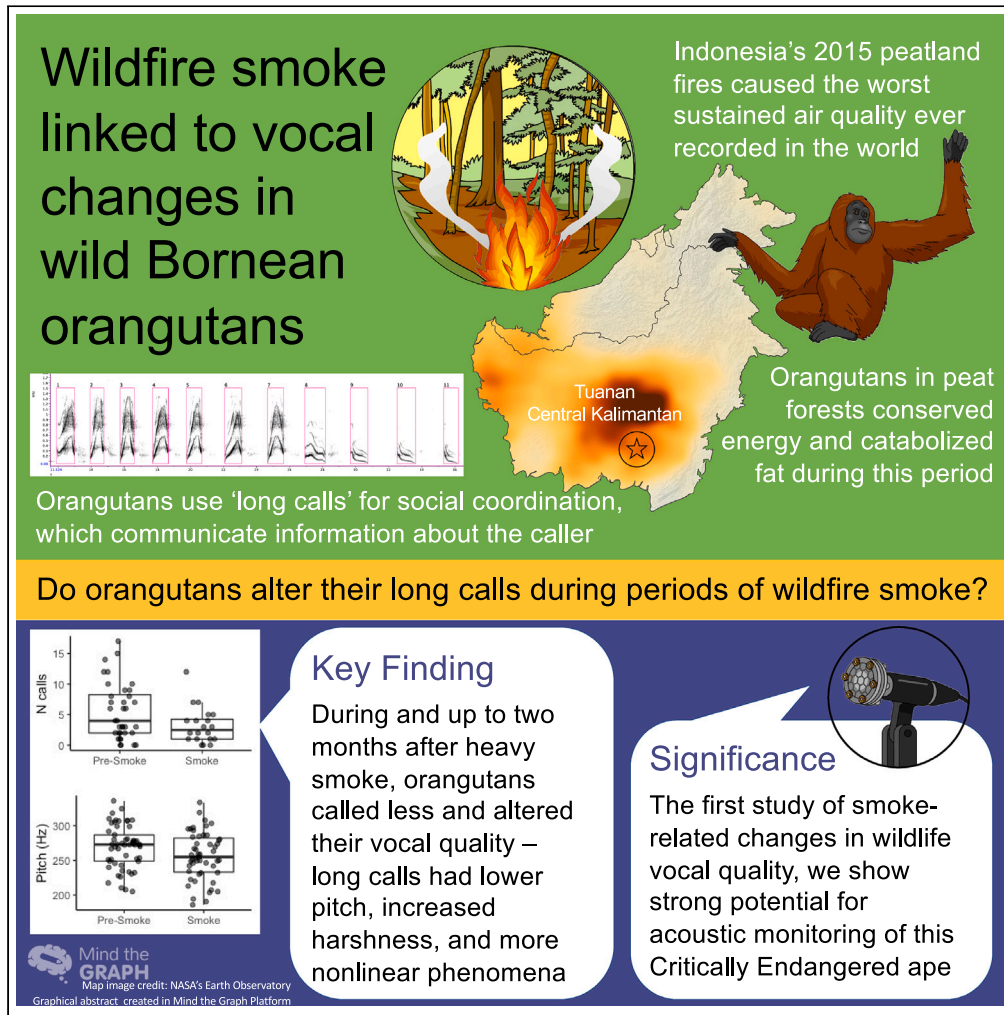


Article

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Highlights

Indonesia's 2015 peatland fires caused the worst sustained air quality ever recorded

During and after the fires, orangutans called less and showed reduced vocal quality

Orangutans' vocal changes likely signal illness or other shifts in their health

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Article

Wildfire smoke linked to vocal changes in wild Bornean orangutans

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SUMMARY

Tropical peatlands are the sites of Earth's largest fire events, with outsized contributions to greenhouse gases, toxic smoke, and haze rich with particulate matter. The human health risks from wildfire smoke are well known, but its effects on wildlife inhabiting these ecosystems are poorly understood. In 2015, peatland fires on Borneo created a thick haze of smoke that blanketed the region. We studied its effects on the long call vocalizations of four adult male Bornean orangutans (*Pongo pygmaeus wurmbii*) in a peat swamp forest. During the period of heavy smoke, orangutans called less often and showed reduced vocal quality—lower pitch, increased harshness and perturbations, and more nonlinear phenomena—similar to changes in human smokers. Most of these changes persisted for two months after the smoke had cleared and likely signal changes in health. Our work contributes valuable information to support non-invasive acoustic monitoring of this Critically Endangered primate.

INTRODUCTION

Worldwide, forested landscapes are increasingly vulnerable to wildfires due to global and regional changes in climate and land-use activities.^{1,2} A major driver of deforestation, fire was associated with nearly 40% of global forest loss between 2003 and 2018, negatively impacting biodiversity, ecosystem services, and climate change.³ Beyond environmental impacts, wildfires and their smoke pose significant economic costs and severe health risks.⁴ In the tropical peatlands of Southeast Asia, wildfires—the vast majority of which occur in Indonesia—have rapidly escalated in their extent, frequency, and severity since the 1980s.⁵ While burning has occurred in Borneo's peat swamps throughout their history, paleoecological analyses demonstrate that fires did not significantly impact the forest vegetation until human forest clearance escalated after the mid-nineteenth century.⁶ Dramatically altered by deforestation and drainage, these vulnerable ecosystems are now the source of the Earth's largest fire events and a major contributor to greenhouse gas emissions.^{7,8}

Peat combustion produces a dense toxic smoke—or haze—that contains a variety of hazardous gasses, as well as particulate matter (PM), a leading cause of global pollution-related mortality.⁹ Compared to other wildfires, fires on peatland can smolder underground for weeks and produce higher emission factors for CO, CH₄, CO₂, HCN, NH₃, and PM.¹⁰ During Indonesia's record-setting 1997 El Niño fires, the Indonesian State Ministry for Environment reported more than 500 haze-related deaths, 1.4 million acute respiratory infections, and 2.4 million lost workdays.¹¹

The impacts of wildfire smoke on the health of wildlife have been poorly studied; however, available research on pets, livestock, and animal models indicates that smoke pollution can have both direct and indirect effects on animal health and behavior.¹² For example, smoke inhalation can damage lung tissue, impair cardiovascular function, and alter immune responses of animals.¹³ Some of these effects are observed even after short periods of smoke exposure (8 h–1 week), causing acute symptoms, such as labored or rapid breathing, wheezing, panting, coughing, and other indicators of respiratory distress.¹⁴ Smoke exposure may also impact other physiological systems. For example, farm animals exposed to smoke show low conception rates, poor weight gain, and decreased milk production.¹⁵ Likewise, 2-to-3-month-old captive infant rhesus macaques (*Macaca mulatta*) exposed to 10 days of high particulate matter (PM_{2.5} = particles measuring < 2.5 μm in diameter) concentrations from wildfire smoke showed reduced lung capacity and weakened immune responses at age three.¹⁶ In that same colony of macaques, pregnant

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females who were exposed to 12 consecutive days of elevated PM_{2.5} concentrations (i.e., exceeding 35 µg/m³) experienced greater pregnancy loss compared to females who were pregnant during periods of healthy air.¹⁷ Surviving infants who were exposed to smoke *in utero* showed a suite of biobehavioral differences—including greater inflammation, blunted cortisol, more passive behavior, and memory impairment—compared to infants conceived after the smoke period.¹⁸

Combined, lung injury and a weakened immune response can lead to inflammation, respiratory infection, and illness.¹⁹ Launching an immune response to illness or infection can be energetically costly, thereby altering animals' energy balance and activity levels.²⁰ Although a direct immune response to smoke has not been studied in wildlife, humans show clear immune responses to wildfire smoke.²¹ To our knowledge, only one study has documented both behavioral and energetic smoke-related changes in wildlife. Adult male Bornean orangutans (*Pongo pygmaeus*) showed energy-conserving behavior, resting more and traveling shorter distances, during smoke and post-smoke periods.²² Despite moving less and consuming more calories, the animals experienced negative energy balance, indicated by increased ketosis (a sign of fat catabolism), possibly signaling energetically costly immune activity triggered by smoke exposure.²² In a later study on the same population, Ashbury and colleagues²³ further explored the indirect effects of wildfires on Bornean orangutans through their impacts on the productivity of orangutan foods. They found that during the extended period of low fruit availability after the 2015 fires, adult female orangutans similarly adopted an energy-conserving strategy (i.e., resting more, traveling less, consuming more fallback foods, and socializing less often) compared to pre-fire low-fruit periods.

Using behavioral observations and passive acoustic monitoring, a handful of studies have also documented changes in wildlife vocal behavior in response to wildfire smoke. For example, during Borneo's El Niño-driven peatland fires of 2006, white-bearded gibbons (*Hylobates albibarbis*) called less often and sang shorter bouts on smoky days, leading the study's author to hypothesize that changes in singing behavior could signal changes in the gibbons' respiratory health.²⁴ During Indonesia's 2015 El Niño-driven fires, biological soundscapes were severely disrupted by the smoke that covered Singapore.²⁵ Acoustic activity declined significantly during the smoke period and had only partially recovered 16 weeks after the smoke had cleared. The authors noted that ecosystems closer to the wildfires in Borneo, where air quality was up to 15 times more hazardous, would likely be more severely affected than those in Singapore. In Washington State, 10 species of birds were less likely to be detected by citizen scientists during periods of haze when PM_{2.5} concentrations were elevated.²⁶ Although they could not tease apart whether results were driven by changes in bird presence, abundance, or perceptibility, the authors noted that wildfire smoke likely influenced the birds' movements and vocal activity.

Smoke-related changes in vocal quality have not been examined in nonhuman animals; however, studies of cigarette smoking in humans may offer some insights for nonhuman primates who share similar respiratory and vocal anatomy. Compared to non-smokers, the voices of smokers have been shown to exhibit lower pitch (mean F0),²⁷ more perturbation in amplitude (shimmer) and frequency (jitter),²⁸ and a lower harmonics-to-noise ratio (HNR or harmonicity).²⁹ A meta-analysis of smoking-related vocal changes concluded that smoking most consistently and strongly altered pitch and maximum phonation time.³⁰ Collectively, these vocal features have been linked to structural and histological changes to the larynx caused by smoking, including drying, irritation, thickening, and inflammation.³¹ Wildfire smoke contains many of the same hazardous components common in cigarette smoke, including PM, carbon monoxide, and carcinogens.³² PM has been linked to both systemic and laryngeal inflammation in humans.⁹ Thus, it is likely that inhaling wildfire smoke could cause some of the same vocal changes in nonhuman primates as inhaling cigarette smoke does in humans.³³

Nonlinear phenomena (NLP) are another class of vocal features that hold great potential to signal the underlying health and condition of wildlife. NLP are abrupt changes in the harmonic structure of sound produced in the larynx that are caused by asynchronous or irregular oscillations of the vocal folds.³⁴ NLP include frequency jumps (abrupt, discontinuous shifts in F0), subharmonics (additional harmonics that suddenly appear as integer fractions of the F0), biphonation (simultaneous occurrence of two or more independent F0's), and deterministic chaos (periods of nonrandom noise). They have been documented in the vocalizations of a vast array of human and nonhuman primates and other mammals and have been linked to the health, physical condition, and affective state of the caller.³⁵ NLP are also particularly common in distress vocalizations, such as alarm calls and fear screams.³⁶

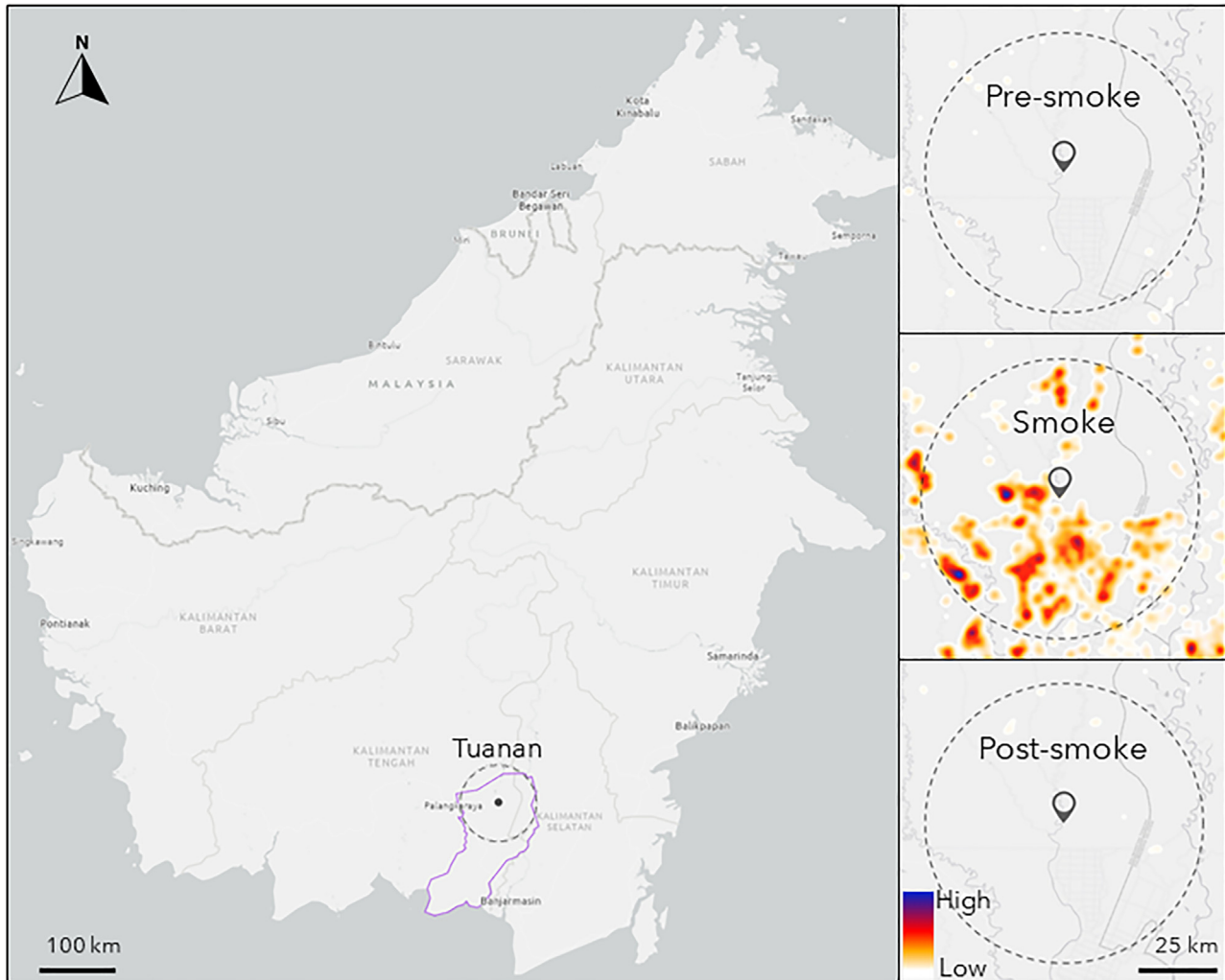


Figure 1. Map of study area and MODIS-derived hotspots of fire locations

Left panel: Tuanan study location within the Ex-Mega Rice Project (purple outline) on Borneo, Right panel: heatmap (color scale) of MODIS-derived fire hotspots during each study period (Pre-Smoke: 15 Mar–7 Jul 2015, Smoke: 4 Sep–17 Oct, Post-smoke: 19 Nov–13 Jan 2016) detected within a 50-km radius (dashed circles). Map created using ESRI ArcGIS Online. Data source: “Archive fires for Indonesia” feature layer created by Global Forest Watch (http://gis-gfw.wri.org/arcgis/rest/services/Fires/FIRMS_ASEAN/MapServer/0).

Our present work aims to document vocal changes in orangutans (*Pongo pygmaeus wurmbii*) during and after an extended period of hazardous air quality caused by wildfires in Central Kalimantan, Indonesia (Figures 1 and 2). Between June and November 2015, nearly 125,000 fire hotspots were detected by satellites in Indonesia, largely concentrated on the peatlands of Sumatra and Borneo. The fires were the direct result of severe drought across the region brought on by the strongest El Niño on record since 1997.³⁷ Burning an estimated 4.6 million ha of land across Sumatra, Kalimantan, and West Papua,³⁸ Indonesia’s 2015 wildfires resulted in the worst sustained air quality ever recorded anywhere in the world³⁹ and Central Kalimantan was a hotspot for PM_{2.5} fire emissions.¹⁰

Our research focused on long calls, which are loud, booming long-distance vocalizations produced by adult males that can propagate more than a kilometer and serve an important role in mate competition and attraction within the orangutans’ dispersed communities.⁴⁰ We hypothesized that orangutan long calls would exhibit changes consistent with shifts in their physical health and condition, as predicted by honest signaling theory. Honest signaling theory posits that signals of quality or competitive ability are constrained by physiological, physical, or production costs that shape the quantity, rate, and features of the signal.⁴¹ Prolonged exposure to high concentrations of PM in wildfire smoke causes detrimental health

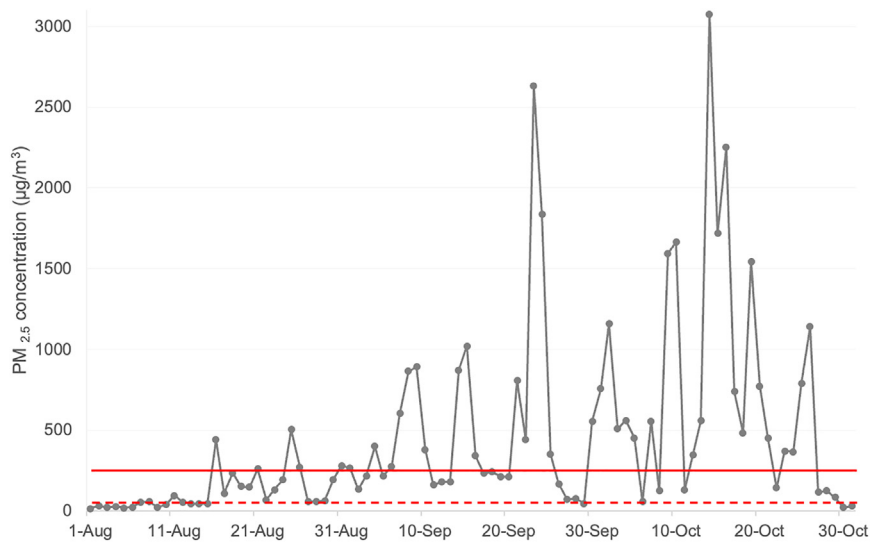


Figure 2. Simulated values of average daily $PM_{2.5}$ concentrations

Plotted $PM_{2.5}$ values from the FINNpeatSM model within the 30-km grid cell containing Tuanan for the period 1 Aug–31 Oct, 2015. “Unhealthy” (dashed red line = $55 \mu\text{g}/\text{m}^3$) and “Hazardous” (solid red line = $255 \mu\text{g}/\text{m}^3$) concentrations, as defined by the United States Environmental Protection Agency, are indicated for reference.

effects to humans and nonhumans, including respiratory distress, infections, systemic inflammation, and laryngitis, all of which could cause changes in vocal behavior and/or acoustics. Therefore, we predicted that during and after the smoke period: (1) males would call less often and make shorter calls, (2) long calls would show changes in vocal quality, including reduced pitch, increased shimmer and jitter, and reduced harmonicity, and (3) orangutan voices would exhibit more NLP compared to the pre-smoke period.

RESULTS

Prediction 1: Decreased long call rates and durations

We found a significant decrease in the number of long calls produced per day during the smoke period (pre-smoke mean = 5.5, smoke mean = 3.2 calls; [Figure 3](#), [Tables 1](#) and [S1](#)) and this reduction persisted into the post-smoke period (mean = 0.6 calls; [Figure 4](#), [Tables 1](#) and [S1](#)). In contrast, there were no changes in the duration of long calls during the smoke period (pre-smoke mean = 51.0, smoke mean = 48.2 s; [Figure 3](#), [Tables 1](#) and [S1](#)), but calls were shorter during the post-smoke period (mean = 42.8 s; [Figure 4](#), [Tables 1](#) and [S1](#)).

Prediction 2: Reduced pitch and vocal quality

Mean pitch was significantly lower during smoke ([Figure 3](#), [Tables 1](#) and [S1](#)), but this effect did not persist post-smoke ([Figure 4](#), [Tables 1](#) and [S1](#)). Jitter was significantly higher during both smoke and post-smoke periods but shimmer was higher only post-smoke ([Figures 3](#) and [4](#), [Tables 1](#) and [S1](#)). Lastly, HNR was lower (i.e., calls were noisier) during both the smoke ([Figure 3](#)) and post-smoke periods ([Figure 4](#), [Tables 1](#) and [S1](#)).

Prediction 3: Increased incidence of nonlinear phenomena

We documented an increase in the presence of biphonation during the smoke and post-smoke period relative to the pre-smoke period ([Figures 3](#), [4](#), and [5](#), [Tables 1](#) and [S1](#)). In contrast, deterministic chaos did not significantly increase during either period ([Figures 3](#), [4](#), and [5](#), [Tables 1](#) and [S1](#)). There were no changes in the relative duration of either biphonation or deterministic chaos across periods.

DISCUSSION

We found evidence that orangutans alter their calling behavior and exhibit vocal changes during periods of wildfire smoke. Most of these changes persisted for the two months we monitored these individuals after the smoke had cleared; and it is presently unknown how long they may have continued beyond our

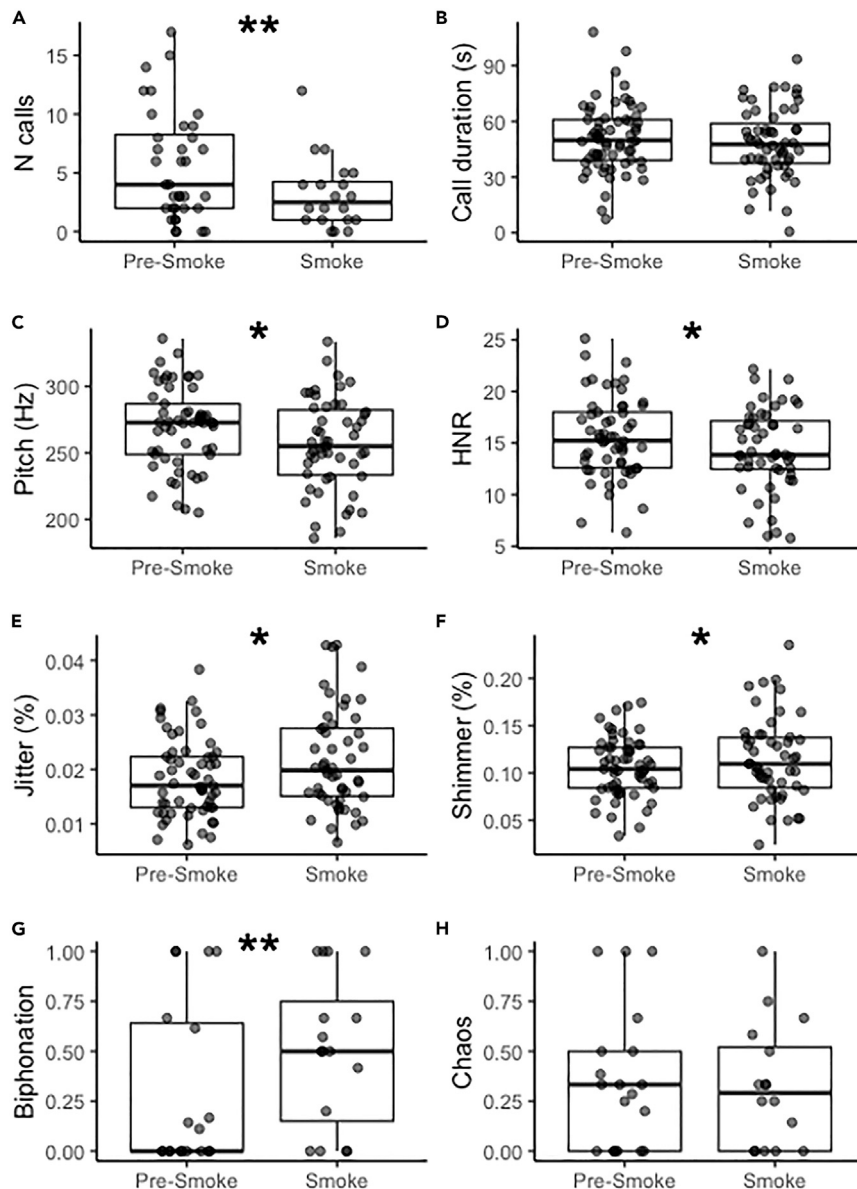


Figure 3. Boxplots depicting immediate changes in long calls

(A) = number of long calls per day, (B) = call duration (s), (C) = pitch (Hz), (D) = harmonics to noise ratio, (E) = jitter, (F) = shimmer, (G) = biphonation, (H) = deterministic chaos. Individual data points are plotted and overlapping values appear darker. Significance of one-tailed tests indicated ** $p < 0.01$, * $p < 0.05$.

study period. At the same time, we recognize the small sample size of this study—only four individuals—greatly limits the interpretation of our results; we further describe these constraints in the Study Limitations. Call rate and duration are key elements of calling effort that can reflect small fluctuations in energy status and physical condition.⁴¹ As we predicted, orangutans reduced their daily calling rate during and after the smoke period. The reduced post-smoke call rate is likely related to the orangutans' shorter travel distances during that period, when they appeared to adopt an energy-conservation strategy by resting more and moving less.²² Indeed, orangutans failed to produce a single long call on 56% of post-smoke observation days, compared to 22% and 25% of days during the pre-smoke and smoke periods, respectively. It is unlikely that the changes observed in the post-smoke period could be attributed to changes in diet or nutrition during this period, since our previous study showed that monthly fruit availability (i.e., the proportion of stems in phenology plots producing fruit) was similar (mean

Table 1. Mean (avg), standard deviation (sd), minimum (min), and maximum (max) values within each study period for each of the variables examined

Variable	Pre-Smoke				Smoke				Post-Smoke			
	avg	sd	min	max	avg	sd	min	max	avg	sd	min	max
Calls/day	5.5	4.6	0	17	3.2	3.0	0	12	0.6	1.1	0	4
Duration (s)	51.0	18.2	7.4	108.1	48.2	18.8	0.7	93.4	42.8	12.8	21.4	57.2
Pitch (Hz)	269.6	30.5	205.2	336.0	256.5	34.2	186.0	333.7	260.0	30.4	209.5	310.7
Jitter (%)	1.8	0.7	0.6	3.8	2.2	0.9	0.7	4.3	2.1	0.6	1.1	3.4
Shimmer (%)	10.6	3.2	3.4	17.4	11.5	4.4	2.4	23.5	11.8	2.9	7.6	18.6
HNR	15.5	3.9	6.3	25.1	14.4	4.0	5.8	22.2	12.7	3.6	6.0	17.8
Biphonation	0.3	0.5	0	1	0.50	0.50	0	1	0.55	0.51	0	1
Chaos	0.3	0.5	0	1	0.36	0.48	0	1	0.20	0.41	0	1

pre-smoke = 2.73%, post-smoke = 3.01%) and energy intake was higher in the post-smoke period compared to the pre-smoke period.²²

Although unchanged during the smoke period, call durations were shorter post-smoke. Call duration is likely influenced by lung volume and capacity⁶³ and shorter calls could signal post-fire reduction in lung function related to smoke inhalation. For instance, adult humans exposed to 50 days of wildfire smoke in Montana (35 days of which had “very unhealthy” PM_{2.5} levels) suffered a significant decrease in lung function that worsened in the year following the fires and persisted for as long as two years in some individuals.⁶⁴ Taken together with research demonstrating reduced lung volumes in rhesus macaques exposed to wildfire smoke during infancy,¹⁶ it appears that exposure to high PM_{2.5} levels can have long-lasting, if not permanent, effects on human and nonhuman primates’ lung function that may emerge later and worsen over time.

During the smoke period, orangutans’ voices exhibited lower pitch and HNR, as well as higher jitter. During the post-smoke period, their voices had higher shimmer and jitter, and lower HNR. Whereas pitch is associated with the mass and tension of vocal folds; jitter, shimmer, and HNR reflect the stability and periodicity of their vibrations.⁶³ Collectively, these features of vocal quality have been linked to histological changes in the larynx of human smokers (e.g., inflammation, mucosal thickness), as well as states of high arousal in animals.⁶⁵ On the one hand, because the pitch-lowering effects of smoking can arise quickly and reverse after two days of smoking cessation,²⁹ the normal F0 values we observed post-smoke are not surprising. On the other hand, we are not aware of studies demonstrating the precise onset and offset times of the physiological changes underlying shimmer, jitter, or HNR and so we are unable to propose a mechanistic explanation for the delayed onset of shimmer relative to the other features.

We found evidence that some NLP increased in response to wildfire smoke. Biphonation, but not deterministic chaos, was significantly more prominent during the smoke period and persisted post-smoke. NLP are commonplace in many primates³⁴ and deterministic chaos has been observed, but not systematically investigated, in orangutans.⁶⁶ In chimpanzees, NLP are commonly observed—with biphonation occurring frequently and deterministic chaos only rarely⁵⁷—in the climax notes of male pant-hoot calls and are thought to serve as an honest signal of caller condition, wherein males in poor condition produce calls with more NLP.⁶⁷ Numerous studies have linked NLP to health in human and nonhuman primates, including metabolic disease in macaques,⁶⁸ malnourishment in human infants,³⁵ and acute laryngitis⁶⁹ and COVID-19 in adults.⁷⁰

Taken together, orangutan long calls exhibit changes consistent with predictions of honest-signaling theory.⁴¹ To our knowledge, ours is the first study to investigate the effects of wildfire smoke on the voice of any nonhuman animal. Long calls are thought to play a central role in the Bornean orangutan mating system, serving to both attract female mates and confront and assess competitor males.⁷¹ Thus, the reductions we documented in both the quantity and quality of these displays could have significant, yet unknown, social and reproductive consequences for the population.

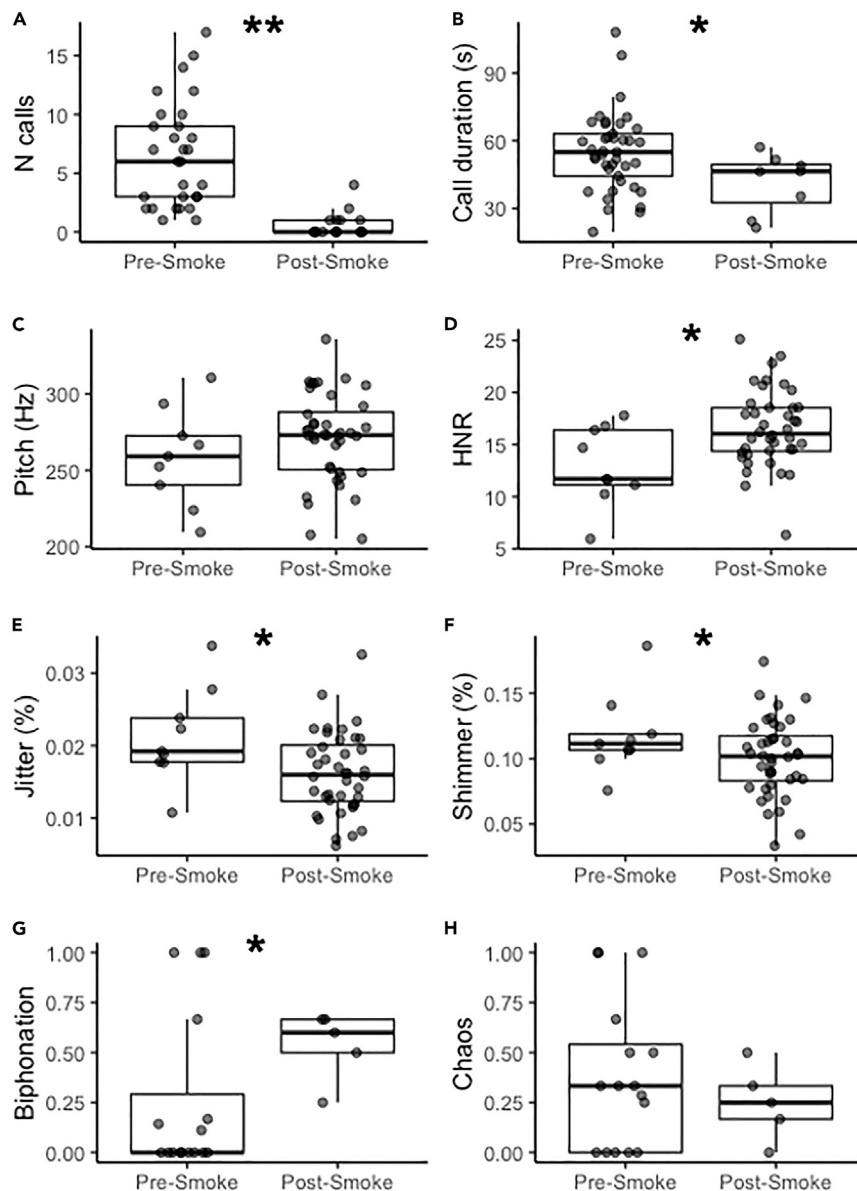


Figure 4. Boxplots depicting persistent changes in orangutan long calls

(A) = number of long calls per day, (B) = call duration (s), (C) = pitch (Hz), (D) = harmonics to noise ratio, (E) = jitter, (F) = shimmer, (G) = biphonation, (H) = deterministic chaos. Individual data points are plotted and overlapping values appear darker. Significance of one-tailed tests indicated ** $p < 0.01$, * $p < 0.05$.

Our previous research showed that these same individuals experienced negative energy balance in the post-smoke period, despite reducing activity levels and increasing caloric intake, likely signaling allostatic load related to a stress and/or immune response.²² During that time, the Borneo Orangutan Survival Foundation's (BOSF) rescue teams reported that wild orangutans across the region were suffering malnourishment, dehydration, and stress.⁷² Further, 16 infants at the BOSF Nyaru Menteng orangutan rehabilitation center in Central Kalimantan were diagnosed with respiratory infections,⁷² indicating that orangutans experience some of the same adverse health effects as humans.

Presently, we cannot identify the precise mechanisms underlying the behavioral, physiological, and vocal changes we have documented. We did not observe any coughing, but there was a non-significant

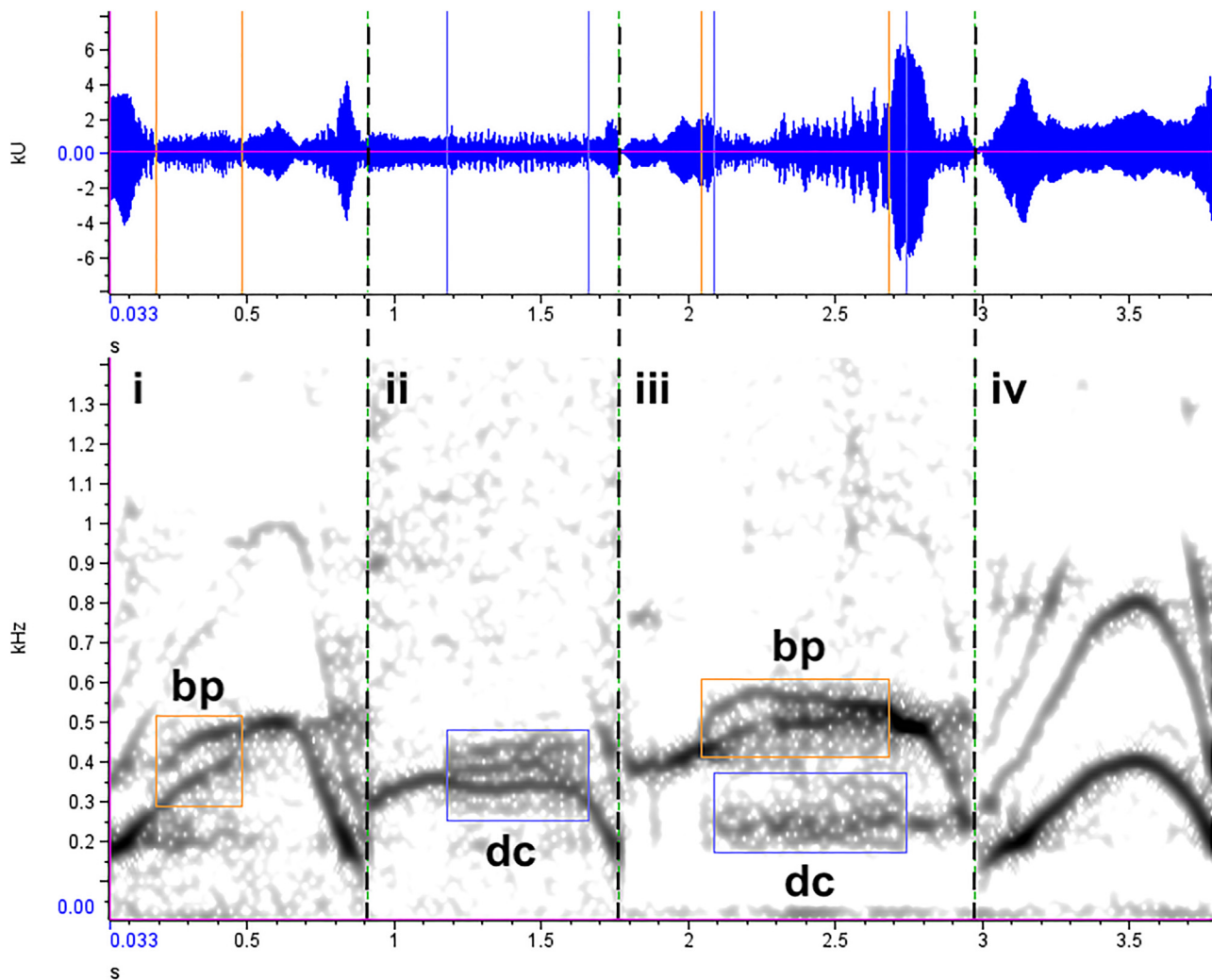


Figure 5. Spectrogram and waveform depicting nonlinear phenomena in long call pulses

Examples of pulse clips recorded from three males during pre-smoke and smoke periods containing annotations of (i) biphonation (bp: orange rectangles), (ii) deterministic chaos (dc: blue rectangles), (iii) both biphonation and deterministic chaos, and (iv) no nonlinear phenomena.

increase in sneezing during and after the smoke compared to the pre-smoke period (Erb, unpublished data: pre-smoke = 0%, smoke = 15%, post-smoke = 10% of observation days). Wildfire smoke, particularly from peatland fires, contains a suite of hazardous and toxic components—from benzene to carbon monoxide—that could cause a range of acute symptoms and lasting health effects that, in turn, affect the voice.⁷³ The region in which our study took place experienced the highest concentrations of PM_{2.5} on the island of Borneo between Sep–Oct 2015, with some models estimating mean concentrations exceeding 800 μg/m³ and demonstrating a strong correlation with carbon monoxide in the atmosphere.¹⁰

As peatland fires in Indonesia and other regions around the world continue to increase in severity and frequency, wildlife are at risk of serious health outcomes from prolonged and repeated exposure to toxic smoke.¹ Emerging evidence that PM_{2.5} exposure from wildfire smoke is linked to increased COVID-19 cases and deaths⁷⁴ amplifies this concern for human and nonhuman animals—including most nonhuman primates—who are vulnerable to SARS-CoV-2 infection and illness.⁷⁵ Thus, there is an urgent need for sustained research into the long-term impacts of wildfire smoke on populations and ecosystems.⁷⁶ By documenting acoustic changes that parallel behavioral and energetic shifts in individuals, our work contributes valuable information that can help scientists and

wildlife managers monitor the health of this critically endangered species, whose populations lost > 100,000 individuals between 1999 and 2015.⁷⁷ The discovery of these linkages highlights the great potential of remote methods, like passive acoustic monitoring, to safely collect population-wide data and deepen our understanding of the short- and long-term effects of wildfire smoke on wildlife populations worldwide.

Limitations of study

We acknowledge that the small number and uneven sampling of individuals included in our study limit the strength of our conclusions. Our manual NLP annotations were conducted by a single experienced observer following lengthy consultation with expert colleagues (see [acknowledgments](#)). Though we took careful measures to address observer bias (i.e., removed information about caller and study period, randomized the order of clips, and conducted all annotations in a single session), our protocol relied on a time-consuming audiovisual approach that could limit reproducibility. Further, the marginal R^2 values (i.e., the proportion of variance explained by the fixed factor alone) for many of our response variables (e.g., jitter, shimmer, and HNR) were somewhat small. These results indicate that smoke period explained a small proportion of the overall variance in these models and suggests that there are other factors contributing to vocal quality that we did not measure in this study. Despite the highly variable nature of vocal quality within these four individuals, it is notable that we documented a statistically significant relationship with the occurrence of wildfire smoke, though the biological relevance of this finding needs further investigation. We note that the period with the worst very poor air quality (October 14–28: estimated mean $PM_{2.5}$ mean = 1,065 $\mu g/m^3$, max = 3,075 $\mu g/m^3$) coincided with when the research team turned our efforts to fighting fires and it is entirely possible that health consequences emerged or intensified during that time. Although we attempted to account for potential social and environmental influences on orangutan long calls, the observational nature of our study limited our ability to disentangle the possible effects of all contributing (including seasonal) factors. Lastly, our interpretations are limited by a lack of direct air quality measurements and clinical data on orangutans to directly link PM to and identify the precise physiological changes underlying the vocal changes we documented. Despite these limitations, in our view, we have presented a rare, valuable dataset, collected under extraordinary circumstances. This work points to new lines of inquiry, identifies testable hypotheses and predictions for future investigation, and highlights the great potential of passive acoustic monitoring to study changes in behavior and vocal quality of wildlife in response to wildfire smoke.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.107088>.

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Cornell University is located on the traditional homelands of the Gayogohónó, members of the Haudenosaunee Confederacy, an alliance of six sovereign Nations with a historic and contemporary presence on this land. The Confederacy precedes the establishment of Cornell University, New York State, and the United

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AUTHOR CONTRIBUTIONS

Conceptualization, W.M.E.; Methodology, W.M.E.; Validation, W.M.E.; Formal Analysis, W.M.E.; Investigation, W.M.E., E.J.B., A.N.H., J.L.L.; Resources, W.M.E., T.M.S., E.R.V.; Data Curation, W.M.E., E.J.B., A.N.H., J.L.L.; Writing – Original Draft, W.M.E., E.J.B., A.N.H., J.L.L.; Writing – Review & Editing, W.M.E., E.J.B., A.N.H., J.L.L., E.R.V.; Visualization, W.M.E.; Supervision, W.M.E., T.M.S., E.R.V.; Project Administration, W.M.E., E.J.B., A.N.H., T.M.S., E.R.V.; Funding Acquisition, W.M.E., E.R.V.

DECLARATION OF INTERESTS

The authors declare no further conflicts of interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Original data deposited for this study	Github repository	https://github.com/wendyerb/wildfire-smoke-orangutan-voice
Software and Algorithms		
Code for model building and evaluation	Github repository	https://github.com/wendyerb/wildfire-smoke-orangutan-voice
R: A language and environment for statistical computing v4.2.2	R Core Team, 2021	http://www.r-project.org
VoiceLab	Feinberg & Cook, 2020	https://voice-lab.github.io/VoiceLab/
Raven Pro 1.6	K. Lisa Yang Center for Conservation Bioacoustics, 2019	https://ravensoundsoftware.com/software/raven-pro/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Wendy Erb (erbivorous@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Original acoustic and environmental data have been deposited at Github and are publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- All original code has been deposited at Github and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Research complied with protocols approved by the Institutional Animal Care and Use Committee of Rutgers, the State University of New Jersey. The data used in this study comprise non-invasive behavioral observations and sound recordings of four wild, free-ranging adult flanged male Bornean orangutans. The precise ages of these individuals is unknown.

METHOD DETAILS

Study site

We conducted research between March 2015 and January 2016 at the Tuanan Orangutan Research Station in Central Kalimantan, Indonesia (2° 09' 06.1" S; 114° 26' 26.3" E: [Figure 1](#)). Located within the Ex-Mega Rice Project (EMRP), the Tuanan trail grid covers approximately 1,200 ha of regenerating peat swamp forest that was selectively logged in the 1990s. EMRP was a failed initiative to convert a million hectares of peatland into rice fields in the late 1990s. Though little rice was ever harvested, more than 4,000 km of canals were cut to dry the peat and precipitated what's been called Indonesia's largest environmental disaster.⁴² In 1997/98, more than half of the EMRP site, the vast majority of which was peatland, burned during the severe El Niño drought that year.⁴³ Today, the area continues to be extremely fire-prone, burning regularly with the

most severe fires occurring during El Niño dry seasons.⁴⁴ Although the 2015 fires and haze were the worst since the 1997/98 megafires, severe fires also occurred in 1982/83, 1987, 1991, 1994, and 2006.⁴⁵ Tuanan is located within an area of the EMRP (Block E) with relatively intact hydrology and healthy forest but, after more than two months of drought in 2015, wildfires burned roughly 90 ha of the study area (Erb, unpublished data).

Study species and subjects

Bornean orangutans (*Pongo pygmaeus*) comprise three subspecies, all of which are endemic to the island of Borneo. Unusual among monkeys and apes, orangutans are semi-solitary and have two distinct adult male morphs: unflanged and flanged males. Whereas unflanged males are only slightly larger in size and similar in appearance to adult females, flanged males are nearly twice their size and develop large fleshy cheek pads (or flanges) as well as expanded throat sacs.⁴⁶ In captivity, Bornean orangutans develop flanges as early as 15–16 years of age,⁴⁷ though this can occur significantly later in wild populations (e.g., one male in Sumatra was >30 when he flanged:⁴⁶). Only flanged males regularly produce long calls and individuals show significant variability in the acoustic properties of their calls.⁴⁸

The present study focuses on data collected from four adult flanged males: Niko, Otto, Tomi, and Wodan. All four males were observed and recorded before and during the fire season and three of them (Niko, Tomi, and Wodan) were also observed in the months after. Although we don't know the precise ages of these males, Niko, Otto, and Tomi were first observed in the study area as fully flanged adults (in 2003, 2008, and 2011, respectively), whereas Wodan was observed with incipient flanges in 2004 and matured to a fully flanged male in 2010.

Data collection and long call recording

Data for the present study were collected between 15 March 2015–13 January 2016. Minimum and maximum temperatures were recorded near the research camp at approximately 18:00 using a minimum-maximum thermometer and rainfall accumulations recorded with a rain gauge at approximately 06:00 and 18:00 each day. WME, EJB, ANH, and local research assistants collected data during 72 full-day (nest-to-nest) and 17 partial-day focal-animal observations of the four adult flanged males. We include all data we collected from these four males within the study period. Notably, the research team was away from the study site in August 2015 and we were additionally unable to collect data during the peak smoke period (14–31 October 2015), when we turned our collective efforts to extinguishing fires in the study area.

Whenever possible, we observed focal animals for five consecutive days separated by at least a month; however, occasionally males were lost before five days of observations had been completed. The distribution of full-day follows disaggregated by male and month is provided in [Figure S1](#). During observations, we used all-occurrences sampling⁴⁹ of long calls, recording whether the call occurred spontaneously or following a stimulus (i.e., within 15 min of another male's long call, an environmental noise, or an approaching animal), the orangutan's height above the ground (mean = 8.4, range = 0–19 m), and the focal-observer distance (mean = 7.6, range = 1–20 m). We opportunistically recorded 86% of these long calls (N = 268 of 313) using a Marantz PMD-660 solid-state recorder (Marantz, Japan, 16 bits, 44,100 Hz sample rate) and Sennheiser directional microphone (Sennheiser, Germany, K6 power module, ME66 recording head). An audio recording and spectrogram of a long call analyzed in this study are provided in the Supplemental information ([Figure S2](#) and [Audio S1](#)).

Acoustic analysis

All recordings were down sampled to 5,512 Hz in Adobe Audition prior to analysis to optimize the frequency resolution for these vocalizations whose dominant frequencies are below 400 Hz and high frequencies are below 1.5 kHz.⁵⁰ Prior to analysis, we removed poor-quality and partial recordings (N = 18) and randomly selected calls stratified by male and period in an effort to balance the dataset across males and study periods (see table below). WME and JLL manually annotated 132 calls from these four males using Raven Pro 1.6⁵¹ by creating selections (N = 1,516) around each pulse, i.e., the longest continuous sound produced on a single exhalation with a duration of ≥ 0.8 s. Selections were made to tightly bound the onset and offset of each pulse ([Figure S2](#)). We calculated call duration from the onset of the first pulse to the offset of the last pulse (excluding 4 recordings for which there was uncertainty about whether the first pulse was recorded, resulting in N = 128 calls for this analysis). Prior to analyzing vocal quality, we excluded (N = 723 of 1,516) any selections (pulses) that contained disturbing background noise as well as so-called huitus-type

pulses (cf.⁵²), since those are characterized by a break in the fundamental frequency contour (i.e., contain a small period of silence) and automated measurements of pitch for this class of pulses are not reliable.

Sample sizes for analyses reported in the present study disaggregated by male ID and study period. Dur = number of long call recordings for which call duration was measured; Voc-C = number of long call recordings for which vocal quality was measured; and Voc-P = number of pulses for which vocal quality was measured

Male ID	Pre-Smoke			Smoke			Post-Smoke		
	Dur	Voc-C	Voc-P	Dur	Voc-C	Voc-P	Dur	Voc-C	Voc-P
Niko	13	13	149	5	7	46	2	3	18
Otto	9	9	68	11	10	98	–	–	–
Tomi	14	8	33	14	12	45	1	1	7
Wodan	28	27	172	25	22	133	6	6	24

WME used Voice Lab⁵³ to automatically measure these individual pulse clips (N = 793). We selected the most common measurements of voice quality in studies of human smokers (reviewed in³⁰) that could be measured on field recordings: Pitch (mean F0), Harmonics-to-Noise Ratio (HNR), Jitter (small perturbations in periodicity), and shimmer (small perturbations in amplitude). Details about these measurements can be found in the Praat manual.⁵⁴ Default settings were used for all measurements. Jitter and shimmer measurements comprise multiple variables, so we calculated the average of ‘local’, ‘rap’ and ‘ppq5’ for jitter; and of ‘local’, ‘apq5’ and ‘apq11’ for shimmer (following the methods of⁵⁵). Since long calls nearly always comprise multiple pulses (mean = 25.5, range = 2–63), we calculated the average of each acoustic feature across all analyzed pulses in each long call and excluded recordings (N = 14 of 132) containing fewer than three measured pulses. The above table shows the final sample size of long calls and pulses analyzed for each male within each study period.

For the final analysis, we randomly selected 156 pulse clips (stratified by males and study periods to better balance the dataset, Table S2). One observer (WME) visually inspected spectrograms in Raven (5,512 Hz sampling rate, 512-point Hann window, 99% overlap). To minimize bias, their order was randomized and the observer was blind to the male ID and the recording period. Frequency jumps and subharmonics were very rare (N = 1 each), so we did not include those variables in the present study. Biphonation was identified as the occurrence of two or more simultaneous independent frequency contours and deterministic chaos was identified as a sudden loss of harmonic structure or episodes of nonrandom noise (Figure 5). We note that some NLP we scored as deterministic chaos could be examples of sidebands⁵⁶ as we were unable to systematically differentiate these classes of NLP. WME created selections to bound the onset and offset of each type of NLP and scored the presence of each in a one-zero fashion (cf.⁵⁷). We calculated the relative duration of each type of NLP by dividing the duration of the NLP by the duration of the entire pulse.

Air quality estimation

We relied on two sources of air quality data: 1) daily PM₁₀ (particles measuring <10 μm in diameter) concentrations collected by the Meteorology, Climatology and Geophysics Council (BMKG) at the Palangkaraya airport (79 km from Tuanan) and 2) hourly simulated surface PM_{2.5} (particles <2.5 μm) concentrations produced by the FINNpeatSM model within the 30-km grid cell containing Tuanan. The FINNpeatSM model incorporates measurements of above-ground vegetation combustion, burned peat mass, and soil moisture to estimate total PM_{2.5} emissions produced by fires. This model of fire emissions best predicted surface observations from air quality monitors and the authors estimated that peat burning contributed 71% of total primary PM_{2.5} emissions from Indonesia’s fires in Sep–Oct 2015.¹⁰ Using the data produced and generously shared by Laura Kiely,¹⁰ we used the R packages ‘ncdf4’ and ‘raster’ to extract hourly simulated concentrations at the Tuanan Research Station. We then calculated the mean daily concentration for each 24-h period from 1 August–31 October, 2015. The United States Environmental Protection Agency’s (EPA) air quality standards for particulate pollution within a 24-h period are 35 μg/m³ for PM_{2.5} and 150 μg/m³ for PM₁₀.⁵⁸ The EPA further defines thresholds for unhealthy (PM_{2.5} > 55.5, PM₁₀ > 255 μg/m³), very unhealthy (PM_{2.5} > 150.5, PM₁₀ > 355 μg/m³), and hazardous (PM_{2.5} > 250.5, PM₁₀ > 425 μg/m³) air quality.

Based on the daily PM₁₀ data from Palangkaraya, the period of unhealthy air quality began 22 August and ended 28 October (67 days). During this period, 93% of days with available measurements (N = 58) exceeded the unhealthy threshold (mean = 784 µg/m³, range = 82–1829 µg/m³). Unhealthy PM₁₀ values were not recorded on any other days during the study period before or after these dates. The simulated PM_{2.5} values within the grid-cell containing Tuanan (Figure 2) indicate a similar range of dates. Unhealthy PM_{2.5} values began 16 August and ended 29 October (75 days), during which time 99% of days exceeded the unhealthy threshold (mean = 542 µg/m³, range = 46–3,075 µg/m³). These air quality thresholds delineated the start (16 August) and end (29 October) of the smoke period and, accordingly, we divided our data into three periods: pre-smoke (15 Mar–7 Jul: mean PM₁₀ = 22 µg/m³), smoke (4 Sep–17 Oct: mean PM₁₀ = 830 µg/m³, mean PM_{2.5} = 693 µg/m³), and post-smoke (19 Nov–13 Jan: mean PM₁₀ = 42 µg/m³).

QUANTIFICATION AND STATISTICAL ANALYSIS

To test our predictions, we constructed linear mixed models for each dependent variable using the ‘lme4’ package in R.⁵⁹ Prior to analysis, we tested for correlations among variables. HNR, jitter, and shimmer were highly correlated with each other (>0.9). Although we report the results of each test to permit comparison with previous studies, we caution that there is clear non-independence among these variables. To examine the immediate effects of smoke, we compared observations and recordings from the pre-smoke and smoke periods and to examine the smoke’s persistent effects, we compared pre-smoke to post-smoke periods. For all models, we included study period as the fixed effect and male ID as a random intercept. As our predictions were directed, we used one-tailed tests for significance testing. General linear models were used for all variables except the number of long calls per day and the presence of NLP, for which we used generalized models specifying Poisson (log-link) and binomial (logit) distributions, respectively. Only jitter required log-transformation prior to analysis. We confirmed that all model residuals conformed to the model assumptions using the DHARMA package in R.⁶⁰ Lastly, we used the R package ‘MuMIn’⁶¹ to calculate conditional and marginal R² for each model.

Since some acoustic features can vary with caller arousal,⁴⁸ we first tested for differences in the duration of spontaneous compared to stimulated (i.e., following another male’s long call, an environmental noise, or an approaching animal) long calls across periods. Stimulated long calls represented 25%, 20%, and 20% of pre-smoke, smoke, and post-smoke calls, respectively, and there were no differences in the rates of stimulated long calls across periods (Table S3, $F_{2, 125} = 0.03$, $p = 0.98$). However, call context significantly affected call duration (Table S4) and we therefore report the results of both (period only and period plus context) models.

Additionally, previous research has shown that hot daytime temperatures and heavy rainfall sometimes reduce primate call rates and durations.⁶² We therefore also tested for differences across periods in maximum daytime temperature and daytime rainfall accumulation (06:00 to 18:00) in our dataset. Temperature varied significantly across study periods ($F_{2, 64} = 31.93$, $p < 0.001$), with the highest temperatures recorded in the post-smoke period. Rainfall was less variable ($F_{2, 69} = 3.17$, $p = 0.03$) and this difference was driven by the drought conditions during the smoke period, whereas the pre-smoke and post-smoke periods did not differ from each other (Table S3). When we included either of these variables in our models, however, no environmental factors significantly influenced call number or duration (Table S4).