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Insights on the effect of aircraft traffic on avian vocal activity

HANNAH VINCELETTE,[1,2]* RACHEL BUXTON,[1,3] NATHAN KLEIST,[1] MEGAN F. MCKENNA,[4] DAVYD BETCHKAL[5] & GEORGE WITTEMYER[1]

[1]*Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO, 80523, USA*
[2]*Migratory Bird Division, U.S. Fish & Wildlife Service Alaska Region, 1011 East Tudor Rd, Anchorage, AK, 99503, USA*
[3]*Department of Biology, Carleton University, Ottawa, ON, K1N 9A7, Canada*
[4]*National Park Service, Natural Sounds and Night Skies Division, 1201 Oakridge Drive, suite 100, Fort Collins, CO, 80521, USA*
[5]*National Park Service, Natural Sounds and Night Skies Division, MP 237 Parks Hwy, Denali Park, AK, 99755, USA*

Aircraft noise is pervasive across the USA, including in national parks, but its effects on wildlife remain unresolved. As with other noise sources, aircraft noise may affect species physiology and behaviour by being perceived as a threat, distracting individuals, or degrading the sensory environment. This study aimed to understand the effect of aircraft traffic and associated noise on the richness of bird vocalization activity in a remote national park in the USA. We used a continent-wide acoustic dataset encompassing over 30:00 h of annotated recordings to identify two geographically similar sites with high rates of bird vocalizations and both high and low rates of aircraft noise. We selected sites in Denali National Park, both of which experience little human presence, and quantified the richness of bird vocalizations before, during and after aircraft events. We present evidence of a community-level behavioural response to aircraft noise, with increased bird vocalization richness after aircraft events at a site with relatively lower aircraft noise. At the site with low rates of aircraft noise, we found bird vocalization richness did not significantly change during an aircraft event but did increase after an aircraft event. At the site with high rates of aircraft noise, bird vocalization richness did not significantly change during or after an aircraft event. This study provides new insights into wildlife responses to aircraft traffic and associated noise and highlights the importance of noise research in the management of relatively quiet and undisturbed landscapes.

Keywords: aircraft noise, Alaska, bird vocalizations, landscape ecology, national park, ornithology, soundscape, species richness.

Commercial aviation in the USA has been growing rapidly for the past 40 years, resulting in widespread air traffic (Barber *et al.* 2010). Air traffic is one of the leading sources of noise pollution in protected areas, contributing to chronic anthropogenic noise (hereafter 'noise') levels in relatively remote landscapes (Buxton *et al.* 2017, 2019). Increased noise in protected areas not only affects visitor experience (Miller *et al.* 2018) but can have negative consequences for the wildlife that uses these habitats (Shannon *et al.* 2016, Deacy *et al.* 2019). Despite its broad distribution, the effects of air traffic noise on wildlife remain largely understudied. As environmental degradation and climate change continue to impact habitat availability (Segan *et al.* 2016), the protection and management of acoustic sensory conditions is increasingly relevant in efforts to maintain natural environments and their ecological functions (Dumyahn & Pijanowski 2011, Dominoni *et al.* 2020).

*Corresponding author.
Email: hdvincelette@gmail.com
Twitter: @hannahdanielleV

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Noise has been shown to affect a variety of taxa (Slabbekoorn 2010). Birds represent a particularly vocal taxon, where vocalizations function in territory establishment and maintenance, mate attraction, predator alarm, the announcement and exchange of food, and the maintenance of social integration (Slabbekoorn 2004). Thus, bird behaviour, occupancy, abundance and reproductive success are strongly influenced by acoustic environments (Francis *et al.* 2009, 2011b, Schroeder *et al.* 2012). Birds are also relatively easy to detect acoustically (Carignan & Villard 2002). Therefore, birds are useful indicators of the ecological consequences of noise and are frequently the subjects of studies regarding the impacts of noise on wildlife (Shannon *et al.* 2016).

Noise is known to impact birds across molecular, behavioural, population and community levels of organization. At the molecular level, evidence suggests anthropogenic noise is associated with telomere attrition (Injaian *et al.* 2019) and oxidative stress in nestlings (Injaian *et al.* 2018), impaired function of the central stress response system and altered nestling growth patterns (Kleist *et al.* 2018). Noise can affect bird behaviour by degrading the sensory environment (Swaddle *et al.* 2015). For example, the frequency of anthropogenic noise can overlap and disrupt auditory environmental cues (e.g. 'masking', Lohr *et al.* 2003). Birds are known to shift the frequency and timing of their vocalizations to avoid masking (Mockford & Marshall 2009, Dominoni *et al.* 2016). Some birds alter time spent singing, the amplitude and structure of vocalizations (Sierro *et al.* 2017), or increase song duration and rate to maximize projection in noisy environments (Díaz *et al.* 2011). Alterations in the rate and type of song in response to noise may alter energy budgets. Moreover, masking can hamper parent–offspring communication (Schroeder *et al.* 2012) and territory defence by males, leading to a reduction in reproductive opportunities and fitness consequences (Zwart *et al.* 2016, Kleist *et al.* 2016).

As bird species do not respond to noise uniformly, noise also has effects at the community level (Francis *et al.* 2011a). Species with high-frequency vocalizations are more likely to adjust the frequency of vocalizations in response to lower frequency noise, whereas species with low-frequency vocalizations are more likely to adjust vocalization timing (Hu & Cardoso 2010) or leave the area to avoid masking effects (Proppe *et al.* 2013). Birds that learn songs or show high song plasticity may adapt more quickly to altered acoustic environments (Ríos-Chelén *et al.* 2012). Some species appear impervious to noise exposure (Yang & Slabbekoorn 2014). In some cases, these species-specific responses may lead to indirect benefits for tolerant species due to decreased avian predator abundance in loud habitats (Francis *et al.* 2009). Ultimately, these variable responses can alter avian community composition and diversity and consequently ecosystem functioning (Francis *et al.* 2012). Community-level changes may become long-lasting as persistent noise exposure creates new selection pressures and drives evolutionary change (Swaddle *et al.* 2015).

Aircraft are the predominant source of noise on National Park Service (NPS) lands (Lynch *et al.* 2011, Buxton *et al.* 2019), the impact of which will expand due to projected continued growth in US air traffic (Federal Aviation Administration 2019). However, little is known of the consequences of aircraft traffic and associated noise on wildlife (Pepper *et al.* 2003). The impacts of aircraft traffic on communities and ecosystems is particularly concerning in wilderness areas, where there are few sources of human disturbance. Among the management bodies of US protected areas, the NPS is particularly concerned with the intrusion of noise on its lands and is mandated to protect natural acoustic environments as a resource (National Park Service 2006). Congressional concern over the impact of aircraft on park lands has been legislatively expressed since 1987, when the National Parks Overflight Act mandated research surrounding the impacts of overflights on parks (Lynch *et al.* 2011).

To the best of our knowledge, no studies have directly quantified the effects of aircraft traffic and associated noise on bird communities in wildland habitats. However, one study found no effect of distance to a large airport on avian community richness (Gil *et al.* 2015). Aircraft overflights have been documented to elicit flushing response in some species of raptors (Stalmaster & Kaiser 1997, Delaney *et al.* 1999) and geese (Ward *et al.* 1999). Subtle effects of aircraft noise on parental behaviour were found in Peregrine Falcon *Falco peregrinus*, but no links to reproductive success have been found (Ellis *et al.* 1991, Palmer *et al.* 2003).

Most previous research specifically addressing bird vocal response to aircraft noise has focused on populations near airports, which were documented

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to alter song composition (Sierro *et al.* 2017, Wolfenden *et al.* 2019) and advance the dawn chorus (Gil *et al.* 2015, Dominoni *et al.* 2016). Another study conducted near a military training area demonstrated changes in the vocal behaviour and species distribution of Harlequin Ducks *Histrionicus histrionicus* in response to jet overflights, with long-term effects on individual energy budget and potentially on fitness (Goudie & Jones 2004). Moreover, avian species richness has been shown to decline in response to other sources of noise, particularly natural gas wells (Francis *et al.* 2009) and motor vehicle noise (Proppe *et al.* 2013, McClure *et al.* 2013, Manzanares Mena & Macías Garcia 2018).

Here, we aimed to understand the effect of the most prevalent source of noise disturbance in national parks – aircraft traffic and associated noise – on the vocal activity of birds using an acoustic dataset collected at two sites in Denali National Park, Alaska. These sites are geographically similar but experience contrasting levels of aircraft overflights, allowing the impact of aircraft noise on the richness of vocalizing bird species to be examined. Similar to studies of other noise sources (Francis *et al.* 2009, Proppe *et al.* 2013, McClure *et al.* 2013, Manzanares Mena & Macías Garcia 2018), we hypothesized fewer species would vocalize during an aircraft event than when the aircraft was absent at selected sites in Denali National Park.

METHODS

Selecting acoustic monitoring sites

We used the National Park Service Natural Sounds and Night Skies Division (NSNSD) national dataset to select sites based on the rates of aircraft noise and bird vocalizations. Detailed methods of acoustic recording collection and analysis are outlined in Lynch *et al.* (2011) and Buxton *et al.* (2019). Briefly, the NSNSD has been monitoring the acoustic environment at sites across the park system since 2000 (National Park Service 2013). Recordings are processed and analysed by trained technicians at the Colorado State University Listening Lab, where sounds are identified to categories in sampled recordings (broad natural and anthropogenic groupings include aircraft, vehicles, people talking, wind, flowing water, insects and birds).

To select appropriate sites for this analysis we used a nationwide dataset of 1 382 133 sound samples from 69 national parks, 226 sites and 38:40 h of recordings. We summarized the nationwide dataset to obtain bird and aircraft audibility – percentages of audio samples containing bird and aircraft sounds (Fig. 1) – from which we selected two close proximity sites with contrasting levels of aircraft activity within Denali National Park for a more detailed analysis. The national dataset indicated the chosen sites in Denali National Park had among the highest occurrence of bird vocalizations and were strongly differentiated in the occurrence of aircraft noise. Due to their remote locations, these sites also excluded other types of anthropogenic noise (vehicles, people talking, watercraft, construction noise, sounds from buildings and domestic animals).

Study sites in Denali National Park

An acoustic inventory of Denali National Park and Preserve was finalized in 2015 and encompassed 60 locations across the Alaska Range. Wolf Creek and Backside Lake were the two sites selected for further analysis. Wolf Creek (63°25'44.7"N, 152°27'08.9"W, elevation 290 m) is in a riparian/wetland area northwest of the Alaska Range. Recording took place from 11 June 2015 to 15 July 2015. The area has stringent standards for anthropogenic disturbance and little motorized activity. Backside Lake (62°51'38.3"N,

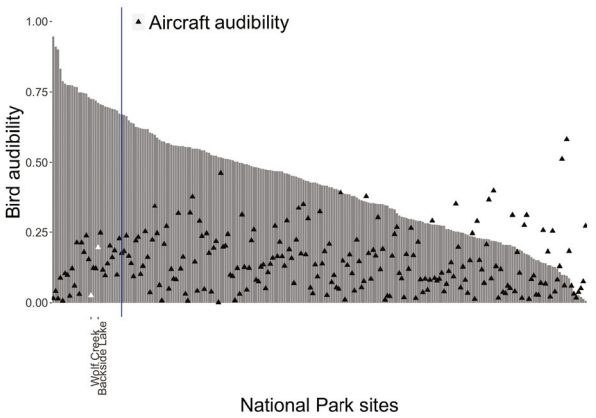

Figure 1. The proportion of time aircraft and birds were audible in 226 NPS sites for which data were collected. Wolf Creek and Backside Lake both ranked in the 90th percentile of most bird-audible sites (denoted by the blue line).

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150°40'49.7"W, elevation 863 m) is in an open subalpine area of the Alaska Range near Ruth Glacier. Recording at this site took place from 15 June 2014 to 11 September 2014. The area has relaxed standards for anthropogenic disturbance and considerable propeller-driven aircraft traffic over the site. Aircraft land and take off from the lake, or less often from the nearby gravel airstrip (Fig. 2). At both sites, aircraft are the only audible anthropogenic noise source. In addition, both sites have similar rates of jet noise, but Backside Lake has about 10 times the rate of propeller noise (Fig. 3).

Data analysis

Using the Sound Pressure Level Annotation Tool from the Acoustic Monitoring Toolbox (developed by the National Park Service 2013), we identified all aircraft in the Wolf Creek and Backside Lake recordings and produced a list of aircraft events (categorized as jet, helicopter or propeller) with associated start and end times. We randomly selected 20 isolated propeller aircraft events during the month of June 2014 at Backside Lake and June 2015 at Wolf Creek. An aircraft event was considered isolated if another aircraft did not occur <12 min before or after the aircraft event.

The acoustic data collected at Wolf Creek and Backside Lake were then analysed in Raven Pro 1.5 (Cornell University, Ithaca, NY, USA) to detect audible bird species richness relative to propeller aircraft events. We manually surveyed 10 min before and 10 min after each aircraft event as well as throughout the duration of the flyover, which ranged from 1 to 9 min with mean ± se length of 4.55 ± 2.42 min at Backside Lake, 5.18 ± 2.12 min at Wolf Creek and 4.86 ± 2.30 min overall. The total sampling effort at Backside Lake and Wolf Creek was 519 min and 520 min, respectively. We calculated audible bird species richness for each minute as the number of unique species heard during a 60-s subsample. The analyst explored the recordings for a month before collecting the data, referencing the Macaulay Sound Library (Cornell University, Ithaca, NY, USA) and Xeno-canto (Xeno-canto Foundation for Nature Sounds, The Hague, Netherlands) to build a 'Sound Library' of common birds at Wolf Creek and Backside Lake. Further, the analyst marked unknown vocalizations with a unique identifier for later identification. To limit human error and observer bias, the same analyst was used for processing all recordings and the samples were analysed in random order.

To model the variation in audible bird species richness we fitted a generalized additive mixed model (GAMM) with a Poisson response using the R package 'mgcv' (Version 1.8). GAMM is a modelling tool for a special case of general linear mixed models (GLMs) with a linear predictor depending on a smooth function of covariates (Wood 2017). The statistical package 'mgcv' allows for the inclusion of parametric and smoothed terms in GAMM functions, offering a convenient method for modelling complex non-linear processes (Wood 2010). The 'wiggliness' of a smooth term is controlled by the number of knots (k), and a penalty on degrees of freedom is incurred with increased k that restricts overfitting. We used the package default of $k = 10$ to fit our smooths.

Given the natural differences between Wolf Creek and Backside Lake (e.g. elevation, community composition, exposure, year of survey), we modelled the sites separately. Our GAMMs included a categorical predictor for time period relative to the aircraft event (*BDA*): 10 min 'before' the event, 'during' the event and 10 min immediately 'after' the aircraft event. We include a response variable for species counted per minute (richness) to control for the potential effect of longer overflights on species accumulation. We also included smooths for Julian date (Julian), hour of day (Hour) and sun position relative to the horizon in radians (SunAltitude). Julian date was calculated as the day of the current year, and we used a cubic regression basis function, which is ideal for numerical data (Table 1). We fitted hour of day using a cyclic cubic regression basis function, which includes the same derivatives for its upper and lower boundaries and is appropriate for time variables (Table 1). Sun altitude – the angle between the horizon and the centre of the sun – was calculated using latitude, longitude and time in the R package 'suncalc' (Thieurmel & Elmarhraoui 2019). We used a cubic regression basis function to fit sun altitude (Table 1). Although time of year and day are known to influence avian vocal activity (Kroodsma 2016), our species counts were taken during the Alaskan summer and around the summer solstice. These extended daylight hours are more accurately defined using sun altitude. We retained the variable for time of day because human activities will still be related to clock time, even when animal behaviour may be

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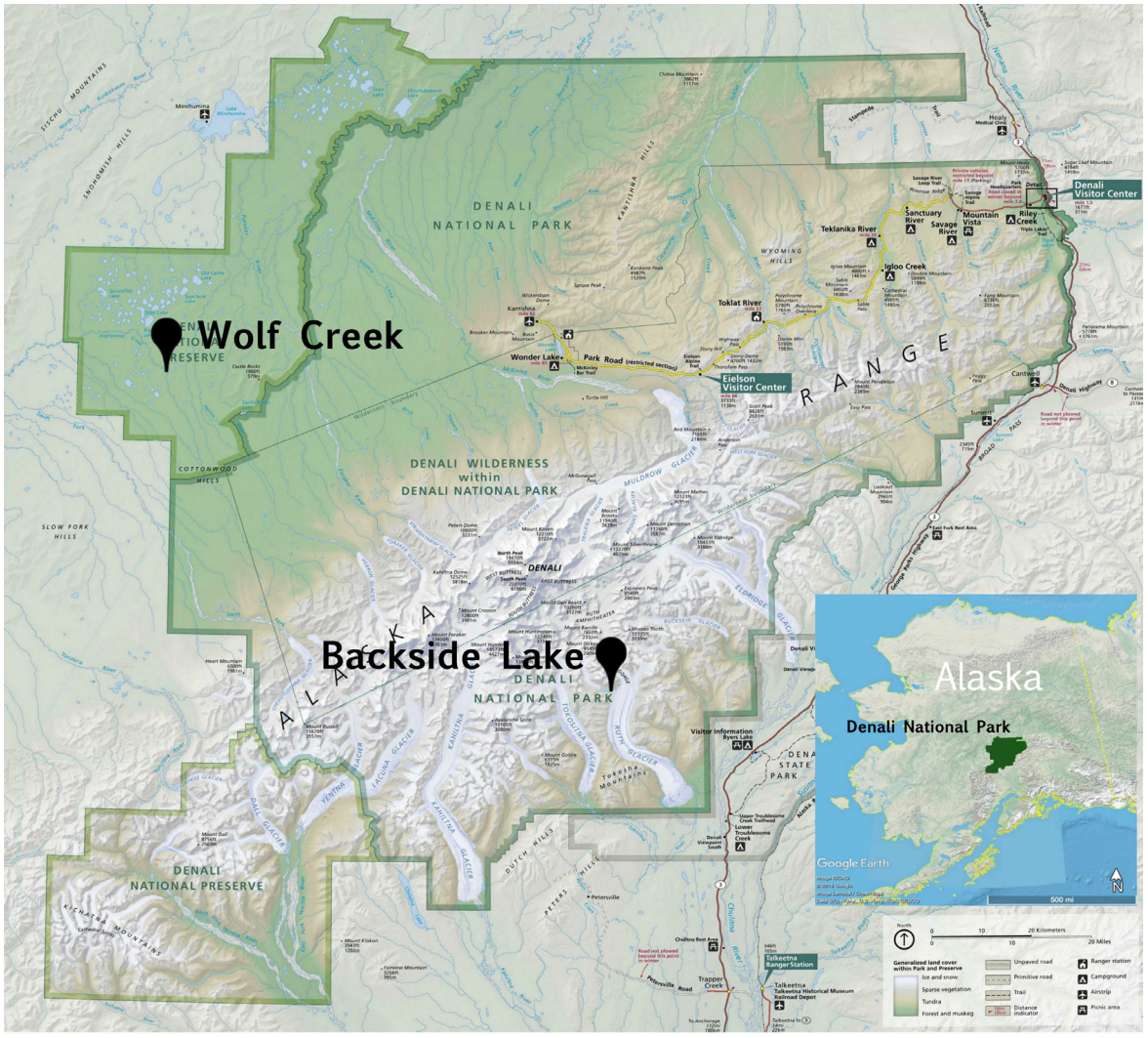

Wolf Creek Backside Lake

Figure 2. Selected sites in Denali National Park. Wolf Creek is the lower elevation, riparian backcountry site with lower aircraft audibility. Backside Lake is the higher elevation, relatively exposed front country site with higher aircraft audibility.

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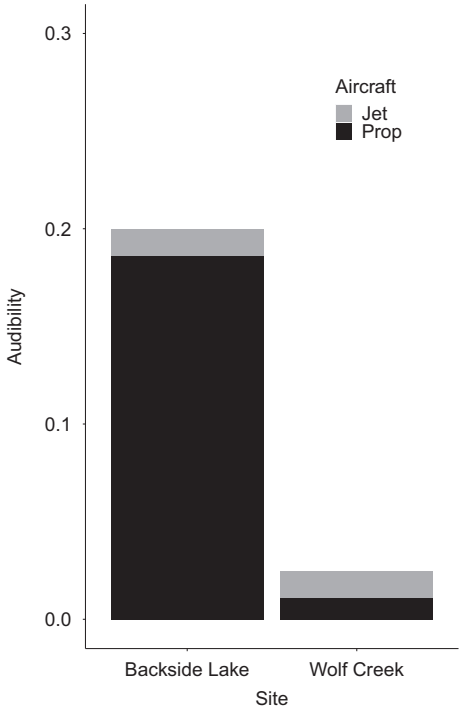

Figure 3. Audibility of aircraft at Backside Lake and Wolf Creek. No other anthropogenic noise sources were present at either site.

more influenced by sunlight conditions. Finally, because our response variable is calculated as species richness for each minute, we include a random effect term to control for potential non-independence of minute-by-minute samples within the same overflight event (AircraftPass).

We conservatively approached fitting GAMMs to our data by employing methods to reduce the chance of overfitting. As model selection procedures, including comparison of Akaike's information criterion (AIC), rarely remove smooth terms from a model, we began the model selection procedure by putting an additional penalty on smoother complexity, which removes uninformative smooth terms from the global model (Marra & Wood 2011). Following smooth term selection, we refitted the model without the extra smooth-term penalty. We then ranked potential models using the *dredge* function from the R package 'MuMIn' (Barton 2020), and considered models < 2ΔAIC of the best model to have support. We also compared top models from each site with a null intercept-only model with random effects using AIC score and log-likelihood methods. We fit all models with maximum likelihood (ML). We checked the best models for overdispersion (Fox & Weisberg 2019). Finally, we used an alpha of 0.05 to determine significant effects of each parametric and smooth term (Wood 2017). We used the R package 'visreg' to produce conditional plots for each term from the best model at each site (Breheny & Burchett 2017). We transformed the output to the response scale to facilitate biological interpretation. All quantitative analyses were performed in program R version 3.5.3 (R Core Team 2019), using the enhanced R distribution from Microsoft R Open version 3.5.3.

RESULTS

Site summary

Wolf Creek and Backside Lake in Denali National Park ranked in the 90th percentile of bird and aircraft audibility among national park sites (Fig. 1). Aircraft was the only noise source at Backside Lake and Wolf Creek. Jets and propeller aircraft were present at both sites, but propeller aircraft were the most common at Backside Lake (Fig. 3). In the Nationwide dataset, at Wolf Creek birds were audible in 72.6% of samples, aircraft in 2.5% of samples and birds in 2.2% of samples when aircraft noise was present. At Backside Lake, birds were audible in 71.2% of samples, aircraft in 19.9% of samples and birds in 14.4% of samples when aircraft noise was present. Vocalizations from 14 species were identified at Backside Lake within the sampling period, with the most common being Golden-crowned Sparrow *Zonotrichia atricapilla* (Fig. S1). Twenty audible species were identified at Wolf Creek, with the most common being Swainson's Thrush *Catharus ustulatus* (Fig. S2). Overall, 28 unique species were identified, with six species heard at both sites (Table S1).

Changes in richness of bird vocalizations

At Wolf Creek (the site with lower aircraft audibility), there was a significant positive effect of the aircraft event after the plane was no longer audible ($\beta_{after} \pm se = 0.19 \pm 0.07$, $P = 0.01$; Fig. 4). Detected species richness was not significantly higher during an aircraft event ($\beta_{during} \pm se = 0.15 \pm 0.08$, $P = 0.07$; Fig. 4). The models < 2ΔAIC of the top models for Wolf Creek

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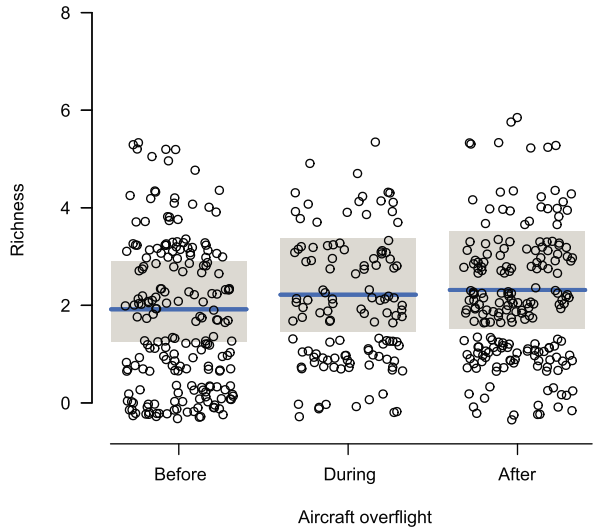

Figure 4. Plot of best model from Wolf Creek. The expected effect of the parametric term, BDA, from the top ranked model for Wolf Creek (Table 1) on observed vocal richness by minute when numerical and categorical terms were held at their median and mode, respectively (n = 520). The points are raw richness count data for each minute sampled, the horizontal bars are model-derived species richness estimates and the shaded areas represent 95% confidence intervals.

included smooth terms for Julian day, hour, sun altitude, and time period relative to the aircraft event (Tables 1 and 2). The term for time period relative to the aircraft event (BDA) was included in all six candidate models. The top ranked model included BDA (df = 20.27, AIC = 1566.75, adjR^2 = 0.39; Table 1). The top model outperformed the null intercept-only model (ΔAIC = –3.04; Table 1).

Detected species richness at Backside Lake (the site with higher aircraft audibility) was not significantly impacted by aircraft overflight. The best model for Backside Lake was the null model (df = 18.92, AIC =1853.56, adjR^2 = 0.46; Table 1). The set of candidate models < 2ΔAIC of the top model included terms for Julian date and hour of day, but these models were not significantly different from the null model (Tables 1 and 2).

DISCUSSION

Our results demonstrated a positive response in the richness of species vocalizing after an aircraft pass in a protected area with less noise intrusion. Unintended noise from aircraft traffic is one of the most pervasive anthropogenic sounds in US National Park units (Buxton *et al.* 2019). Despite the ubiquity of aircraft, little assessment of its ecological impacts has been attempted. To help rectify this lack of information, we explored changes in bird vocalization richness in response to aircraft overflights at two close proximity, bird-rich sites in Denali National Park with different levels of exposure to aircraft. In Denali National Park, the bird community at the site with lower aircraft activity showed increased vocalization richness after the aircraft passed, whereas birds at the site with greater rates of overflight did not demonstrate a response. The heightened vocal activity at Wolf Creek (the site with lower aircraft audibility) suggests aircraft noise is perceived as a threat by the bird community or has a masking effect. The apparent lack of response to aircraft noise at Backside Lake (the site with higher aircraft audibility) potentially indicates the bird community has become habituated to noise or comprises noise-tolerant species, and/or site-specific features alter aircraft noise propagation and perception. Our results provide evidence of a bird community changing vocal behaviour in response to aircraft noise in a remote park and highlight the complex nature of community response to anthropogenic noise.

Site differences in response to aircraft

Audible bird species richness increased after aircraft noise ceased at Wolf Creek, the site with lower aircraft audibility. The direction of response to aircraft noise at Wolf Creek was unexpected. The periods during and after an aircraft event showed an increase in the number of species vocalizing, although this was only significant in the period after the event (Fig. 4). Based on past noise research, we predicted species richness would decline because part of the bird community would respond by decreasing vocalizations in the presence of aircraft noise (Francis *et al.* 2009, Proppe *et al.* 2013, McClure *et al.* 2013, Manzanares Mena & Macías Garcia 2018). However, some bird species have demonstrated a heightened vocalization response to noise due to masking or risk perception (Potash 1972, Brumm 2004, Patricelli & Blickley 2006, Díaz *et al.* 2011, Ríos-Chelén *et al.* 2012, Dominoni *et al.* 2016, Wolfenden *et al.* 2019), in an attempt either to overcome noise disrupting environmental cues ('masking', Lohr *et al.* 2003) or to draw attention to a potential threat

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Table 1. Selection of general additive mixed models describing acoustic detection of bird species richness before, during and after aircraft events at Backside Lake and Wolf Creek. Models are presented in order of support, and variables describe the main effects from each model. Each model included the random effect term AircraftPass. The smooth terms include a basis function used to fit the smooth (Wood 2017). Akaike information criterion (AIC) scores and degrees of freedom were calculated with the function *aic.gam* and log likelihoods with *logLik.gam*.

Model Rank	Model variables	df	logLik	AIC	ΔAIC	R^2(adj)
Wolf Creek						
1	BDA	20.17	–763.20	1566.75	–	0.39
2	BDA + s(Hour, cc)	20.17	–763.20	1566.75	0.00	0.39
3	BDA + s(SunAltitude, cr)	20.20	–763.39	1567.19	0.44	0.39
4	BDA + s(Hour, cc)+s(SunAltitude, cr)	20.20	–763.39	1567.19	0.44	0.39
5	BDA + s(Julian, cr)	20.42	–763.43	1567.70	0.95	0.39
6	BDA + s(Julian, cr)+s(Hour, cc)	20.42	–763.43	1567.71	0.96	0.39
7	Null	18.18	–766.72	1569.79	3.04	0.39
Backside Lake						
1	Null	18.92	–907.85	1853.56	–	0.46
2	s(Julian, cr)	19.17	–907.84	1854.02	0.46	0.46
3	s(Hour, cc)	17.73	–909.81	1855.07	1.52	0.46

AIC, Akaike information criterion; BDA, 'before/during/after' an aircraft event; cc, cyclic cubic; cr, cubic regression; h, hour of day; Julian, Julian date; SunAltitude, sun position relative to the horizon in radians.

Table 2. Wald tests of the significance of parametric and smooth terms for top models at Backside Lake and Wolf Creek. The top ranked model from each site is reported (Table 1). The overall best-fit model for Backside Lake did not include the variable BDA (#4; Table 1).

Site	Model variables	df	edf	Chi-square	*P*-value
Wolf Creek	BDA	2	–	7.00	0.03
	AircraftPass	–	16.72	170.70	<0.001
Backside Lake	AircraftPass	–	17.46	217.00	<0.001

AircraftPass, random effect term for each overflight event; BDA, 'before/during/after' an aircraft event; edf, estimated degrees of freedom.

(risk perception, Halfwerk *et al.* 2018). Increased vocal activity of some species may increase their detection and ultimately drive community-level trends (Swaddle *et al.* 2015, Patricelli & Blickley 2006).

In our study, the most common species counted at Wolf Creek, Swainson's Thrush, has been reported to increase vocalizations during experimental vehicle traffic noise (Hennigar *et al.* 2019). However, removal of this species from our analysis did not change the result and further implies a community-level response to aircraft disturbance. Because we did not distinguish between songs and calls, it is possible that the heightened vocal response of the Wolf Creek bird community was driven by increased use of alarm calls, which would suggest aircraft were perceived as a threat.

In contrast to results from Wolf Creek, there was no evidence for an effect of aircraft noise on bird vocal activity at Backside Lake, where aircraft activity was more prevalent. One explanation for this site-specific trend could be habituation to more consistent aircraft overflights at Backside Lake, resulting in a dampened vocal response (Blumstein 2014). Backside Lake experiences almost 10× the number of propeller plane overflights as Wolf Creek. If birds do not associate overflights with a threat, the community at Backside Lake may have gradually reduced their response following repeated exposures (Brown 1990, Grubb *et al.* 1992, Conomy *et al.* 1998). Lower aircraft exposure at Wolf Creek might imply a reduced impact. However, relatively infrequent overflights reduce the potential for habituation and may be driving a stronger behavioural response (e.g. novel stimulus effect; Ditmer *et al.* 2019).

As discussed previously, another possible cause for the difference in responses to aircraft noise across sites could be related to differences in avian community structure. In our study, the sites had very different vocal bird communities, and the noisier site – Backside Lake – had lower bird vocalization richness (Table S1). Previous studies have

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shown that gradients of noise exposure between urban and forest habitats (Slabbekoorn 2013), within cities (Manzanares Mena & Macías Garcia 2018) and across wildlands (Francis *et al.* 2009, 2011a) drive community structure by reducing species richness at noisier sites. Frequent aircraft disturbance at Backside Lake could reduce habitat use by noise-sensitive species, resulting in the observed lower species richness. Under such a mechanism, the filtering of noise-sensitive species would explain the observed lack of a community response to overflights. However, we can only speculate as to these effects, as we only examined vocal response at two sites and the habitat differences between Backside Lake and Wolf Creek are stark. To properly tease out the interaction between habituation, community structure and aircraft response, future research could examine response at multiple sites.

Environmental factors influence audible bird species richness

Sun altitude was included in two models < 2ΔAIC of the top model at Wolf Creek, but there was no supported effect of sun altitude at Backside Lake. Wolf Creek is forested and less exposed to sunlight, so the bird community may be more sensitive to shifts in sun altitude at this site. The effects of time of day and Julian date were selected for inclusion in candidate models at both Wolf Creek and Backside Lake (Table 1). However, the null model outperformed all other candidate models at Backside Lake. Aircraft activity at Wolf Creek and Backside Lake predominately occurred between 08:00 and 20:00 h (note day length was 20 h during the study period), during which bird vocalization richness was lower at Backside Lake when controlling for other factors (Fig. S3). This may reflect the natural reduction of vocal activity associated with daytime activity or may indicate the absence of noise-sensitive species during hours of high aircraft activity. The trend for Julian date was generally positive at both sites (Fig. S4). This may be explained by the arrival of migrant species over the course of the sampling period or a seasonal environmental shift (e.g. time of sunrise) that caused more species to vocalize.

Although Backside Lake and Wolf Creek are both located in Denali National Park, they have many contrasting features that make direct comparison difficult (e.g. geological features, vegetation, exposure and aspect; see *Study sites in Denali National Park* in Methods). It is also important to note the acoustic data at Backside Lake and Wolf Creek were collected during different years – 2014 and 2015, respectively. One dissimilarity of particular interest is that Backside Lake is located at a higher elevation compared with Wolf Creek (863 and 290 m, respectively) and previous research has demonstrated an inverse relationship between avian species richness and elevation (Terborgh 1977, Rosenzweig & Abramsky 1993, Herbers *et al.* 2004, Handel *et al.* 2009). We must also consider the potential effect of habitat features on the propagation of aircraft noise and how that may alter perception across the landscape; birds equidistant from an aircraft may not hear the same sound. In addition to spreading loss (sound degradation due to distance alone; Attenborough 2002), the amplitude of a sound signal may be attenuated, refracted or scattered due to interactive effects of climate, topography, land cover and other site-specific features (Forrest 1994, Embleton 1996, Attenborough 2002, Zaporozhets *et al.* 2011, Larsen & Radford 2018). These processes are not exclusive and may magnify or dampen sound levels.

It is important to note that the propagation of biophony and geophony may also be affected by habitat features and temper the effect of aircraft noise (Mennitt *et al.* 2014). For example, wind-induced vegetation noise may mask bird communication and further reduce vocalization richness during an aircraft event. Furthermore, atmospheric conditions have also been shown to impact aircraft engine operations and the sound levels produced at the source (Zaporozhets *et al.* 2011). Soundscape dynamics are invariably influenced by habitat features and change on yearly and daily timescales. This may result in disparate impacts of aircraft noise between sites and within sites over the course of the sampling period. Although these and many other factors may influence community response, we reiterate that the simplest explanation for the documented increase of bird vocalization richness in the period following an aircraft event at Wolf Creek is the presence of the aircraft itself, regardless of modulation by site-specific effects.

Future considerations

While we were able to explore the effect of aircraft noise on bird community vocal activity, it is

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important to point out areas within this study that limit interpretations. Our study design was not able to isolate mechanisms driving the results in the study. For instance, our approach could not differentiate between when a species stopped vocalizing from when a species left the area. However, passive acoustic recording of remote habitats removes the presence of humans from monitoring efforts and may improve overall detection of species, especially those sensitive to human disturbance.

Finally, it is important to keep in mind that this study focused on bird vocalization richness, not diversity. As noise exposure can promote the abundance of noise-adapted species (Manzanares Mena & Macías Garcia 2018), it may be necessary to measure shifts in the relative abundance of vocalizing species within the 1-min subsamples to detect trends more accurately. Our study also did not take into account vocalization frequency, amplitude, type, structure or rate (within the 1-min samples), which would offer insight into the quality of the vocal response observed. Using a presence/absence study design limits our ability to detect finer changes in the bird community.

CONCLUSION

Protected areas encompass some of the most remote and quietest parts of the USA, making them even more vulnerable to long-term ecological impacts of aircraft noise (Lynch *et al.* 2011). We investigated how birds respond to aircraft noise at sites with different levels of aircraft disturbance and found evidence of a community-level response to aircraft noise; bird vocalization richness increased after an aircraft passed over the site with lower aircraft activity. There are a variety of explanations for our results. While each has different implications for management, all scenarios are linked to potential long-term biodiversity loss. This underlines the need to explore aircraft noise as a potential driver of biodiversity loss and identify mechanisms to fine-tune conservation objectives.

A major concern for places such as Denali National Park is the potential for community- and ecosystem-level change in the face of anticipated global increases in air traffic and associated noise (Federal Aviation Administration 2019). Chronic loud noise can impose selection pressure on the avian community and alter species composition, drive evolutionary change, and ultimately affect ecosystem functioning (Swaddle *et al.* 2015). This makes further research into the impact of aircraft and other noises crucial to inform management of protected areas both in the USA and globally.

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AUTHOR CONTRIBUTION

Hannah Vincelette: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Project administration (equal); Software (equal); Validation (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Rachel Buxton:** Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Software (lead); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Nathan Kleist:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Software (lead); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Megan F. McKenna:** Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Davyd Betchkal:** Data curation (equal); Investigation (equal); Writing-review & editing (supporting). **George Wittemyer:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (supporting); Supervision (supporting); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (equal).

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DATA AVAILABILITY STATEMENT

The data that support the findings are available at osf.io/xaqnc.

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SUPPORTING INFORMATION

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

Figure S1. Sound sample of a Golden-crowned Sparrow *Zonotrichia atricapilla* song at Backside Lake. This sample was recorded on 6 June 2014 at 02:25 h. The sonogram visually represents the sound with frequency (kHz) over time (s). A Darker colour indicates higher amplitude, or a louder sound.

Figure S2. Sound sample of a Swainson's Thrush *Catharus ustulatus* song and call at Wolf Creek. This sample was recorded at 27 June 2015 at 00:47 h. The sonogram visually represents the sound with frequency (kHz) over time (s). A Darker colour indicates higher amplitude, or a louder sound.

Figure S3. The association between time of day and bird vocalization richness at Backside Lake. This figure represents the covariate 's(Hour)' from the third ranked model for Backside Lake (Table 1).

Figure S4. The association between Julian date and bird vocalization richness at Wolf Creek (A) and Backside Lake (B). This figure represents the covariate 's(Julian)' from the fifth and second ranked candidate models for Wolf Creek and Backside Lake, respectively (Table 1).

Table S1. Occurrence of audible species at Backside Lake and Wolf Creek. Total Count is the number of 1-min subsamples during which a species occurred across all periods. Before, During and After reflect the count in the respective periods. Before is the 10-min period before the aircraft event, During is the period during the aircraft event. After is the 10-min period after the aircraft event. Total Frequency is the species occurrence out of the entire time assessed (49 h 4 min) and at each site (29 h 38 min at Wolf Creek, 20 h 3 min at Backside Lake).

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