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Acorn woodpecker movements and social networks change with wildfire smoke

Allison E. Johnson^{1,5,6,*}, Sahas Barve^{2,3,5}, Lindsay Dreiss⁴, Daizaburo Shizuka¹, and Eric L. Walters²

Climate change has contributed to increased wildfires^{1,2}. Wildfire smoke exposes wildlife to hazards and mortality from particulate matter on a scale larger than the area impacted by fire^{3,4}. Using automated radiotelemetry, we illustrate how smoky conditions are associated with changes in behavior of acorn woodpeckers (*Melanerpes formicivorus*), a flagship species of oak (*Quercus* spp.) savannas of western North America. On smoky days, birds spent more time at their home territory and reduced visitation to others, especially to distant territories. Associations between birds decreased, and individuals were less assorted by group in co-visitation networks, suggesting less inter-individual coordination on smoky days. We show that between 2016 and 2020, ~14% of the acorn woodpecker population in the US experienced fire, potentially exposing on average 89.42% of the range to atmospheric smoke annually. These findings highlight how potential effects of smoke on animal behavior may be widespread and exacerbate negative impacts of increasingly common “megafires”, even in fire-adapted ecosystems.

Acorn woodpeckers are cooperatively breeding birds that live on year-round territories. Non-breeding helpers become breeders by inheriting their natal territory, filling a breeding vacancy, or founding a territory⁵. Helpers and breeders make daily extra-territorial forays to track changes in composition of neighboring groups, often as coalitions of same-sex helpers, to discover dispersal opportunities⁶. Extra-territorial movements are thus an essential behavior that connects individuals within a population-wide social network⁷.

An automated radiotelemetry system has tracked radio-tagged acorn woodpeckers at Hastings Natural History Reservation (HNHR), California since 2017⁶. During summer 2020, two wildfires created smoky conditions at HNHR; the River Fire burned ~1/4 of the reserve and the Dolan Fire burned in close proximity. Automated radiotelemetry data of 37 individuals from 20 groups gathered before, during, and after these fires allowed us to assess the relationship between smoke, movement and social associations. We gathered daily smoke data over HNHR from the Hazard Mapping System Fire and Smoke Product (HMS) of the National Oceanic

and Atmospheric Administration (<https://www.ospo.noaa.gov/Products/land/hms.html>) during 30 days from 1 August to 30 September 2020. The HMS uses opacity of satellite images to qualitatively categorize smoke plumes as “thin”, “medium” and “thick” polygons. While smoke polygons represent smoke present throughout the atmospheric column, we used them as a proxy to reflect ground-level conditions⁸. As a conservative estimate, we considered “medium”, “thick” or overlapping plumes as smoke presence and “thin” or no smoke as absence. Though 9 individuals lived on territories within 200 m of the River Fire, no territories burned. Removal

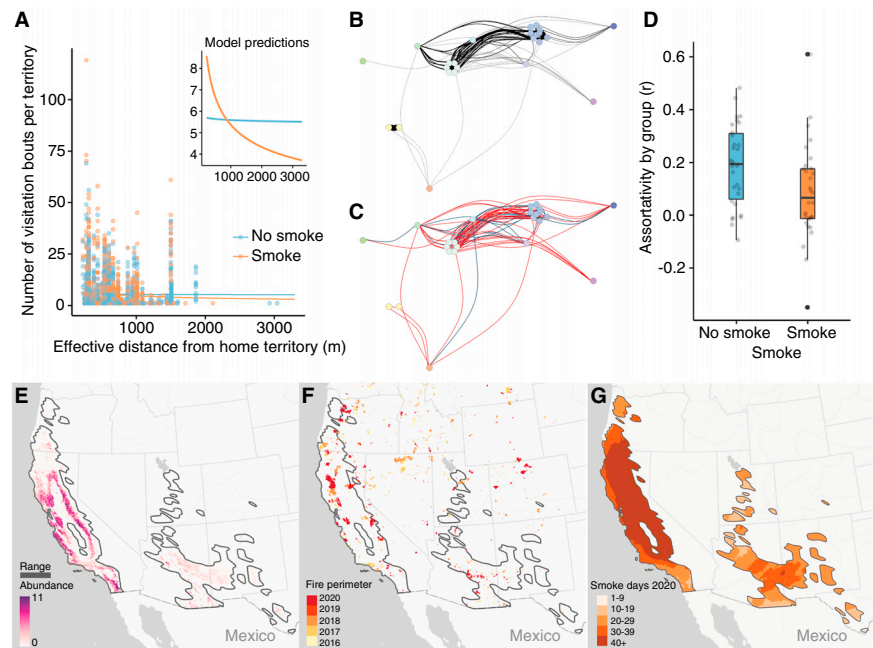


Figure 1. Smoke alters patterns of acorn woodpecker foraging and co-visitation.

(A) Number of visitation bouts per territory per bird ($N = 23$) per day ($N = 61$; 1 August–30 September 2020) is impacted by an interaction between the distance of the territory visited from a bird’s home territory and smoke conditions. Inset shows model predictions (lines) without overlaid data. Blue and orange indicate days without and with smoke, respectively. (B) Social network generated across days without smoke, where nodes are individuals and lines indicate co-visitation. Nodes are colored by group; groups spatially closer are colored similarly. Thicker lines denote larger association index. (C) A subtracted network illustrating smoke impact, where red lines indicate edges that lost weight and blue lines indicate edges that gained weight on smoke days relative to (B). (D) Assortativity by group was higher on days without smoke (blue) than smoky days (orange). Horizontal lines indicate medians, boxes represent interquartile range, whiskers represent 1.5 x interquartile range. Data points are transparent and jittered. (E–G) Impact of fire and smoke across the acorn woodpecker range in the United States. (E) Species abundance from eBird, where darker pixels indicate greater woodpecker counts. (F) Fire perimeters in 2016–2020, data provided through the Wildland Fire Decision Support System administered by the U.S. Geological Survey. Reds indicate fires in more recent years. (G) Distribution of “medium” or “thick” smoke days across the range between 1 June and 31 October for the year 2020 from National Oceanic and Atmospheric Administration. Greater smoke frequency (in days) is represented by darker reds. The distribution of smoke days for 2020 is depicted here because this year corresponds with the behavioral data collected from Hastings Natural History Reservation; however, distributions for each year can be seen in [Figure S1](#).



of these individuals did not alter the results (Supplemental information and Data S1F–H); thus, all individuals were retained in final analyses.

On smoky days, birds spent a greater proportion of time detected at their home territory than on forays (GLMM: $\beta \pm SE = 0.4 \pm 0.01$, $p < 0.001$; Data S1A). While the number of bouts (periods of continuous presence) per unique territory was higher (GLMM, smoke effect: $\beta \pm SE = 2.09 \pm 0.17$, $p < 0.001$), visitations were skewed to territories closer to their home territory during smoky days (distance \times smoke interaction: $\beta \pm SE = -0.31 \pm 0.03$, $p < 0.001$; Data S1B and Figure 1A). Birds also visited fewer unique territories on smoky days (GLMM: $\beta \pm SE = -0.09 \pm 0.04$, $p = 0.01$; Data S1C).

We generated social networks based on duration of associations during extra-territorial forays to understand patterns of co-visitation⁷. The pairwise strength of associations decreased from no smoke to smoky conditions (Wilcoxon signed rank test: $V = 4475$, $p < 0.001$; no smoke mean \pm SD: 0.004 ± 0.012 ; smoke mean \pm SD: 0.003 ± 0.008 ; Figure 1B,C), suggesting birds had less frequent social interactions during forays on smoky days. Associations were also less assorted by social group (Mann-Whitney: $U = 428$, $p = 0.01$; no smoke mean \pm SD: 0.19 ± 0.16 ; smoke mean \pm SD: 0.09 ± 0.18 ; Figure 1D), indicating foraging coalitions were less common⁶.

Spatial analyses show that fire and smoke occur broadly across the range of Acorn Woodpeckers within the continental US (512,340 km²; data from the HMS, US Wildland Fire Decision Support System and eBird, respectively)^{9,10}. From 2016 to 2020, a mean \pm SD of 2.87% \pm 2.29% of the population and 1.57% \pm 1.14% of the species range (over 516,084 km²) was within annual fire perimeters (Figure 1E,F and Table S2; range: 0.60% in 2019 to 3.65% in 2020). Cumulatively, from 2016 to 2020, 13.93% of the population and 3.75% of the species' range burned. By contrast, at the 1 km² scale, an average of 89.42% (minimum of 82.28% in 2019 and a maximum of 100% in 2020) of their US range was within "medium" or "thick" HMS atmospheric smoke polygons for one or more days annually during peak fire season (1 Jun–31 Oct; minimum of 1 day and a maximum of 77 days annually), illustrating the spatial extent of smoke (Table S2 and Figure S1 for

annual distribution of smoke days from 2016–2020; Figure 1G for 2020 smoke distribution). While this illustrates smoke occurs across most of the range annually, its effect on behavior likely depends on ground-level intensity.

Our work demonstrates how smoke may alter the behavior of acorn woodpeckers. During smoky days, foray distances were reduced, and social connectivity and coordination of movements decreased. Our data demonstrate the potential for smoke to alter behavior, but we cannot resolve the precise relationship between smoke intensity and degree of behavioral change. Determining this relationship with remote sensing that measures intensity of smoke and resulting pollutant concentrations will become ever more important as wildfires become more severe¹ and days with intense smoke increase.

SUPPLEMENTAL INFORMATION

Supplemental information includes one figure, one table, one data file, inclusion and diversity statement, supplemental experimental procedures, and supplemental results, and can be found with this article online at <https://doi.org/10.1016/j.cub.2023.08.096>. Data and code for social network and acorn woodpecker visitation behavior are available on Dryad at <https://doi.org/10.5061/dryad.ghx3ffbv4>.

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AUTHOR CONTRIBUTIONS

A.E.J. conducted analyses and wrote and edited the manuscript. S.B. conducted fieldwork, filtered the data, raised funds, and wrote and edited the manuscript. L.D. analyzed range-wide data and wrote and edited the manuscript. D.S. edited the manuscript and aided in analyses.

E.L.W. raised funds for the study, conducted fieldwork, and edited the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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¹School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588, USA. ²Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA. ³Avian Ecology Program, Archbold Biological Station, 123 Main Drive, Venus, FL 33960, USA. ⁴Defenders of Wildlife, Center for Conservation Innovation, Washington, DC 20036, USA. ⁵These authors contributed equally. ⁶Lead contact.

*E-mail: aj.petrochelidon@gmail.com