The Scientific Naturalist

Ecology, 103(1), 2022, e03552

Megafires and thick smoke portend big problems for migratory birds

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Manuscript received 10 February 2021; revised 8 June 2021; accepted 23 July 2021. Corresponding Editor: John Pastor.

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Citation: Overton, C. T., A. A. Lorenz, E. P. James, R. Ahmadov, J. M. Eadie, F. Mcduie, M. J. Petrie, C. A. Nicolai, M. L. Weaver, D. A. Skalos, S. M. Skalos, A. L. Mott, D. A. Mackell, A. Kennedy, E. L. Matchett, and M. L. Casazza. 2022. Megafires and thick smoke portend big problems for migratory birds. Ecology 103(1):e03552. 10.1002/ecy.3552

Key words: birds; energetics; migration; movement; population connectivity; smoke; telemetry; wildfire.

In 2020, the fire season affecting the western United States reached unprecedented levels. The 116 fires active in September consumed nearly 20,822 km^2 (https://inciweb.nwcg.gov/accessible-view/ Accessed 2020-09-29) with 80% of this footprint (16,567 km^2) from 68 fires occurring within California, Oregon, and Washington. Although the 2020 fire season was the most extreme on record, it exemplified patterns of increased wildfire size, number, timing, return frequency, and extent, which are linked to climate-driven changes in precipitation and temperature affecting fire ignition and severity (Westerling 2016, Goss et al. 2020, Weber and Yadav 2020). In addition, wildfire smoke and particulate pollution have expanded greatly in recent decades throughout western North America, posing a threat to both human and ecological health (Burke et al. 2021). Wildfires have increasingly coincided with the start of fall migration (Westerling 2016, Goss et al. 2020) and may present a growing risk to migrating birds in the Pacific Flyway. Migrating birds across several western states were observed dead and dying in 2020. Within the Central Flyway, starvation of insectivorous birds that were recovered in Arizona, Colorado, and New Mexico was linked to a record cold-weather storm in the Rocky Mountains (Fox 2020). But causes of the nearly simultaneous bird mortalities of larger granivorous species (Fig. 1) further west in the Pacific Flyway, where fires were occurring, remain unclear.

Birds are especially vulnerable to disruption during migration as this is one of the most energetically demanding periods of the life cycle (McWilliams et al. 2004). Migration both follows and precedes periods of increased foraging activity and unanticipated energy deficits may have short-term carry-over effects on subsequent demographic processes (Newton 2006). Physiological and atmospheric constraints limit where, how high, and how long birds can fly. However, behavioral and physiological adaptations that make migration more efficient, such as using navigational cues, altering flight elevation to take advantage of winds, and efficient blood oxygenation are widespread across avian taxa (McWilliams et al. 2004). Some bird species fly in formation. which provides physical efficiencies (Mirzaeinia and Heppner 2020), but also maintains social cohesion within family groups, which is particularly strong in geese (Kölzsch et al. 2020). Many migrating species exhibit strong site fidelity to a limited number of stopover locations and travel routes (Weber and Houston 1999) potentially resulting in adverse demographic outcomes if traditional sites are not available (Klaassen et al. 2006). Such patterns of low "migratory diversity" are associated with greater probabilities of population decline while species with greater diversity may respond more robustly to climate change (Gilroy et al. 2016) or stochastic events. Temporary faculative migration from breeding ranges in advance of severe storms has been implied from light level loggers on songbirds that are otherwise obligate migrants (Streby et al. 2015), but a similar response was not evident for resident scavenging birds following volcanic eruption (Alarcón et al. 2016). It is less understood how actively migrating species respond

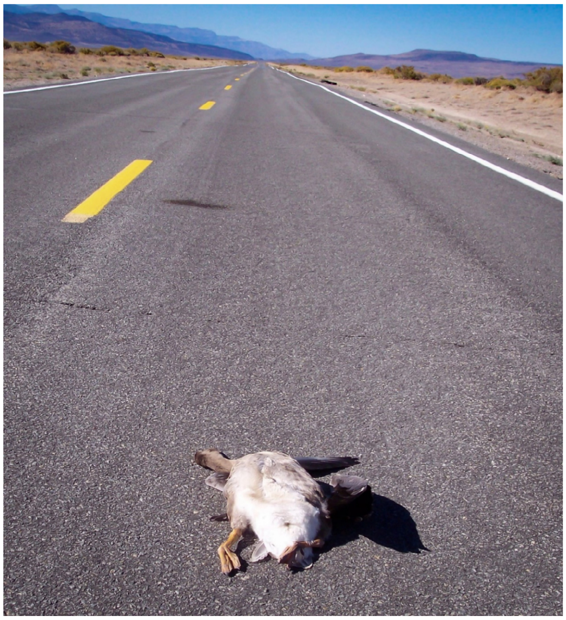

FIG. 1. Goose mortality during migration. Juvenile greater white-fronted goose (*Anser albifrons*) without external injury and weighing nearly half (˜1 kg) of a healthy bird's expected weight (˜1.8–2 kg) was found dead in the arid desert of northern Nevada following recent wildfires. Cause of mortality is presumed to be starvation occurring during migration. Photograph by Bill Henry (retired USFWS).

to similar large-scale disruptions, particularly in the context of route finding and energy expenditure to traditionally used stopover regions.

Ecological investigations on the impact of wildfire on migration and movement have generally focused either on the energetic needs and foraging strategies of individuals or the impact of habitat or patch loss in the landscape. Wildfire impacts on actively migrating animals, particularly effects that extend beyond direct habitat loss within the fire perimeter, are not well documented due to the difficulty in obtaining migration information that spatially and temporally coincides with large fires. Beginning in 2018, we have marked tule greater white-fronted geese (*Anser albifrons elgasi*; tule goose) with collar-mounted GPS-enabled cellular transmitters to study movements and behaviors (Overton and Casazza 2021). With only 14,700 individuals (Yparraguirre et al. 2020), the tule goose is a Species of Special Concern in California and exhibits near absolute fidelity to a primary stopover site at the Summer Lake Wildlife Area in central Oregon, USA (96%; Yparraguirre et al. 2020). Typical fall migration, as observed from five radio-marked individuals in 2019, starts as a nearly direct route from the Cook Inlet in Alaska to Summer Lake that takes just over 4 d. The first half of fall migration between Alaska and Washington consists of flights over, and occasional short rests upon, the Pacific Ocean. Beginning September 12, 2020, all four tule geese were still transmitting, including a single individual that provided a migration track in 2019, and encountered dense smoke either while flying overland into southern Washington or while flying off the coast of Vancouver Island, British Columbia, Canada and Washington, USA.

The three-dimensional smoke forecast from NOAA's High-Resolution Rapid Refresh coupled with the Smoke (HRRR-Smoke) model (Ahmadov, 2017) were compared with bird movements to investigate any potential impacts of smoke upon migration patterns. Elevational gradients of smoke concentrations were linearly interpolated for every GPS location from each goose to allow interpretation of individual movement behavior relative to vertical distribution of smoke density. Geese responded to dense smoke concentrations averaging 161 $\mu g\ m^{-3}$ (Fig. 2) by either stopping migration or altering direction and/or altitude of flights, which resulted in increased total flight time and distance. Three birds migrating over water stopped and rafted for 52–72 h before the smoke cleared and then moved inland. Landward migration of geese through smoke or directly over fires resulted in disorganized paths including both tangential and recursive flights, acute increases in altitude to 4,000 m to over-fly the smoke plume, and stopovers in non-traditional habitats occurring far from traditional migratory pathways (Fig. 3). Social cohesion of migrating flocks may also have been affected. Pairs of marked individuals migrated together twice, but groups separated each time that flocks were stopped in the smoke. One individual (Bird #192587) transited the fires but continued following prevailing winds within the smoke plume away from Summer Lake, arriving in Idaho where tule goose occurrence has never been confirmed (Fig. 3). Ultimately, all individuals arrived at Summer Lake after delays caused by smoke which more than doubled average migration duration (4.18 d in 2019 vs. 9.11 d in 2020; +118%) and extended the average flightpath during migration by 757 km (+27%).

Total energetic deficit resulting from delayed arrival at Summer Lake and extra distance flown was estimated using values from existing literature (see Appendix S1: Section S3). Total increased energetic expenditure averaged 950 kcals (3,977 kJ; observed range 404–1,118 kcals) which is equivalent to nearly 4.4 d of thermally neutral metabolism or 2.27 d encompassing normal activities during the winter. The duration of additional foraging needed to compensate for this caloric deficit is 27.5–42 h. Pre-breeding Canada geese (*Branta canadensis*) increase time spent feeding five-fold to nearly 31% of the day implying that even when feeding at behavioral extremes these energetic deficits would take 4–6 days before recovery. Energy deficits such as we describe, especially when occurring in the context of incomplete knowledge of available food resource locations, can lead

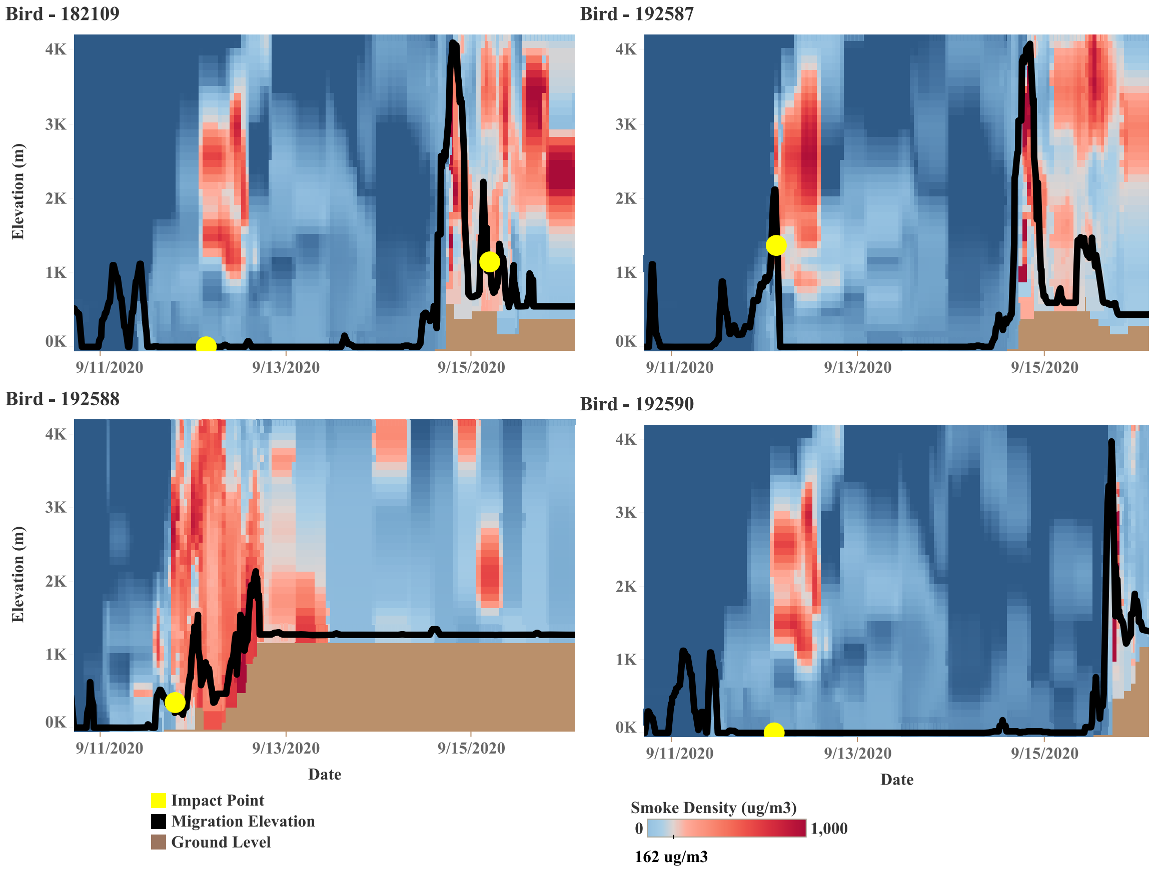

FIG. 2. Examples of migratory flights relative to wildfire smoke plumes. Elevation of four tule greater white-fronted geese migration routes (black lines) to Summer Lake Wildlife Area and vertical distribution of predicted smoke (PM2.5) density. Average smoke concentrations within migration flight elevations (<4,000 m) greater than 160 μg m^{-3} (red) resulted in disruption of typical migratory behavior; including extended at-sea rafting, novel stopover site use, recursive migration paths ("impact points"; yellow circles). Overflight of wildfire by three birds on September 15 and 16 included migration elevations (4,000 m) exceeding the smoke injection height (3,900 m). Ground level at location obtained from ASTER digital elevation model when over land or mean sea level when over the ocean.

to increased mortality or reproductive rates insufficient to maintain goose populations (Klaasen et al. 2005).

We observed impacts to individual migratory behavior at smoke concentrations averaging 161 μg m^{-3}. At ground surface elevations, smoke concentrations exceeded this threshold across a geographic extent 27 times greater than the area burned by wildfires. However, at observed migration altitudes (<4,000 m), this smoke concentration covered an area 44 times larger than the wildfires themselves, encompassing 64% of four western states (California, Nevada, Oregon, and Washington) and effectively transecting the Pacific Flyway (Fig. 3).

Peak migration through the Pacific Flyway states of Washington, Oregon, and California, occurs when wildfires have become more intense, larger, and more frequent due to climatic variation and anthropogenic influences such as fire suppression and invasive plants (Goss et al. 2020, Weber and Yadav 2020). Wildfires in 2020 produced substantial barriers to bird navigation and movement across wide geographic extents, affecting route selection and energy expenditure sufficient to produce long-lasting effects. Limitations in high quality stopover sites due to continuing reductions in wetland extent within the Northern Great Basin (Donnelly et al. 2019) may exacerbate the impacts to migrating birds of larger and later occurring wildfires in western North America. Other species of geese, ducks, shorebirds, and passerines rely on similar traditional pathways and navigational cues and face comparable physiological and energetic constraints. The results we report for tule greater white-fronted geese may reflect significant challenges faced by a broader constituency of migrating birds, particularly those with low migratory diversity

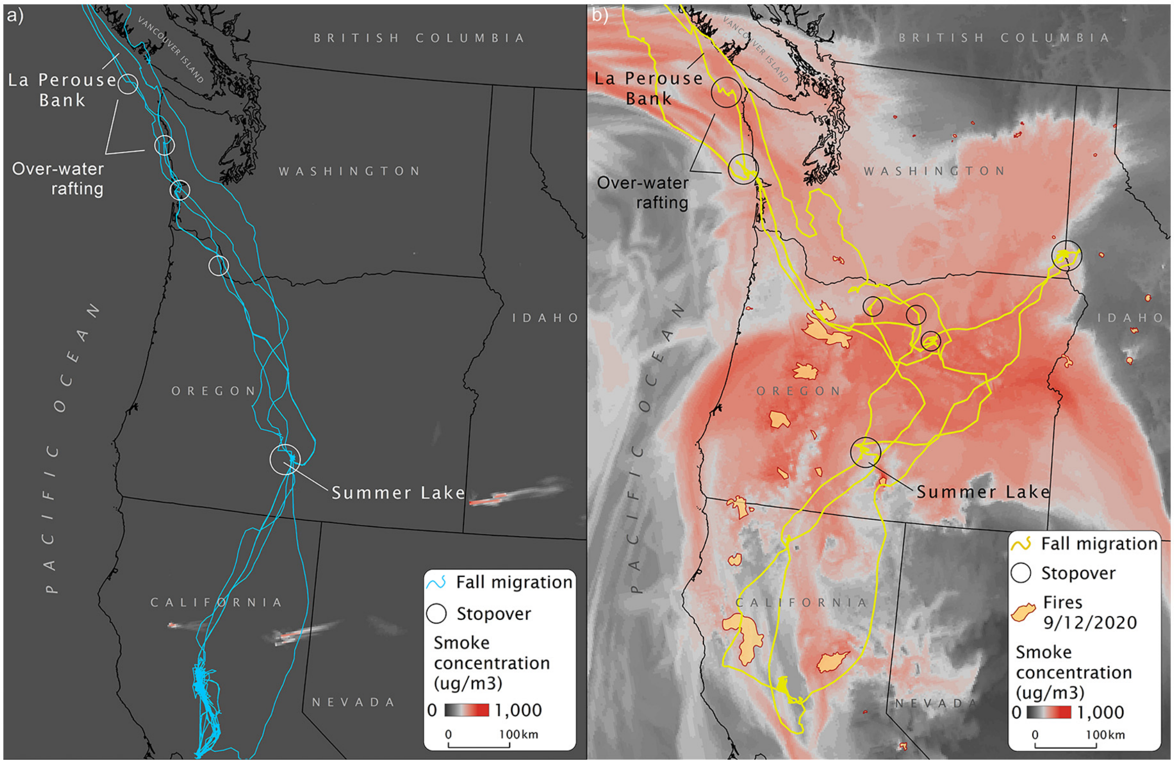

FIG. 3. Maximum smoke extent and migratory paths of tule geese. Tule goose (*Anser albifrons elgasi*) fall migration routes in 2019 (a; $n = 5$) and in 2020 (b; $n = 4$) through arrival at Summer Lake Wildlife Area, Oregon, USA across areas experiencing massive wildfires in 2020 which resulted in aberrant migration behavior, increased energetic demands, and increased mortality risk. Routes during 2020 encountered smoke plumes initially over the Pacific Ocean or Olympic Peninsula. Maximum extent impacted by wildfire smoke of sufficient concentration to disrupt waterfowl migration (>161 μg m^{-3}; red) encompassed an area equal to 64% of four western states (California, Nevada, Oregon, and Washington) on September 12, 2020 and was >44 times larger than the combined area directly impacted by the wildfire. Basemap source: Esri, HERE, Garman, Open StreetMap contributors, and the GIS user community.

(Gilroy et al. 2016) and portend a future of increased challenges (Pickrell and Pennisi 2020) for migratory bird populations.

Acknowledgments

We are grateful for the support and project development of C. Feldheim. B. Reishus, M. St. Louis, K. Walton, D. Yparraguirre and the Oregon Department of Fish and Wildlife assisting with capture and marking birds, to B. Henry for photograph documentation, and M. Falcon for photo-editing. We thank the California Department of Water Resources, Ducks Unlimited, Inc., and U.S. Geological Survey, Western Ecological Research Center for funding field work, analysis and manuscript preparation. R. Ahmadov and E. James thank NOAA's JPSS PGRR program for funding and the rest of the HRRR-Smoke team and collaborators for helping with the model development. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3552/suppinfo

Open Research

Data (Overton and Casazza 2021) are available in the USGS ScienceBase Data Catalog: https://doi.org/10.5066/P9IE7YCH.