthropogenic effects into trophic ecology: Predator-prey interactions in a human-dominated landscape. *Philosophical Transactions of the Royal Society B*, 282, 20151602.
- Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., Ramey, R. R., & McCullough, D. R. (2005). Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters*, 8, 1029–1038.
- Fauvelle, C., Diepstraten, R., & Jessen, T. (2017). A meta-analysis of home range studies in the context of trophic levels: Implications for policy-based conservation. *PLoS One*, 12(3), e0173361.
- Fernández-Juricic, E. (2016). The role of animal sensory perception in behavior-based management. In D. Saltz & O. Berger-Tal (Eds.), *Conservation behaviour: Applying behavioural ecology to wildlife conservation and management* (pp. 149–175). Cambridge: Cambridge University Press.
- Goller, B., Blackwell, B. F., DeVault, T. L., Baumhardt, P., & Fernández-Juricic, E. (2018). Assessing bird avoidance of high-contrast lights using a choice test approach: Implications for reducing human-induced avian mortality. *PeerJ*, 6, e5404.
- Grippio, M., Hayse, J. W., & O’Connor, B. L. (2015). Solar energy development and aquatic ecosystems in the southwestern United States: Potential impacts, mitigation, and research needs. *Environmental Management*, 55, 244–256.
- Halfwerk, W., & Slabbekoorn, H. (2015). Pollution going multimodal: The complex impact of the human-altered sensory environment on animal perception and performance. *Biology Letters*, 11, 20141051.
- Hardesty-Moore, M., Deinet, S., Freeman, R., Titcomb, G. C., Dillon, E. M., Stears, K., ... McCauley, D. J. (2018). Migration in the Anthropocene: How collective navigation, environmental system and taxonomy shape vulnerability of migratory species. *Philosophical Transactions of the Royal Society B*, 373, 20170017.
- Hausberger, M., Boigné, A., Lesimple, C., Belin, L., & Henry, L. (2018). Wide-eyed glare scares raptors: From laboratory evidence to applied management. *PLoS one*, 13, e0204802.
- Hawlena, D., Saltz, D., Abramsky, Z., & Bouskila, A. (2010). Ecological trap for desert lizards caused by anthropogenic changes in

- habitat structure that favor predator activity. *Conservation Biology*, 24, 803–809.
- Hernandez, R. R., Easter, S. B., Murphy-Mariscal, M. L., Maestre, F. T., Tavassoli, M., Allen, E. B., ... Allen, M. F. (2014). Environmental impacts of utility-scale solar energy. *Renewable and Sustainable Energy Reviews*, 29, 766–779.
- Ho, C. K. (2016). Review of avian mortality studies at concentrating solar power plants. *AIP Conference Proceedings*, 1734, 070017.
- Holloran, M. J., Kaiser, R. C., & Hubert, W. A. (2010). Yearling greater sage-grouse response to energy development in Wyoming. *The Journal of Wildlife Management*, 74, 65–72.
- Horváth, G., Blahó, M., Egri, A., Kriska, G., Seres, I., & Robertson, B. (2010). Reducing the maladaptive attractiveness of solar panels to polarotactic insects. *Conservation Biology*, 24, 1644–1653.
- Horváth, G., Kriska, G., Malik, P., & Robertson, B. (2009). Polarized light pollution: A new kind of ecological photopollution. *Frontiers in Ecology and the Environment*, 7, 317–325.
- Hufbauer, R. A., Facon, B., Ravigné, V., Turgeon, J., Foucaud, J., Lee, C. E., ... Estoup, A. (2011). Anthropogenically induced adaptation to invade (AIAI): Contemporary adaptation to human-altered habitats within the native range can promote invasions. *Evolutionary Applications*, 5, 89–101.
- Huso, M., Dietsch, T. & Nicolai, C. (2016). Mortality monitoring design for utility-scale solar power facilities. U.S. Geological Survey Open-File Report 2016-1087, 44.
- International Energy Agency (IEA). (2019). World Energy Outlook 2019. Retrieved from <https://www.iea.org/reports/world-energy-outlook-2019>.
- IRENA. (2019). Renewable Power Generation Costs in 2018, International Renewable Energy Agency. https://doi.org/10.1007/SpringerReference_7300
- Islam, M. T., Huda, N., Abdullah, A. B., & Saidur, R. (2018). A comprehensive review of state-of-the-art concentrating solar power (CSP) technologies: Current status and research trends. *Renewable and Sustainable Energy Reviews*, 91, 987–1018.
- Jacob, J. (2008). Response of small rodents to manipulations of vegetation height in agro-ecosystems. *Integrative Zoology*, 3, 3–10.
- Jeal, C., Perold, V., Ralston-Paton, S., & Ryan, P. G. (2019). Impacts of a concentrated solar power trough facility on birds and other wildlife in South Africa. *Ostrich*, 90, 129–137.
- Jeal, C., Perold, V., Seymour, C. L., Ralston-Paton, S., & Ryan, P. G. (2019). Utility-scale solar energy facilities: Effects on invertebrates in an arid environment. *Journal of Arid Environments*, 168, 1–8.
- Jessop, T. S., Smissen, P., Scheelings, F., & Dempster, T. (2012). Demographic and phenotypic effects of human mediated trophic subsidy on a large Australian lizard (*Varanus varius*): Meal ticket or last supper? *PLoS one*, 7, e34069.
- Kagan, R. A., Viner, T. C., Trail, P. W., & Espinoza, E. O. (2014). *Avian mortality at solar energy facilities in southern California: A preliminary analysis*. Ashland, OR: National Fish and Wildlife Forensics Laboratory Retrieved from <http://www.ourenergypolicy.org/avian-mortality-at-solar-energy-facilities-in-southern-california-a-preliminary-analysis/>
- Kristan, W. B., & Boarman, W. I. (2003). Spatial pattern of risk of common raven predation on desert tortoises. *Ecology*, 84, 2432–2443.
- Loss, S. R., Dorning, M. A., & Diffendorfer, J. E. (2019). Biases in the literature on direct wildlife mortality from energy development. *BioScience*, 69, 348–359.
- Lovich, J. E., & Daniels, R. (2000). Environmental characteristics of desert tortoise (*Gopherus agassizii*) burrow locations in an altered industrial landscape. *Chelonian Conservation and Biology*, 3, 714–721.
- Lovich, J. E., & Ennen, J. R. (2011). Wildlife conservation and solar energy development in the desert southwest, United States. *BioScience*, 61, 982–992.
- Martin, G. R. (2011). Understanding bird collisions with man-made objects: a sensory ecology approach. *IBIS*, 153(2), 239–254. <https://doi.org/10.1111/j.1474-919X.2011.01117.x>.
- May, R., Reitan, O., Bevanger, K., Lorentsen, S. H., & Nygård, T. (2015). Mitigating wind-turbine induced avian mortality: Sensory, aerodynamic and cognitive constraints and options. *Renewable and Sustainable Energy Reviews*, 42, 170–181.
- McCrary, M. D., McKernan, R. L., Schreiber, R. W., Wagner, W. D., & Sciarrotta, T. C. (1986). Avian mortality at a solar energy power plant. *Journal of Field Ornithology*, 57, 135–141.
- Merkle, J. A., Fortin, D., & Morales, J. M. (2014). A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters*, 17, 924–931.
- Moore-O'Leary, K. A., Hernandez, R. R., Johnston, D. S., Abella, S. R., Tanner, K. E., Swanson, A. C., ... Lovich, J. E. (2017). Sustainability of utility-scale solar energy—Critical ecological concepts. *Frontiers in Ecology and the Environment*, 15, 385–394.
- National Renewable Energy Laboratory (NREL). (2019). Renewable Portfolio standards: Understanding costs and benefits. Retrieved from <https://www.nrel.gov/analysis/rps.html>.
- National Renewable Energy Laboratory (NREL). (2020). Q4 2019/Q1 2020 solar industry update. Retrieved from <https://www.nrel.gov/docs/fy20osti/77010.pdf>.
- NC Clean Energy Technology Center (NCCETC). (2020). Database of incentives for renewables and efficiency. Retrieved from <https://www.dsireusa.org/>.
- Northrup, J. M., & Wittemyer, G. (2013). Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters*, 16, 112–125.
- Pazheri, F. R., Othman, M. F., & Malik, N. H. (2014). A review on global renewable electricity scenario. *Renewable and Sustainable Energy Reviews*, 31, 835–845.
- Peterson, E. K., Buchwalter, D. B., Kerby, J. L., LeFauve, M. K., Varian-Ramos, C. W., & Swaddle, J. P. (2017). Integrative behavioral ecotoxicology: Bringing together fields to establish new insight to behavioral ecology, toxicology, and conservation. *Current Zoology*, 63, 185–194.
- Phillips, S. E., & Cypher, B. L. (2019). Solar energy development and endangered species in the San Joaquin Valley, California: Identification of conflict zones. *Western Wildlife*, 6, 29–44.
- Reimers, E., Dahle, B., Eftestøl, S., Colman, J. E., & Gaare, E. (2007). Effects of a power line on migration and range use of wild reindeer. *Biological Conservation*, 134, 484–494.
- Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, 87, 1075–1085.
- Ruegg, K. C., Anderson, E. C., Paxton, K. L., Apkenas, V., Lao, S., Siegel, R. B., ... Smith, T. B. (2014). Mapping migration in a songbird using high-resolution genetic markers. *Molecular Ecology*, 23, 5726–5739.

- Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: A review. *Conservation Biology*, 5, 18–32.
- Sawyer, H., Kauffman, M. J., & Nelson, R. M. (2009). Influence of well pad activity on winter habitat selection patterns on mule deer. *Journal of Wildlife Management*, 73, 1052–1061.
- Schmitt, M. H., Shuttleworth, A., Ward, D., & Shrader, A. M. (2018). African elephants use plant odours to make foraging decisions across multiple spatial scales. *Animal Behaviour*, 141, 17–27.
- Seamans, T. W., Martin, J. A., & Belant, J. L. (2013). Tactile and auditory repellents to reduce wildlife hazards to aircraft. In T. L. DeVault, B. F. Blackwell, & J. L. Belant (Eds.), *Wildlife in airport environments: Preventing animal-aircraft collisions through science-based management*. Baltimore, MD: Johns Hopkins University Press in association with The Wildlife Society.
- Shepherd, S., Hollands, G., Godley, V. C., Sharkh, S. M., Jackson, C. W., & Newland, P. L. (2019). Increased aggression and reduced aversive learning in honey bees exposed to extremely low frequency electromagnetic fields. *PLoS One*, 14, e0223614.
- Smith, J. A., & Dwyer, J. F. (2016). Avian interactions with renewable energy infrastructure: An update. *The Condor*, 118, 411–423.
- Spencer, W. D. (2012). Home ranges and the value of spatial information. *Journal of Mammalogy*, 93, 929–947.
- Stoms, D. M., Dashiell, S. L., & Davis, F. W. (2013). Siting solar energy development to minimize biological impacts. *Renewable Energy*, 57, 289–298.
- Swaddle, J. P., Moseley, D. L., Hinders, M. K., & Smith, P. E. (2016). A sonic net excludes birds from an airfield: Implications for reducing bird strike and crop losses. *Ecological Applications*, 26, 339–345.
- Száz, D., Mihályi, D., Farkas, A., Egri, A., Barta, A., Kriska, G., ... Horváth, G. (2016). Polarized light pollution of matte solar panels: Anti-reflective photovoltaics reduce polarized light pollution but benefit only some aquatic insects. *Journal of Insect Conservation*, 20, 663–675.
- Thomas, K. A., Jarchow, C. J., Arundel, T. R., Jamwal, P., Borens, A., & Drost, C. A. (2018). Landscape-scale wildlife species richness metrics to inform wind and solar energy facility siting: An Arizona case study. *Energy Policy*, 116, 145–152.
- Tsoutsos, T., Frantzeskaki, N., & Gekas, V. (2005). Environmental impacts from the solar energy technologies. *Energy Policy*, 33, 289–296.
- Tuomainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, 86, 640–657.
- Turney, D., & Fthenakis, V. (2011). Environmental impacts from the installation and operation of large-scale solar power plants. *Renewable and Sustainable Energy Reviews*, 15, 3261–3270.
- USEIA. (2019). International Energy Outlook, U.S. Energy Information Administration. Retrieved from <https://www.eia.gov/outlooks/ieo/pdf/ieo2019.pdf>
- Vale, C. G., & Brito, J. C. (2015). Desert-adapted species are vulnerable to climate change: Insights from the warmest region on earth. *Global Ecology and Conservation*, 4, 369–379.
- Vistnes, I., Nellemann, C., Jordhoy, P., & Strand, O. (2004). Effects of infrastructure on migration and range use of wild reindeer. *Journal of Wildlife Management*, 68, 101–108.
- von Seckendorff Hoff, K., & Marlow, R. W. (2002). Impacts of vehicle road traffic on desert tortoise populations with consideration of conservation of tortoise habitat in southern Nevada. *Chelonian Conservation and Biology*, 4, 449–456.
- Walston, L. J., Jr., Rollins, K. E., LaGory, K. E., Smith, K. P., & Meyers, S. A. (2016). A preliminary assessment of avian mortality at utility-scale solar energy facilities in the United States. *Renewable Energy*, 92, 405–414.
- Wilcove, D. S., & Wikelski, M. (2008). Going, going, gone: Is animal migration disappearing. *PLoS Biology*, 6, e188.
- Wilkening, J., & Rautenstrauch, K. (2019). Can solar farms be wildlife friendly? A facility in the southwest hopes to find the answer. *Wildlife Professional*, 13, 46–50.
- Wyszkowska, J., Shepherd, S., Sharkh, S., Jackson, C. W., & Newland, P. L. (2016). Exposure to extremely low frequency electromagnetic fields alters the behaviour, physiology and stress protein levels of desert locusts. *Scientific Reports*, 6, 36413.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Chock RY, Clucas B, Peterson EK, et al. Evaluating potential effects of solar power facilities on wildlife from an animal behavior perspective. *Conservation Science and Practice*. 2020;e319. <https://doi.org/10.1111/csp2.319>