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Reducing avian collisions with human-made structures: A sensory ecology approach to open-air settings

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ABSTRACT

Billions of birds fatally collide with human-made structures each year. These mortalities have impacts on species of conservation concern and potentially on avian populations as a whole. This source of human-wildlife conflict also places economic and operational constraints on various human industries. Furthermore, with continued increases in urbanization, the rate and extent of collisions continues to increase. Efforts to reduce collisions have largely centered on making structures more visible to birds but have been met with limited success. Currently, there is a call for solutions to be tailored to both the environmental context of hazardous structures and to the sensory ecology of at-risk birds.

In Chapter 1, we review how and why sensory ecology will help reduce in-flight collision risk for birds. A growing understanding of the sensory systems of birds and of the interface between these systems and the environment will enable the design of appropriate warning and deterrent signals. In particular, we review avian auditory and visual sensory ecology to better understand the susceptibility of birds to collisions and to recommend effective signal design. We highlight the ubiquity and salience of multi-modal signals in avian ecology and evolution, particularly as warning signals, and propose the use of multi-modal signals in mitigating collisions. We encourage the use of animal behavior frameworks to assess collision risk and collision mitigation approaches. Behavioral analyses offer numerous advantages over traditional collision measures, such as mortality estimates. Behavioral data can be generated quickly, render large sample sizes, and allow more nuanced perspectives of the context-dependence of collisions.

In Chapter 2, we investigate the use of acoustic signals to reduce avian collisions with structures in open airspace. Birds have largely evolved without tall human-made structures in their flight paths and, consequently, avian perception and behavior may not be suitably primed to detect these novel hazards. Our previous work in captive settings showed that acoustic signals aid in drawing the attention of flying birds to potential collision hazards, influencing flight behavior. The current work corroborates these findings in a field setting. We projected acoustic signals into open airspace surrounding communication towers and quantified movement patterns of birds, to indicate potential collision avoidance behavior. Our results show a ~15% reduction in overall bird activity surrounding towers during sound treatment conditions, compared with control trials. Furthermore, flight movement patterns during sound treatments were characterized by significantly greater distances from and greater displacement of travel direction relative to towers, compared with control trials. Flights during sound treatments also showed significantly slower velocities, compared with control trials. Lower frequency sound stimuli (4-6 kHz) produced larger effect sizes than higher frequency stimuli (6-8 kHz). Results also co-varied with tower location and data collection date, reinforcing an appreciation of the context-dependent nature of collision risk. Our findings will inform the field of avian sensory ecology and help to assess the use of acoustic signals in collision mitigation measures.

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Chapter 1

Sensory and behavioral ecology will help reduce in-flight collision risk for birds

As part of broader human-wildlife conflicts, billions of birds fatally collide with human-made structures each year. These mortalities have known impacts at local scales, particularly on species of conservation concern, but potentially also influence broader-scale population trends. Collisions also place economic and operational constraints on various human industries, such as the building and energy sectors. With continued increases in urbanization and habitat alteration, the rate and extent of collisions will continue to increase. Here we review how and why sensory and behavioral ecology will help reduce in-flight collision risk for birds. A growing understanding of the sensory systems of birds and of the interface between these systems and the environment will enable the design of appropriate warning and deterrent signals. In particular, we review avian auditory and visual sensory ecology to better understand the susceptibility of birds to collisions and to recommend effective signal design. We highlight the ubiquity and salience of multi-modal signals in avian ecology and evolution, particularly as warning signals, and propose the use of multi-modal signals in mitigating collisions. We encourage the use of animal behavior frameworks to assess collision risk and collision mitigation approaches.

Introduction

Interactions between wildlife and humans are increasing, driven primarily by increases in both human population size and anthropogenic modification of the environment (Sih et al., 2011). Direct mortality of wildlife due to physical interactions with anthropogenic structures is a significant source of human-wildlife conflict (Nyhus, 2016). One form of direct mortality is physical collisions between wildlife and human-built structures. Mortality from collisions has been documented in a wide range of taxa including mammals (Arnett et al., 2016; Collins & Kays, 2011), amphibians (Glista et al., 2008), and birds (Loss et al., 2015). Furthermore, collisions occur with a diversity of structures, including mobile features such as automobiles (Glista et al., 2008; Hill et al., 2020), aircraft (Cleary et al., 2006), wind turbine blades (Loss et al., 2013), and also static structures including windows (Klem, 2010), buildings (Loss et al., 2014), power lines, and communication towers (Longcore et al., 2012). Such collisions negatively impact numerous species of conservation concern, across taxa (Glista et al., 2008; Pagel et al., 2013; Stehn & Wassenich, 2008), and can have impacts at the population level (Everaert & Stienen, 2007; Hunt & Hunt, 2006). Collisions are also associated with significant operational and economic cost to numerous sectors of human society, including agriculture, travel, and energy (Allan, 2000; Snyder & Kaiser, 2009). Consequently, there is policy and lobbying both for and against socioeconomic development associated with wildlife conflicts. For example, the costs of site-assessment studies for wind energy development are substantial and have largely come about by lobbying from conservation groups. The widespread occurrence of collisions, across both taxa and structure types, and the associated societal and economic costs, render collisions a prominent source of human-wildlife conflict. Characterizing the nature of collisions across these diverse contexts is an important step in developing effective mitigation approaches to this conflict.

While collisions have been documented in a range of taxa, some wildlife are particularly susceptible to collisions with anthropogenic structures. Flying animals, for example, are much more prone to lethal collisions due to the force with which they may strike structures and due to physiological limitations in their ability to avoid unexpected structures while flying. Billions of birds die annually from collisions with human-made structures including communication towers, wind turbines, buildings, windows, power lines, and fences (Klem, 2010; Longcore et al., 2012; Loss et al., 2013, 2014). The conservation implications of collisions for birds have been debated and much work remains to be done on characterizing spatial and temporal trends at a large scale. However, it is already clear that collisions can be a threat to species of conservation concern on a local scale, as has been documented with Golden Eagles (*Aquila chrysaetos*) near Altamont pass, California (Pagel et al., 2013), migrating Whooping Cranes (*Grus americana*) in the central U.S. (Stehn & Wassenich, 2008), or Blue Cranes (*Anthropoides paradiseus*) in South Africa (Shaw et al., 2010). As in these case studies, collisions can have notable population-level consequences for some species. At particular risk may be longer-lived, low-producing species for which increased mortalities can have a marked effect in a relatively short amount of time (Everaert & Stienen, 2007; Hunt & Hunt, 2006). The effect of collisions on migratory species is particularly difficult to ascertain given their large geographic ranges. However, current levels of habitat degradation and loss already severely threaten migratory birds (Runge et al., 2015). Even when the consequences of collisions are unclear at broader scale population levels, local losses in avian abundance can have functional costs for populations, communities, and ecosystems (Anderson et al., 2011; Rosenberg et al., 2019). Furthermore, local population declines can contribute to an overall more restricted geographical range for a species, which can eventually lead to extinction (Diamond, 1989). Lastly, the true incidence of bird collisions, even at local scales, is likely underreported (Longcore et al., 2008; Smallwood et al., 2010) but is nonetheless recognized as a leading source of human-caused avian mortality and is projected to increase alongside continued human developments (Drewitt & Langston, 2000; Klem, 2010).

Factors that influence the likelihood of in-flight collisions

The incidence of in-flight collision with human-made structures is influenced by the features of the hazard itself and how the hazard is situated. For example, the geographic location of a structure greatly determines collision risk. Structures located on or near key foraging, roosting or breeding habitats, or within flyways used extensively for migrations or local movements, are associated with higher collision incidence (Everaert & Stienen, 2007; Henderson et al., 1996; Hunt & Hunt, 2006). Also, the physical extent and arrangement on the landscape of structures affects collision risk. Specifically, the height of tall structures, such as towers and turbines, significantly influences the incidence of collisions (Crawford & Engstrom, 2001; Winkelman, 1992). Additionally, structural lighting is associated with collisions, particularly at night. Artificial light can attract and disorient birds by disrupting navigation behaviors and physiology (Bruderer et al., 1999; Gauthreaux & Belser, 2006; Verheijen, 1985). This renders birds susceptible to direct mortality through collisions and indirect mortality through exhaustion, starvation, or predation (Avery et al., 1976; Beason, 1999; Verheijen, 1985). Some types of hazards, such as communication towers or wind turbines, extend high above surrounding landscapes into open airspace and are isolated from surrounding features. These types of structures, which occupy previously highly predictable environments, may present evolutionarily novel hazards to flying birds.

In addition to the properties and densities of hazards themselves, there are certain taxa that are disproportionately more likely to collide with certain structures. For example, morphology and flight characteristics correlate with collision risk. Some species are aerodynamically and biomechanically limited in responding to unexpected hazards (Bevanger, 1998; Herrera-Alsina et al., 2013; Janss, 2000). Also, there are differences in sensory physiology among taxa which may underlie differential collision risk. Species with good binocular but poor lateral vision appear to be more susceptible to collisions with power lines and fences (Bevanger, 1994, 1998), while species with optimized lateral vision may be at higher risk to collisions with communication towers or wind turbines (Martin, 2011). Additionally, flight behavior is an important factor influencing collision risk. Birds using thermals or prevailing winds, engaging in aerial displays, or pursuing prey or competitors have all been observed colliding with structures in several studies (Alonso & Alonso, 1999; Barrios & Rodríguez, 2004; Faanes, 1987; Richardson, 2000). Finally, individual variation within taxa such as in age and experience, can also influence collision risk. First year migrants or recently fledged or dispersing birds are at higher risk of collision when moving through unfamiliar environments (Alonso & Alonso, 1999; Rose & Baillie, 1989).

It is also clear that environmental factors interact with the properties of hazards and of taxa to influence collision incidence. For example, there are notable temporal (season and time of day) patterns to collisions. Some gregarious species form winter flocks, while migratory species often move en masse. These high concentrations of birds, perhaps with decreased attention to surrounding features as they follow a lead bird, are associated with increases in collisions during specific times of year (Alonso & Alonso, 1999; Barrios & Rodríguez, 2004; Richardson, 2000). Another environmental factor that influences collision risk is ambient lighting. Many species, both in their daily movements as well as in migrations, concentrate movements at night or in the early hours of the day, when collision risk may be augmented by lower visibility. High collision incidence at these times of day is particularly evident with migratory passerines in North America (Drewitt & Langston, 2000; Longcore et al., 2013). Also, weather conditions influence collisions risk. In particular, overcast conditions force birds to fly at lower heights with compromised visibility increasing their risk of colliding with structures (Avery et al., 1977; Elkins, 1983). Higher wind speeds, anomalous prevailing wind conditions and extremes of temperature have also all been associated with higher collision incidence in local examples (Elkins, 1983; Henderson et al., 1996; Newton, 2007; Winkelman, 1992).

A synthetic example of the structural, taxonomic and environmental drivers of collisions risk can be provided with open-air structures such as towers and turbines. Higher collision incidence has been reported when these structures are located in migratory flyways or near key habitats (Everaert & Stienen, 2007; Hunt & Hunt, 2006), when structures are taller (Crawford & Engstrom, 2001; Winkelman, 1992), and when structures are associated with artificial lighting (Avery et al., 1976). A diverse range of species have been documented as collision victims with open-air structures, but migratory passerines appear to be disproportionately susceptible (Drewitt & Langston, 2000; Longcore et al., 2013). These collisions show temporal associations, with passerine collisions peaking during migrations, particularly, for example, southward fall migration in North America, when many birds are first time migrants (Longcore et al., 2013). Most passerine collisions also occur at night or in the early hours of the morning, when visibility may be hindered by lower light conditions or when artificial light on structures may disorient or attract migrants (Longcore et al., 2013). The visual systems of most birds are described as having higher resolution and acuity in the lateral fields of view, particularly as vision relates to navigating environments (Martin, 2007, 2009). Furthermore, when flying at higher altitudes, the attention of birds is likely focused on terrestrial features, as they navigate or survey habitats. Thus, the behavior of birds in open airspace, and the adaptations of their visual systems, may not adequately detect these open-air structures, which occupy what was, at least evolutionarily, a highly predictable environment for birds.

Current approaches to assessing risk of collisions

It is common to estimate the number and rate of collisions with hazards by local collection of data. Local measures are then scaled-up or combined, through meta-analytical techniques, to generate landscape-, regional-, or global-scale estimates. These generalized estimates inform our understandings of the broad patterns of avian collisions and can be used as the basis for conservation management practices and socio-economic development regulations and policy. For these reasons, it is vitally important that local estimates of collisions are accurate and informative.

Currently, much of the local data on collisions is estimated through direct observations of mortality. Researchers conduct surveys of carcasses around the hazard, sometimes supplemented by anecdotal reporting from non-systematic survey methods (e.g. Klem, 1989). These methods of data collection likely lead to under-estimates of actual collisions as they can often ignore the influence of scavengers, delayed mortalities, or carcass persistence and detectability (Barrientos et al., 2018; Loss et al., 2012; Santos et al., 2016). Additionally, surveys of carcasses are rarely conducted throughout the entire year, rather focusing on peak collision periods such as during migrations. However, collisions at other times of year can be significant and should be incorporated to render more accurate estimates of mortality (Loss et al., 2013). Furthermore, not all collisions are fatal yet may still negatively impact wildlife. For example, both local and larger-scale movements hindered by the presence of collision hazards may confer energetic costs to wildlife (Lennox et al., 2016). A variety of anthropogenic structures have also been shown to increase stress levels in wildlife by, for example, limiting access to resources such as food or by disrupting communication systems (Lennox et al., 2016). These indirect effects likely contribute to the overall deleterious impacts of collision hazards on wildlife but are difficult to estimate or understand using current methods (i.e. surveys of carcasses).

How can we improve on local surveys of carcasses to better assess the risks of in-flight collisions for birds? We suggest that analyzing the behaviors of wildlife may help to remedy the current methodological shortcomings (Blackwell et al., 2016). Successful mitigation of human-wildlife conflicts relies on a sound mechanistic understanding of how wildlife responds to anthropogenic disturbance and much of that response is behavioral. The application of behavioral frameworks to understanding and mitigating collisions is particularly appropriate, given the high context dependence of these events. Continued contributions to characterizing the behavior of wildlife in anthropogenically modified contexts is crucial to successfully managing human-wildlife conflicts.

Much of the work aimed at reducing human wildlife conflict has focused on deterring wildlife from areas of conflict, either completely or at specific times when deleterious interactions may be highest (e.g. Hedges & Gunaryadi, 2010; Mahjoub et al., 2015; Noatch & Suski, 2012). The same can be noted with work on reducing avian collisions (e.g. Blackwell et al., 2018; Swaddle et al., 2016). Absolute deterrence is an understandable approach, especially when conflicts pose severe hardships to human livelihood. For example, the threat and occurrence of collisions between birds and airplanes, and the actions taken to mitigate this conflict, cost the U.S. civil aviation industry up to $937 million annually (Cleary et al., 2006). Complete deterrence, however, is a less nuanced approach compared with, for example, aiming to elicit certain behaviors from wildlife which may decrease the severity or incidence of conflict, but not permanently displace local wildlife populations. Furthermore, complete deterrence is not easily achievable, given the high value of some resources for wildlife and the extent of human activities into almost all environments. For example, human agricultural areas, which have continually extended into areas previously inhabited by diverse wildlife, can often provide a valuable food resource for remaining wildlife populations and the conflict between humans and wildlife over these resources can be tense (Nyhus, 2016). Complete deterrence in these examples is either of limited success, given the high value of the resource, or leads directly to the declines, and even extinctions, of wildlife populations (Nyhus, 2016; Rosenberg et al., 2019). In an example with avian collisions, migratory species are likely significantly threatened by wind farms with which they indirectly compete for the resource of air movements. Wind farms are strategically placed to maximize exposure to prevailing wind streams, while migrating birds heavily rely on the same resource to successfully complete energetically costly migrations (Drewitt & Langston, 2000; Everaert & Stienen, 2007; Hunt & Hunt, 2006; Richardson, 2000). Sustained deterrence of birds from these areas is difficult, given their adaptation to the use of this resource, and deterrence efforts could also drive avian mortality, possibly contributing to population and species declines.

Avian sensory and behavioral ecology as an integrative solution

Behavior mediates the interactions between individuals and their environments. Thus, approaches to mitigating human-wildlife conflicts should include a focus on influencing the behavior of wildlife. However, behaviors are often transient or flexible, particularly when under strong environmental pressures including anthropogenic modification of the environment (Levis & Pfennig, 2016; Sih et al., 2011; Slabbekoorn & den Boer-Visser, 2006; West-

Eberhard, 2005). Therefore, ideally, efforts that influence behavior should continually monitor behavioral variation and be flexible themselves.

One of the reasons behaviors respond flexibly is through feedback via the sensory systems of wildlife. In the case of in-flight collisions, mitigation efforts have targeted the visual systems of birds (Martin, 2011) because birds navigate their environments visually (Gill, 2007). While this interpretation may largely still be true, our understanding of the visual systems of birds has been revised markedly in recent decades. Recent work has explored aspects of avian visual systems including spectral sensitives, spatial resolution and acuity, and how visual systems interface with ecology (e.g. Butler et al., 2018; Ensminger & Fernández-Juricic, 2014; Harness et al., 2016; Martin, 2007; Potier et al., 2018). In some instances, these advances have been incorporated into mitigation work. For example, hazards such as communication towers are now illuminated with discontinuous lighting; a modification from sustained lighting which was shown to attract rather than deter birds, particularly nocturnal migrants (Gauthreaux & Belser, 2006; Ogden, 1996). Some visual warning signals now encompass short wavelength, ultra-violet stimuli, following work characterizing widespread avian spectral sensitivities in this portion of the electromagnetic system (Harness et al., 2016; Hart & Hunt, 2007). However, many more mitigation efforts do not yet incorporate recent advances in understanding avian sensory systems and ecology.

The visual systems of most birds generally have higher resolution and acuity in the lateral fields of view, particularly as it relates to navigating surroundings (Martin, 2007, 2017a). Binocular vision, on the other hand, appears to be more associated with physically proximate tasks, such as perching or landing, obtaining food, preening, and provisioning young (Martin, 2009, 2017a). Furthermore, as previously mentioned, birds moving through open airspace may direct their attention primarily to terrestrial features as they navigate a landscape. Hazards such as communication towers or wind turbines may thus occupy an effective blind spot for birds in these contexts (Martin, 2011). Simply making these structures more visually conspicuous, particularly in the regions where they may be less noticeable such as near the tops of these structures, may be an ineffective mitigation approach. Stokke et al. (2020) showed how visual signals placed at the base of wind turbines were as effective in mitigating collision risk as signals placed nearer the top of structures, illustrating a potentially more effective targeting of the context-dependent behavior of at-risk birds in these open-air contexts. Characterizing the ecological context of behaviors is necessary to create effective collision mitigation solutions.

Our current interpretations of how avian visual systems function in variable ecological contexts is particularly lacking. Most work characterizing avian visual systems, both physiologically and behaviorally, has been conducted in captive settings with potentially little ecological relevance. Furthermore, much of our current knowledge of avian sensory systems is gleaned from data collected from immobile specimens (e.g. Fernandez-Juricic et al., 2004; Martin, 2007; Potier et al., 2018), while much less has been obtained from birds during flight (e.g. Bhagavatula et al., 2011). However, it is important to assess how birds perceive their environment while they are in flight. This is of particular consequence for work aiming to address collisions by flying birds, where our current understanding of their sensory system sensitivities or the interactions between those sensitivities and variable environments may be significantly ill-informed.

We have a much deeper understanding, compared to vision systems, of how avian auditory systems mediate responses to environmental changes. This may primarily be driven by the extensive work on bird song and vocal-auditory communication. We have investigated the effects of these responses for populations and communities (e.g. Francis et al., 2009, 2011) as well as their evolutionary consequences (e.g. Derryberry et al., 2016; Luther & Derryberry, 2012). Furthermore, we have investigated the mechanisms by which auditory systems themselves respond to changes both in the short term, such as through behavioral or physiological flexibility (e.g. Arroyo-Solís et al., 2013; Derryberry et al., 2017), and long term, such as through developmental plasticity (Peters et al., 2012) or local adaptation (Bueno-Enciso et al., 2015; Slabbekoorn & den Boer-Visser, 2006). Understanding avian auditory ecology has helped mitigate human wildlife conflicts, such as in deterring birds from airfields and agricultural sites using signals intended to mask avian communications (Mahjoub et al., 2015; Swaddle et al., 2016). Furthermore, this communication-disrupting deterrence has produced a sustained behavioral response in birds. This proves more effective than signals designed to simply alarm birds, and which consequently experience deteriorating efficacy as birds become accustomed to the disturbance (Belant et al., 1998; Bomford, 1990).

Despite potentially more extensive work on avian auditory ecology, much of this work has once again been conducted in captive and laboratory settings. This is particularly true for work on auditory physiology, but also includes behavioral studies (e.g. Dooling & Prior, 2017; Henry et al., 2016). Furthermore, as with work on visual systems, there is less explicit focus on how avian auditory systems function while birds are in flight. For collision mitigation work, aiming to tailor methods to the sensory ecology of at-risk birds, this context specific applications are vitally important. Investigating the use of sensory stimuli to mitigate avian collisions therefore comes with the opportunity to explore a less-understood area of avian sensory ecology.

In reality, birds use multiple senses simultaneously while attempting to avoid hazards in flight. Specifically, we propose that combining our understanding of visual and auditory ecology will lead to more effective mitigation strategies. Multi-modal signals increase the salience and efficacy of communication by augmenting detectability and decreasing the influence of unintended signals and background noise (Partan & Marler, 2005; Stevens, 2013). The baseline reaction times of birds may often be insufficient to be able to avoid anthropogenic collision hazards. For example, Blackwell et al. (2009)

showed that the reactions times of brown-headed cowbirds (*Molothrus ater*) and mourning doves (*Zenaida macroura*), to rapidly approaches vehicles was not sufficient to avoid collisions. One of the challenges in collision mitigation work is extending the detectability of hazards or their warnings enough so that flying birds will have enough time and space to react and avoid these hazards. Multi-modal signals may have high applicability for collision scenarios, where a high detectability of warning signals is required. Swaddle & Ingrassia (2017) show how the presentation of a conspicuous acoustic signal, together with the presence of a visually apparent collision hazard, produced the highest degree of collisions avoidance flight behavior in flying birds, compared to either the visual or acoustic signals alone. The use of multi-modal signals in collision mitigation work merits further exploration.

Conclusion

Knowledge of avian sensory ecology, particularly that of visual and auditory systems, will allow suitable solutions to be tailored to the context dependent nature of both hazards themselves and at-risk birds. Interpreting the response of birds to hazards using behavioral measures will provide higher resolution data, to inform larger scale measures of collisions incidence and risk, and more adequately evaluate mitigation approaches. Furthermore, interpretation of behavioral responses will allow continual fine tuning of mitigation techniques to match the short term and long-term changes in the behavior of wildlife. The study of avian collisions provides an opportunity to further our understanding of the interplay between avian sensory systems and the environment, as well as affording further insight into the responses of birds to anthropogenic change.

Chapter 2

Using acoustic signals to reduce avian collisions with human-made structures in open airspace: An informed sensory ecology approach

Introduction

It is estimated that billions of wild birds die annually from collisions with human-made structures such as communication towers, wind turbines, power lines and buildings (Klem et al., 2009; Longcore et al., 2012; Loss et al., 2013, 2014). These collisions are one of the largest sources of human-caused avian mortality world-wide. Such collisions can be a significant threat to species of conservation concern on a local scale (e.g. Pagel et al., 2013; Shaw et al., 2010; Stehn & Wassenich, 2008) and likely have larger scale impacts too, though these trends remain difficult to estimate. However, with the known impacts of habitat loss and degradation on birds, collisions likely have an added detrimental effect on populations, particularly of migratory species (Runge et al., 2015). Furthermore, losses in avian abundance can have functional costs for populations, communities, and ecosystems, for example by changing predator-prey dynamics (Anderson et al., 2011; Rosenberg et al., 2019; Thaker et al., 2018) and local population declines can contribute to restricted geographical ranges and eventually extinction (Diamond, 1989).

In addition to effects on wildlife, avian collisions are costly to numerous sectors of human society, including agriculture, travel, and renewable energy (Allan, 2000; Snyder & Kaiser, 2009). For example, the threat and occurrence of collisions between birds and airplanes, and the actions taken to mitigate this conflict, cost the U.S. civil aviation industry up to $937 million annually (Cleary et al., 2006). There is costly policy and lobbying both for and against socioeconomic development and operations which have been linked with avian collisions. The widespread occurrence of collisions, across both taxa and structure types, and the associated societal and economic impacts, render collisions a prominent source of human-wildlife conflict. Furthermore, with continued increases in urbanization, the incidence of bird collisions will continue to rise (Hager et al., 2017).

Unsurprisingly, there have been substantial efforts to reduce the incidence of bird collisions with human-made structures. Many of these efforts have centered on making structures more visible to birds (e.g. Barrientos et al., 2012; Klem & Saenger, 2013). Some methods have been successful, such as the use of various types of markings on glass windows (Rössler et al., 2015) or dynamic lighting atop towers at night and in overcast conditions (Blackwell et al., 2018; Goller et al., 2018). However, many of these examples often lack transferability and replicability - not being as successful in other settings of even similar scenarios (Longcore et al., 2012; Loss et al., 2014). The prevalence of visually oriented mitigation methods is likely due to their relative ease of implementation, but it is also due to the perspective that birds predominantly navigate their environments visually (Frank B. Gill, 2007b). Making structures more visible, however, has often been informed by a human, not avian, perspective. Through studies of avian sensory ecology, we now know that birds view their worlds quite differently from humans (Martin, 2011; Martin & Shaw, 2010). As a result, there is increasing realization that solutions to collisions need to center on understanding the world from the perspective of avian sensory ecology, by incorporating knowledge about both the environmental context of hazards and the sensory systems of at-risk birds (Blackwell et al., 2016; Madliger, 2012; Martin, 2011).

Second only to windows collisions, large human-made structures such as wind turbines and communication towers pose significant collision threats to birds (Allan, 2000; Longcore et al., 2012; Loss et al., 2014; Pagel et al., 2013). These structures extend dozens to hundreds of meters vertically into open airspace and are often isolated from surrounding features. The incidence of collisions with these structures is influenced by features of the hazard itself and how the hazard is situated. For example, the height of tall structures significantly affects collision risk (Crawford & Engstrom, 2001; Longcore et al., 2008), structural lighting is associated with collisions, particularly at night (Gauthreaux & Belser, 2006; Longcore et al., 2008), and the geographic location of a structure greatly determines collision incidence. As examples of the latter, structures located on or near key foraging, roosting or breeding habitats, or within flyways used extensively in migrations or local movements, are associated with higher collision incidence (Everaert & Stienen, 2007; Henderson et al., 1996; Hunt & Hunt, 2006). There is evidence to suggest that perceptual limitations of flying birds may be a strong explanatory factor for the prevalence of collisions with these open-air structures (Martin & Shaw, 2010). Birds generally have eyes located laterally on their skulls which dictates aspects of their visual physiology, such as field of view and focal acuity. For many species, it appears as though lateral vision may serve predominantly for navigation behaviors while binocular vision is concerned with more proximate tasks such as landing, perching, feeding, and provisioning of young (Martin, 2007, 2009). The visual attention of birds during high altitude flight may be more focused towards terrestrial features as part of navigating, foraging, or other surveying behaviors, and these behaviors may primarily use the lateral rather than forward-facing, binocular fields of view. Bird visual physiology and behavior may not be adequately primed for the detection of structures in open airspace, which may be directly in line with a bird's flightpath (Martin, 2011, 2017b). Finally, avian physiology and behavioral ecology have evolved mostly in the absence of human-made structures extending vertically into open airspace, and these structures present evolutionarily novel hazards for flying birds (Martin, 2017b; Swaddle et al., 2015).

Understanding the potential perceptual limitations of flying birds to open-air hazards will allow for the development of more suitably designed mitigation measures. Birds use multiple senses simultaneously while attempting to avoid hazards in flight. One way to increase the detectability of a hazard is to stimulate more than one sensory modality. Multi-modal signals increase the saliency and efficacy of communication signals by augmenting their detectability and decreasing the influence of unintended signals and background noise (Partan &

Marler, 2005; Stevens, 2013). For these reasons, multi-modal signals are prevalent in nature, particularly as warning signals (Rojas et al., 2019; Rowe & Halpin, 2013), and have also been used to mitigate other human-wildlife conflicts, such as in deterring birds from conflict areas (e.g. Lecker et al., 2015). One of the challenges in collision mitigation work is extending the detectability of hazards or their warnings enough so that flying birds have ample time and space to react and avoid hazards.

Multi-modal signals may be highly applicable for collision scenarios, where a greater detectability of warning signals is required. Specifically, we propose that combining an understanding of visual and auditory avian ecology will lead to more effective warning signal design and collision mitigation strategies. Swaddle and Ingrassia (2017) demonstrated how the presentation of a conspicuous acoustic signal, together with the presence of a visually apparent collision hazard, produced the highest degree of collision avoidance behavior in flying birds, compared to either the visual or acoustic signals alone. A potential collision-mitigating approach in open-air settings may be to use conspicuous acoustic signals, which could aid in drawing the attention of flying birds towards collision hazards. Combining knowledge about avian auditory physiology and behavior with that of sound propagation characteristics could lead to the development of acoustic signals that are effective in the context of open-air collisions. Much previous work has detailed the auditory physiology of birds as well as characteristics of sound transmission through the environment (e.g.

Dooling et al. 2002; Bradbury and Vehrencamp 1998; Gill and Bierema 2013). However, somewhat less is known about the sensory ecology of birds during flight. Conducting tests on mitigating collision risk in flying birds using auditory and visual signals provides a compelling opportunity to expand upon our understanding of avian sensory ecology and behavior during flight.

The use of acoustic signals in mitigating collisions in open-air scenarios has begun to receive some attention, predominantly in addressing collisions with wind turbines (H. T. Harvey and Associates, 2018; May et al., 2015). However, there is ample room for increased testing and a lack of peer-reviewed studies conducted by third party research groups. Our research group previously highlighted the effectiveness of multi-modal signals (auditory and visual) in influencing the flight behavior of birds in a captive setting (Swaddle & Ingrassia, 2017).

The first aim of the current study is to test the efficacy of conspicuous acoustic signals at reducing the risk of collisions with visually-obvious tall structures in a field setting. We projected acoustic signals into the air-space surrounding communication towers and evaluated the collision risk of flying birds in sound treatment and control conditions.

The second aim of the current study is to begin testing what specific characteristics of acoustic signals elicit higher degrees of collision-avoidance behavior. We tested two types of acoustic signals, to evaluate frequency-dependent behavioral responses.

The third aim of the current study is to develop behavioral analyses to interpret collision risk and evaluate the efficacy of mitigation techniques. Much of the current data on collisions is estimated through direct observations of mortality. Researchers conduct surveys of carcasses around the hazard, sometimes supplemented by anecdotal reporting from non-systematic survey methods (e.g. Klem, 1989). These methods of data collection likely lead to under-estimates of actual levels of collisions, often struggling to account for the influences of scavengers, delayed mortalities, or carcass persistence and detectability (Barrientos et al., 2018; Loss et al., 2012; Santos et al., 2016). Furthermore, not all collisions are fatal and yet may still negatively impact birds through, for example, increased energetic costs in avoiding hazards (Lennox et al., 2016). Therefore, a behavioral approach offers to generate greater amounts of data and enables a more nuanced interpretation of the context-dependency of collision risk and mitigation efficacy, compared with traditional, mortality-based, estimates. We analyzed the flight behaviors of birds during sound treatment and control conditions, using videographic three-dimensional modeling techniques.

Methods

Ethics statement

Our experiments were conducted at communication tower sites in Virginia, USA. Authorization to access sites was obtained from entities with ownership or operational privileges. Permission to access towers was granted by the Delmarva

Educational Association for the site in Townsend, VA, and by the Virginia State Police for the site in Eastville, VA. The field experimental protocol was approved by the William & Mary Institutional Animal Care and Use Committee. No additional public or private permits were required.

Study area

Experiments were conducted between September and November 2019 at communication tower sites on the Delmarva Peninsula in Virginia. The tower in Eastville, VA is a 107 m high, self-supported structure (hereafter, *VSP* tower). The tower in Townsend, VA is 161 m high and supported by equally angled guy lines (hereafter, *DEA* tower). Both towers extend into isolated open airspace above surrounding landscapes and are located in semi-rural settings with no buildings within 150 m and proximate landcover featuring a mix of forest and open multipurpose or agricultural land (Figure 1). The Delmarva Peninsula is an important part of the Atlantic migratory flyway, with heavily used stopover habitat and consequently high avian diversity and abundance during the North American fall migration (Buler & Dawson, 2014). There are numerous communication towers along this peninsula as well as current and planned near- and off-shore wind energy development, which will all pose collision risks to birds (Musial & Ram, 2010; Watts, 2010).

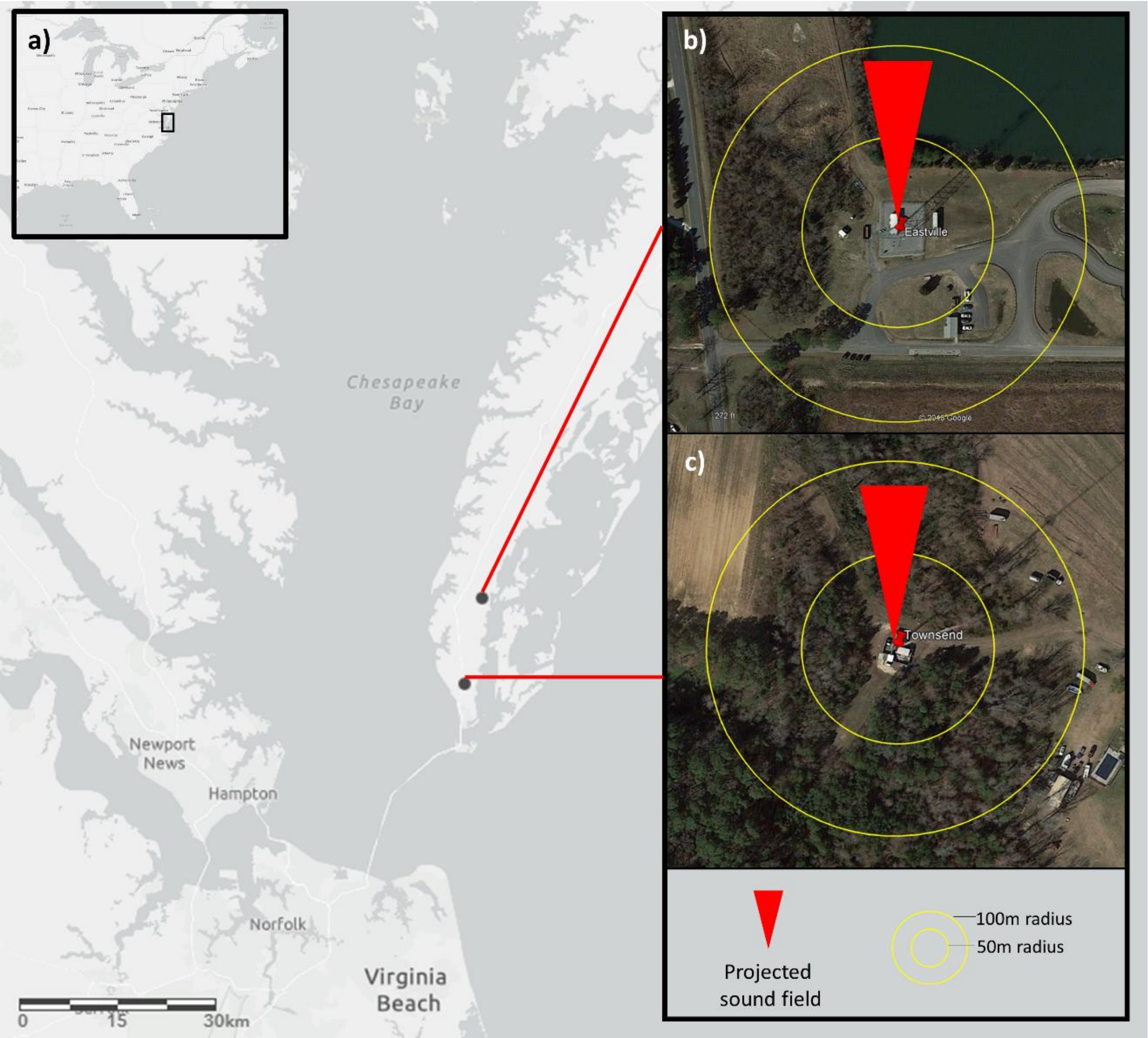
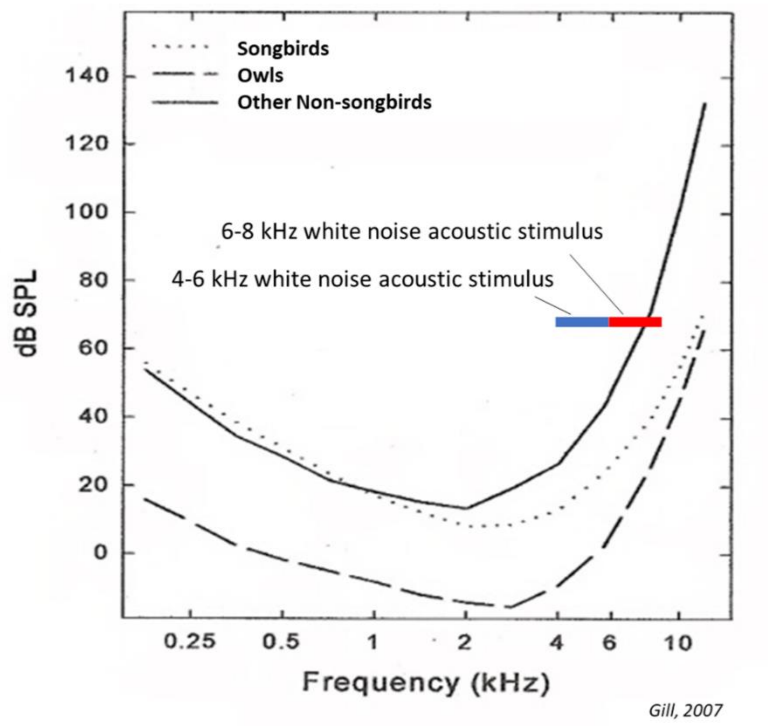


Figure 1. Communication tower sites in Virginia. Inset a) indicates location of Delmarva Peninsula. Inset b) indicates location of the *VSP* tower site in Eastville, VA. Inset c) indicates location of the *DEA* tower site in Townsend, VA. Data were collected between September and November 2019. Towers are located in semi-rural settings with no nearby buildings and proximate landcover featuring a mix of forest and open multipurpose or agricultural land. Sound fields were oriented northwards to match the general southward movements of migrating birds.

Sound stimuli

We tested two different stimuli to determine if frequency affected the efficacy of the signal. All stimuli were generated in PRAAT (ver. 5.3.55; Boersma

& Weenik, 2013) and further edited in Audacity(R) version 2.4.1. We created two types of stimuli intended to target general avian auditory sensitivities, to propagate with relatively low degradation through open-air environments, and to be minimally masked by background noise (Figure 2; Gill, 2007; Wiley & Richards, 1978). Two stimuli were created by band-pass filtering white noise, between 4 and 6 kHz for one stimulus (treatment condition *4-6 kHz*) and between 6 and 8 kHz (treatment condition *6-8 kHz*) for the other stimulus. Silent periods of matching duration were also created on the audio files (treatment condition *control*). Stimuli were projected at an intended intensity of >70 dBA SPL at 50 m, by adjusting speaker output to 100 dBA SPL at 3 m from the speaker and assuming an average attenuation rate of -6dB per doubling of distance through open-air.



Gill, 2007

Figure 2. Sound stimuli design and avian auditory sensitivity. 4-6 kHz (blue bar) and 6-8 kHz (red bar) band-pass filtered white noise stimuli were generated. These stimuli are intended to target general avian auditory sensitivities, to propagate with relatively low degradation through open-air environments, and to be minimally masked by background noise. Signals were projected with an intended intensity of >70 dBA SPL at 50m.

General experimental procedure

Experiments were conducted using a fully factorial design between site location and stimulus type: Each site location (*DEA* and *VSP*) experienced each stimulus type (4-6 kHz and 6-8 kHz) on three separate day replicates. Thus, data were collected on 6 separate days over the course of the season. Experiments were run on pairs of consecutive days, with one stimulus type being used at both sites on the first day and the second stimulus type being used at both sites on the subsequent day. The order of stimulus type use in a pair of days was continually counterbalanced through the course of the season.

We conducted our field experiments in the early to mid-morning hours as, for daytime collisions, this has been shown to be a time period of high collision incidence (Hager et al., 2017; Klem, 2010). Within a day, data were collected between 05:00 and 11:00. We projected sound fields from the base of each tower using a highly directional speaker (LRAD 100X) positioned at an angle of 45° from the horizon. The sound field was oriented northwards, to match the general southward movements of migrating birds in autumn. We alternated 30-min periods of sound stimuli projection with 30-min periods of silent control. Treatment and control periods were separated by 15-min buffer intervals, intended to minimize any spill-over effect between treatment periods. We collected video data from two GoPro cameras (Hero7 Black) positioned 1.2 m either side of the directional speaker, at the base of the tower. Both cameras were angled upwards at an angle of 45° from the horizon and angled inwards toward a focal point 3 m in front of the speaker, to triangulate on the area of interest around the tower encompassing the sound field (Figure 3). Stereographic video data (at 30 frames per second) were computed to recreate the three-dimensional (3D) coordinates of bird flights surrounding towers, using methods available in the open-source Argus packages implemented in Python 3.6.2 (Jackson et al., 2016). In order to maximize coverage of the airspace around towers, we used a wide angle (focal length: 15 mm) setting on the cameras. Trials began with the playback of conspicuous audio tones, for later use in synchronizing video footage. A 1 m calibration wand (a wooden dowel with painted polystyrene balls on either end, measuring 1 m) attached to a drone was flown through the focal area and video recorded at the start of each experimental day.

For each day of data collection and each tower location, we extracted average daily temperature (°C) and precipitation (mm) from the PRISM Climate Group gridded dataset (Oregon State University, http://www.prism.oregonstate.edu) and scored cloud cover (oktas) from aggregate video data. Experiments were not conducted on days with heavy precipitation or average wind speeds above 2 m/s, in an effort to minimize variation in abiotic variables between sampling times.

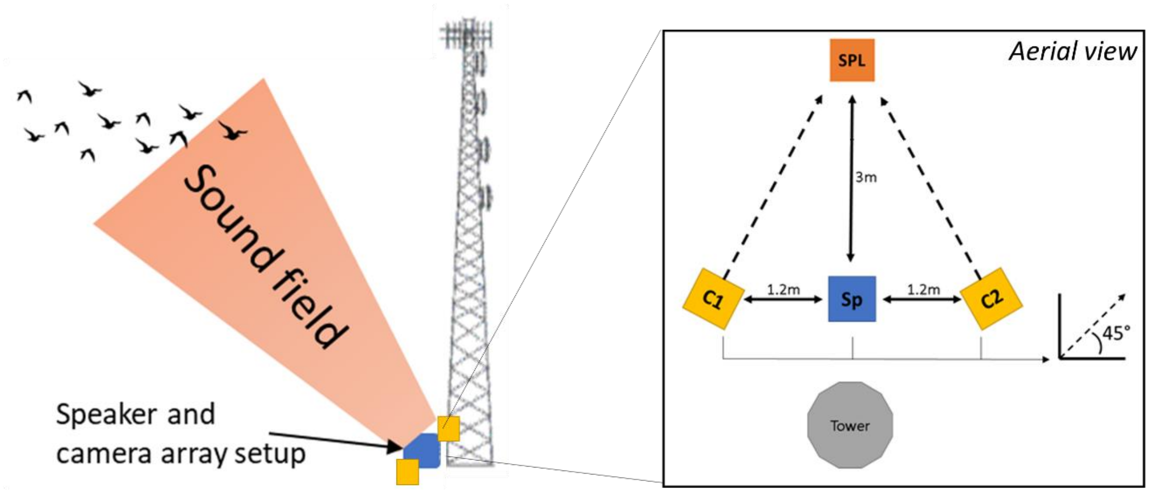


Figure 3. General experimental layout. Sound fields were projected from the base of towers at 45° from the horizon. Video cameras (yellow squares) were positioned 1.2 m either side of the directional speaker (blue squares), at the base of the tower. Cameras were angled upwards at 45° from the horizon and angled inwards toward a focal point 3 m in front of the speaker, to triangulate on the area of interest around the tower encompassing the sound field.

Flight analyses

We visually inspected all video recordings to classify the general size of birds (*small* (generally songbird-sized) or *large* (generally medium-size birds such as *Corvidae* and larger)), the group size (*single* or *flock* of any size), time of the flight, and the number of bird flights around each tower during each treatment period of the experiment. Further, we identified flights for analysis where the bird(s) flew centrally through the fields of view of video cameras, below the maximum height of the towers but at least 5 m above the ground, and where birds did not perch on surrounding vegetation or on the towers or guy ropes themselves. This procedure allowed us to identify 'at risk' flights where birds were most likely to have not recently interacted with the tower (i.e., they did not perch) and were at most risk of collision with the tower.

We analyzed the ‘at risk’ flights to further describe flight behaviors. First, we synchronized video footage using both acoustic and visual cues. We corrected for lens distortion due to the wide-angle mode using the DWarp Argus package (Jackson et al., 2016) implemented in Python 3.6.2. To recreate 3D flight paths of all birds, we calibrated the cameras and airspace using a wand-based, direct linear transformation (DLT) technique with sparse-bundle adjustment (SBA), implemented in the Argus packages in Python 3.6.2 (Jackson et al., 2016). In both camera views, we manually digitized the centroid of each bird for every frame during a flight to determine the 3D positions with respect to time. To reduce digitization noise, these raw data were first smoothed using a quintic spline function. The spline error tolerances were weighted by error variances extracted from the 3D reconstruction uncertainty at every data point.

We derived a set of three flight metrics from smoothed 3D positional data to characterize the flight behavior of birds. Horizontal distance (d) from the tower was calculated for every frame of a bird’s flightpath:

$$d = \sqrt{x^2 + y^2}$$

where x and y are the coordinates of a bird in the horizontal plane, with the tower as the origin, for a given frame. Velocity (v) was estimated as the first derivative of position with respect to time from the quintic spline polynomial. 3D absolute velocity was calculated from the derived positions for each frame of a bird's flightpath:

$$v = \sqrt{V_x{}^2 + V_y{}^2 + V_z{}^2}$$

where V_x, V_y and V_z are the estimated velocities in each 3D plane. Horizontal angle between a bird's momentary flight trajectory and the tower (Θ_{tower}) was calculated for every frame of a bird's flightpath:

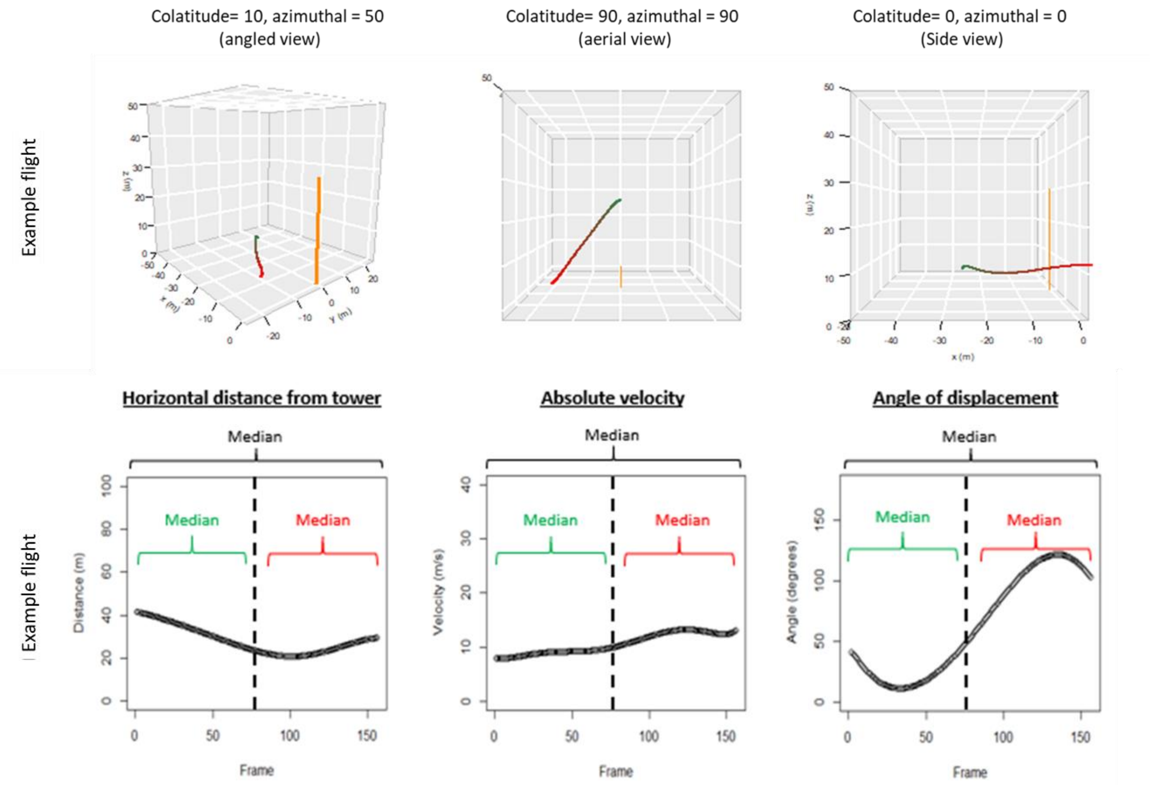
$$\Theta_{tower} = \cos^{-1}\left(\frac{(\vec{A} \cdot \vec{O}\,)}{\|\vec{A}\|\;\|\vec{O}\|}\right)$$

where $\vec{A}$ is a vector between consecutive 3D positions in a bird's flightpath and $\vec{O}$ is the vector between the same starting position and the tower.

Each metric was then represented for every flight by taking the median measure of all the frame-by-frame estimates. A secondary set of measures were derived to capture changes in these flight behavior metrics through the course of a bird's flight. To achieve this, a bird's flight path was divided equally into its temporally earlier and later halves of their flight, capturing how the bird responds to the sound cue and proximity to the communication tower. Each of the three metrics (d, v, Θ_{tower}) was summarized for both halves of the flight. Finally, the change in the median measure from the earlier half of the flight to the later half (e.g. change in median distance (Δd) = median $d_{later\ half}$ – median $d_{earlier\ half}$) of the flight were calculated for each metric. Table 1 summarizes all flight metrics and calculations. An example flight and its derived metrics are presented in Figure 4. Calculations were executed using R (R Core Team, 2019) statistical software.

Metric	Formula	Overall flight	Overall flight interpretation	Within-flight change	Within-flight interpretation
Horizontal distance from tower	d = $\sqrt{x^2 + y^2}$	MED_d = median(d)	Higher values of d mean greater distances from towers, conferring less collision risk	ΔMED_d = MED_d(latter) – MED_d(ealier)	Negative values of Δd mean flights approach towers. Lower negative values mean flights approach towers less, conferring less collision risk
Absolute velocity	v = $\sqrt{V_x^2 + V_y^2 + V_z^2}$	MED_v = median(v)	Lower values of v mean slower flight velocities, conferring less collision risk	ΔMED_v = MED_v(latter) – MED_v(ealier)	Positive values of Δv mean acceleration of flights. Lower positive values mean less acceleration, conferring less collision risk
Angle of displacement from tower	$\Theta_{tower} = \cos^{-1}\left(\frac{(\vec{A} \cdot \vec{o})}{\lVert\vec{A}\rVert \, \lVert\vec{o}\rVert}\right)$	$MED_{\Theta tower}$ = median(Θ_{tower})	Higher values of Θ mean greater angles of displacement, conferring less collision risk	$\Delta MED_{\Theta tower}$ = $MED_{\Theta tower}$(latter) – $MED_{\Theta tower}$(ealier)	Positive values of ΔΘ mean increased angles of displacement from towers. Higher positive values mean greater increased angles, conferring less collision risk

Table 1. Summary of all flight metrics and calculations. d is the horizontal distance from towers; v is the absolute velocity; Θtower is the horizontal angle between the momentary flight trajectory and a reference trajectory to towers. Interpretations describe potential metric outcomes and their predicted influence on collision risk.



Change in metric = latter median measure – earlier median measure

Overall flight metrics	Median distance from tower	Median velocity	Median angle of displacement
Within-flight metrics	Change in median distance from tower	Change in median velocity	Change in median angle of displacement

Figure 4. Example flight and derived behavioral metrics. The top row of graphs illustrates a smoothed 3D reconstruction of a bird flight path around a tower. Flight behavior was characterized using measures of horizontal distance from the tower (d), absolute velocity (v), and horizontal displacement angle from the tower (Θ_{tower}). These measures were summarized for an entire flight path using the median. Changes in flight behavior over the course of a bird's flight were summarized using the change in the median from the earlier to latter half of the bird's flight.

Statistical analysis

We analyzed flight behavior metrics using multiple linear regression analysis implemented in R (R Core Team, 2017). Specifically, we modeled the 6 median measure flight metrics summarized in Table 1. All outcome metrics met the normality assumption of linear regression. Treatment condition (*4-6 kHz, 6-8 kHz, control*), date (6-levels), tower site (*DEA, VSP*), bird size (*small*, *large*), and bird group size (*single*, *flock*) were treated as categorical fixed factors. A set of candidate models was built from a priori hypotheses and from explorations of non-linearity and collinearity between predictors and between predictors and response variables (Table 2). The same initial set of candidate models was used for all outcome variable analyses.

Candidate model linear predictor
1
treatment
site
date
treatment + site
treatment + date
site + date
treatment + site + treatment*site
treatment + date + treatment*date
site + date + site*date
treatment + site + date
treatment + site + date + site*date
treatment + site + date + treatment*site
treatment + site + date + treatment*date
treatment + site + date + treatment*site + treatment*date
treatment + site + date + treatment*site + treatment*date + site*date
treatment + bird_size
treatment + bird_group
site + bird_size
site + bird_group
treatment + site + bird_size
treatment + site + bird_group
treatment + site + date + bird_size
treatment + site + date + bird_group
treatment + bird_size + treatment*bird_size
treatment + bird_group +treatment*bird_group

Table 2. Set of candidate models. The same set of candidate models was applied to all outcome flight behavior metrics. Structure of linear predictors was based on a-priori hypotheses and exploration of non-linearity and collinearity between predictors and between predictors and response variables

Models were selected based on Akaike's information criteria (AIC) with small sample bias adjustment, AICc. AICc weight was used to rank model suitability and models performing worse than the null model were subsequently excluded from analyses. All models performing better than the null model were used to calculate model averaged beta coefficients and 95% confidence intervals (Burnham & Anderson, 2002). Predictor variable parameter estimates were averaged from only those models in which a given predictor occurs (subset averaging). Model averaged estimates of parameter beta coefficients were used to compute model-averaged predictions of outcome variables, with standard errors.

Results

General bird activity around towers

We collected data on 6 sampling days from two tower locations, for three hours each day, generating 9 hours of video footage at each tower site for each sound frequency. We inspected the rate of detected bird flights (number of flights per minute) around each tower during each treatment period of the experiment (Figure 5). Overall, 1585 interactions between towers and birds were logged. The rate of detected interactions (birds per minute) was higher at the VSP tower, averaging 2.68 (SE ± 0.13), compared with the DEA tower, averaging 0.36 (SE ± 0.08).

By treatment, there was a 16.2 % decrease in the mean rate of detections during 4-6 kHz sound treatment periods (mean = 1.29; SE ± 0.34) compared to control periods (mean = 1.54; SE ± 0.31), and a 11.7 % decrease in the mean rate of detections during 6-8 kHz sound treatment periods (mean = 1.36; SE ± 0.5) compared to control periods (Figure 5a).

At the DEA tower site, there was a 30.6 % decrease in the mean rate of detections during 4-6 kHz sound treatment periods (mean = 0.34; SE ± 0.06) compared to control periods (mean = 0.49; SE ± 0.14), and a 85.7 % decrease in the mean rate of detections during 6-8 kHz sound treatment periods (mean = 0.08; SE ± 0.04) compared to control periods (Figure 5b). At the VSP tower site, there was a 15.1 % decrease in the mean rate of detections during 4-6 kHz sound treatment periods (mean = 2.43; SE ± 0.22) compared to control periods (mean = 2.86; SE ± 0.21), and a 7.4 % decrease in the mean rate of detections during 6-8 kHz sound treatment periods (mean = 2.64; SE ± 0.28) compared to control periods (Figure 5b).

Across the 6 sampling days, there was a decrease in detection rate during sound treatment periods, irrespective of stimulus type, compared to control periods, on all sampling days except for one, where there was an increase in detection rate during 4-6 kHz sound treatment periods compared to control periods. On this particular day, the mean detection rate during 4-6 kHz sound treatment periods was lower compared to control periods at the DEA tower site, while the mean detection rate during 4-6 kHz sound treatment periods was higher compared to control periods at the VSP tower site.

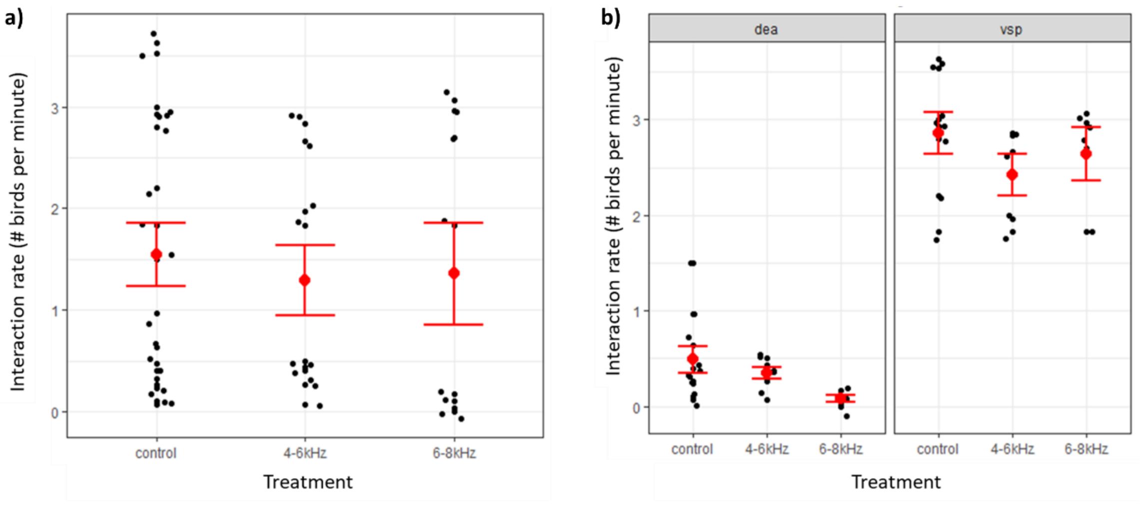


Figure 5. General bird activity around towers by treatment conditions and tower site location. Panel a) shows the overall rate of detections by treatment condition. Panel b) shows the overall rate of detections by treatment condition within each tower site. Solid black dots represent detection rates per 30-minute sampling period. Solid red dots and error bars represent mean detection rate ± standard error of the mean.

Flight behavior metrics

Of the 1585 total interactions between birds and towers, 145 (9.1 %) were deemed “at-risk” flights, for subsequent behavioral analysis. 106 of these flights occurred at the VSP tower, with a mean “at-risk” interaction rate of 0.21 birds per minute (SE ± 0.02) and 39 occurred at the DEA tower, with a mean “at-risk” interaction rate of 0.07 birds per minute (SE ± 0.01). The mean “at-risk” interaction rate (birds per minute) was 0.12 (SE ± 0.02) during control periods, 0.13 (SE ± 0.03) during 4-6 kHz treatment periods, and 0.14 (SE ± 0.05) during 6-8 kHz treatment periods. Despite overall differences in general bird activity between tower sites, the rate of “at-risk” interactions did not vary substantially between treatment conditions periods within tower sites.

Flight behavior metrics: Overall distance from towers

The 4-6 kHz treatment condition significantly influenced overall distance from towers compared to the control condition, with model-averaged 95% confidence intervals not overlapping zero (Table 3). The effect size of this parameter estimate was related to an estimated 5.25 m greater mean overall distance from towers during 4-6 kHz treatment conditions, compared to control conditions. The 6-8 kHz treatment condition parameter was related to an estimated 0.63 m lesser mean overall distance from towers, compared to control conditions, though this effect was not significant according to 95% confidence intervals (Table 3). The influence of sampling date on overall distance from towers was notable, with multiple dates indicating significant or marginally significant differences compared to the randomly assigned reference date (Table 3). This indicates an influence of sampling date variation on the overall median distance of birds from towers.

Parameter	beta coefficient	Lower 95% CI	Upper 95% CI
(Intercept)	21.8	16.1	27.5
treatment4-6kHz	5.25	0.422	10.1
treatment6-8kHz	-0.634	-7.54	6.28
siteVSP	3.21	-1.32	7.75
siteVSP:treatment4-6kHz	-1.71	-9.90	6.47
siteVSP:treatment6-8kHz	-8.74	-22.5	5.01
date100119	4.56	-1.14	10.2
date110319	12.2	5.25	19.2
date110419	6.03	0.404	11.7
date92419	-1.88	-8.65	4.89
date93019	7.47	-0.133	15.1

Table 3. Overall median distance model-averaged parameter estimates. Subset of all model-averaged parameter estimates based on a-priori interest and estimated parameter importance. Parameter estimates with 95% confidence intervals not overlapping zero are highlighted in dark gray. Parameter estimates with 95% confidence intervals marginally overlapping zero are highlighted in light gray.

Table 4 presents the results of the candidate models fit to the overall median distance outcome variable, ordered by delta AICc value and derived model weight. The relative contribution of individual parameters to the final averaged model are listed in Table 5. Sampling date was the top-performing parameter of importance in the averaged overall median distance model. Treatment condition and tower site were the second and third most important parameters in the averaged model, respectively.

Model	ΔAICc	weight
treatment + site + date	0	0.245
treatment + date	0.246	0.217
site + date	1.019	0.147
treatment + site + date + bird_group	1.362	0.124
date	1.507	0.115
treatment + site + date + bird_size	2.138	0.084
treatment + site + date + treatment * site	3.101	0.052
treatment + site + date + site * date	7.293	0.006
site + date + site * date	8.672	0.003
treatment + site + date + treatment * date	8.834	0.003
treatment + date + treatment * date	9.151	0.003
treatment + site + date + treatment * site + treatment * date	12.263	0.001

Table 4. Overall median distance model selection table. AICc weight was used to rank model suitability. Models performing worse than the null model were excluded from subsequent analyses.

	date	treatment	site	bird_group	bird_size	site:treatment
Sum of weights:	1	0.73	0.67	0.12	0.08	0.05
N containing models:	13	19	15	4	4	4

Table 5. Overall median distance model-averaged parameter importance. AICc weights are summed for each model containing the parameter of interest to indicate the relative importance of individual parameters within the averaged model. Shown are parameters with sum of weights >0.01

The averaged model was used to generate model-based estimates of the outcome variable. Figure 6 plots these model-based estimates of overall median distance against treatment conditions (Figure 6a) and against treatment conditions within site (Figure 6b).

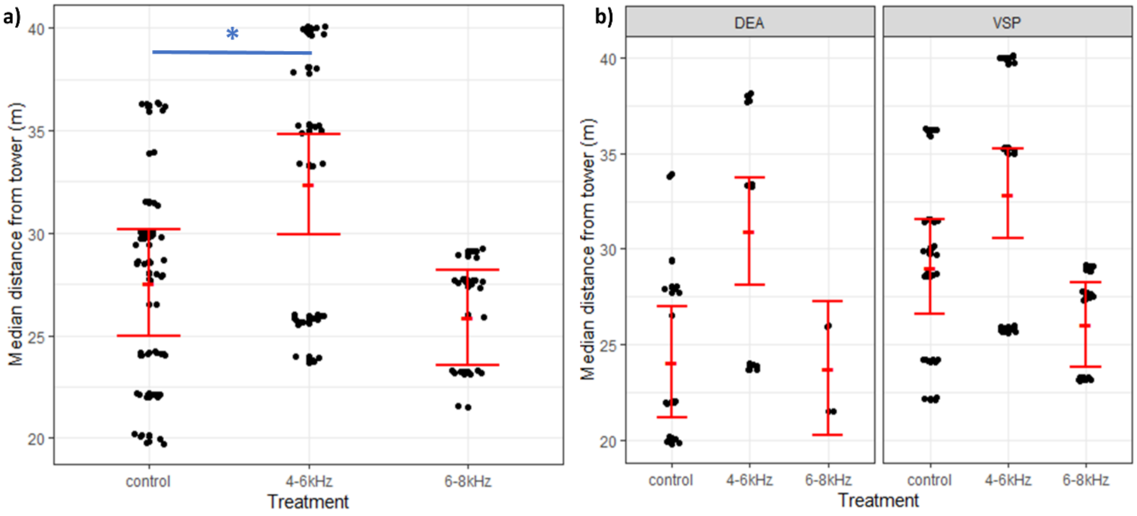


Figure 6. Overall median distance by treatment condition and tower site location. Panel a) shows the overall median distance from tower by treatment condition. Panel b) shows the overall median distance from tower by treatment condition within each tower site. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Blue asterisks indicate statistically significant influence of model-averaged parameter estimates according to 95% confidence intervals.

Flight behavior metrics: Overall velocity

The 4-6 kHz and 6-8 kHz treatment conditions significantly influenced overall velocity compared to the control condition, with 95% confidence intervals not overlapping zero (Table 6). The effect size of the 4-6 kHz parameter was related to an estimated 1.48 m/s lower mean velocity during 4-6 kHz treatment conditions compared to control conditions. The effect size of the 6-8 kHz parameter was related to an estimated 1.88 m/s greater mean velocity during 6-8 kHz treatment conditions compared to control conditions. The influence of sampling date on overall velocity was somewhat notable, with some dates indicating marginally significant differences compared to the randomly assigned reference date (Table 6). This indicates some influence of sampling date variation on the overall median distance of birds from towers.

Parameter	beta coefficient	2.5% C.I.	97.5% C.I.
(Intercept)	7.12	4.98	9.26
treatment4-6kHz	-1.48	-2.80	-0.162
treatment6-8kHz	1.89	0.163	3.61
siteVSP	-0.336	-2.66	1.99
siteVSP:treatment4-6kHz	1.16	-1.36	3.68
siteVSP:treatment6-8kHz	-3.40	-8.08	1.30
date100119	-1.06	-4.82	2.70
date110319	3.13	-0.376	6.64
date110419	2.67	-0.933	6.27
date92419	0.942	-1.64	3.52
date93019	-1.35	-4.69	1.99

Table 6. Overall median velocity model-averaged parameter estimates. Subset of all model-averaged parameter estimates based on a-priori interest and estimated parameter importance. Parameter estimates with 95% confidence intervals not overlapping zero are highlighted in dark gray. Parameter estimates with 95% confidence intervals marginally overlapping zero are highlighted in light gray.

Table 7 presents the results of the candidate models fit to the overall median velocity outcome variable, ordered by delta AICc value and derived model weight. The relative contribution of individual parameters to the final averaged model are listed in Table 8. Treatment condition was the top-performing parameter of importance in the averaged overall median velocity model. Tower site and sampling date were the second and third most important parameters in the averaged model, respectively.

Model	ΔAICc	weight
treatment + site + date + site * date	0	0.842
treatment + site + date + bird_size	6.072	0.04
treatment + site + date + bird_group	6.787	0.028
treatment + site + date	7.392	0.021
treatment + site + date + treatment * site	8.491	0.012
treatment + site + date + treatment * site + treatment * date + site * date	8.575	0.012
treatment + site + bird_size	9.165	0.009
treatment + site + bird_group	9.26	0.008
treatment + site	9.277	0.008
site + date + site * date	10.662	0.004
treatment + site + treatment * site	10.729	0.004
treatment + bird_size	11.15	0.003
treatment + date	11.473	0.003
treatment + bird_group + treatment * bird_group	11.512	0.003
treatment + bird_group	13.158	0.001
treatment	13.281	0.001

Table 7. Overall median velocity model selection table. AICc weight was used to rank model suitability. Models performing worse than the null model were excluded from subsequent analyses.

	treat	site	date	Date: site	bird_ size	bird_ group	site: treat	date: treatment
Sum of weights:	1	0.99	0.96	0.86	0.05	0.04	0.03	0.01
N containing models:	19	15	13	3	4	4	4	4

Table 8. Overall median velocity model-averaged parameter importance. AICc weights are summed for each model containing the parameter of interest to indicate the relative importance of individual parameters within the averaged model. Shown are parameters with sum of weights >0.01

The averaged model was used to generate model-based estimates of the outcome variable. Figure 7 plots these model-based estimates of overall median velocity against treatment conditions (Figure 7a) and against treatment conditions within site (Figure 7b).

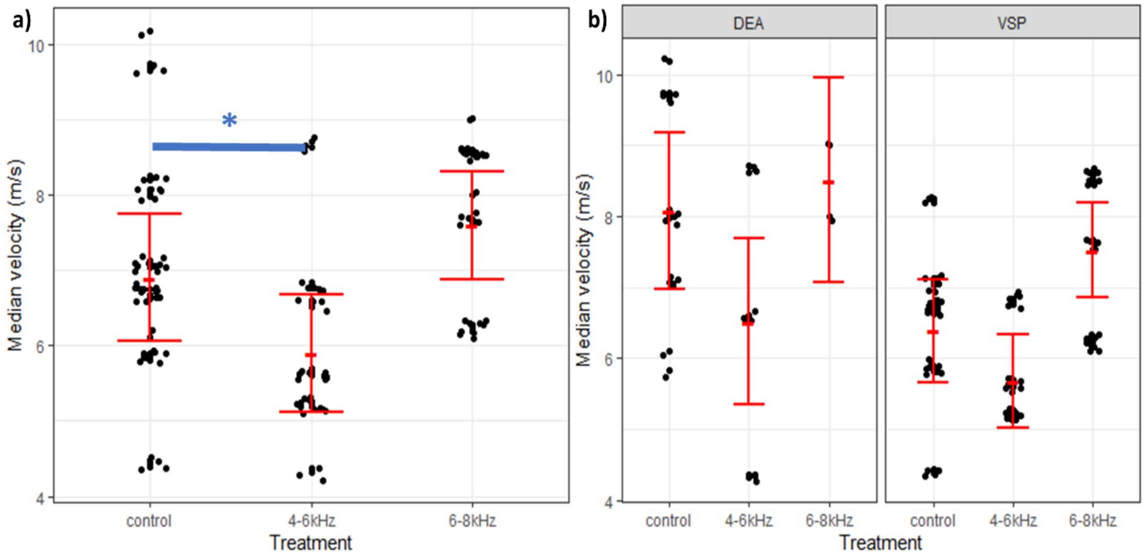


Figure 7. Overall median velocity by treatment condition and tower site location. Panel a) shows the overall median velocity by treatment condition. Panel b) shows the overall median velocity by treatment condition within each tower site. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Blue asterisks indicate statistically significant influence of model-averaged parameter estimates according to 95% confidence intervals.

Flight behavior metrics: Overall angle of displacement

The 6-8 kHz treatment condition significantly influenced the overall angle of displacement from towers compared to the control condition, with the 95% confidence interval not overlapping zero (Table 9). The effect size of the 6-8 kHz parameter was related to an estimated 19.4° increase in the mean angle of displacement from towers, compared to control conditions. The 4-6 kHz treatment condition marginally influenced overall median angle of tower avoidance compared to the control condition, based on the 95% confidence intervals (Table 9). The effect size of the 4-6 kHz parameter was related to an estimated 10.7° increase in the mean angle of displacement from towers, compared to control conditions.

Parameter	beta coefficient	2.5% C.I.	97.5% C.I.
(Intercept)	56.7	48.9	64.5
treatment4-6kHz	10.7	-0.718	22.2
treatment6-8kHz	19.4	3.27	35.5
siteVSP	-1.53	-12.2	9.18
siteVSP:treatment4-6kHz	3.62	-16.9	24.1
siteVSP:treatment6-8kHz	28.6	-5.98	63.2
bird_sizesmall	0.114	-11.4	11.7
bird_sizesmall:treatment4-6kHz	14.6	-4.54	33.7
bird_sizesmall:treatment6-8kHz	-21.3	-41.2	-1.32

Table 9. Overall median angle of displacement from tower model-averaged parameter estimates. Subset of all model-averaged parameter estimates based on a-priori interest and estimated parameter importance. Parameter estimates with 95% confidence intervals not overlapping zero are highlighted in dark gray. Parameter estimates with 95% confidence intervals marginally overlapping zero are highlighted in light gray.

Table 10 presents the results of the candidate models fit to the overall median angle of tower avoidance outcome variable, ordered by delta AICc value and derived model weight. The relative contribution of individual parameters to the final averaged model are listed in Table 11. Treatment condition was the top-performing parameter of importance in the averaged overall median angle of tower avoidance model. Bird size and the interaction between bird size and treatment condition were the second and third most important parameters in the averaged model, respectively.

Model	ΔAICc	weight
treatment + bird_size + treatment * bird_size	0	0.709
treatment	3.88	0.102
treatment + bird_group	5.457	0.046
treatment + bird_size	5.996	0.035
treatment + site	6.023	0.035
treatment + site + bird_group	7.641	0.016
treatment + site + treatment * site	7.683	0.015
treatment + site + bird_size	8.149	0.012
treatment + bird_group + treatment * bird_group	8.625	0.009
treatment + date + treatment * date	9.383	0.007
treatment + date	9.581	0.006
treatment + site + date + treatment * date	11.844	0.002
treatment + site + date	11.929	0.002
site	13.486	0.001
treatment + site + date + bird_group	13.497	0.001
treatment + site + date + treatment * site	13.518	0.001
treatment + site + date + bird_size	13.666	0.001
treatment + site + date + treatment * site + treatment * date	14.27	0.001

Table 10. Overall median angle of displacement from tower model selection table. AICc weight was used to rank model suitability. Models performing worse than the null model were excluded from subsequent analyses.

	treat	Bird _size	bird_size: treatment	site	Bird _group	date	site: treatment
Sum of weights:	1	0.76	0.71	0.09	0.07	0.02	0.02
N containing models:	19	4	1	15	4	13	4

Table 11. Overall median angle of displacement from tower model-averaged parameter importance. AICc weights are summed for each model containing the parameter of interest to indicate the relative importance of individual parameters within the averaged model. Shown are parameters with sum of weights >0.01

The averaged model was used to generate model-based estimates of the outcome variable. Figure 8 plots these model-based estimates of overall median tower angle against treatment conditions (Figure 8a) and against treatment conditions within site (Figure 8b).

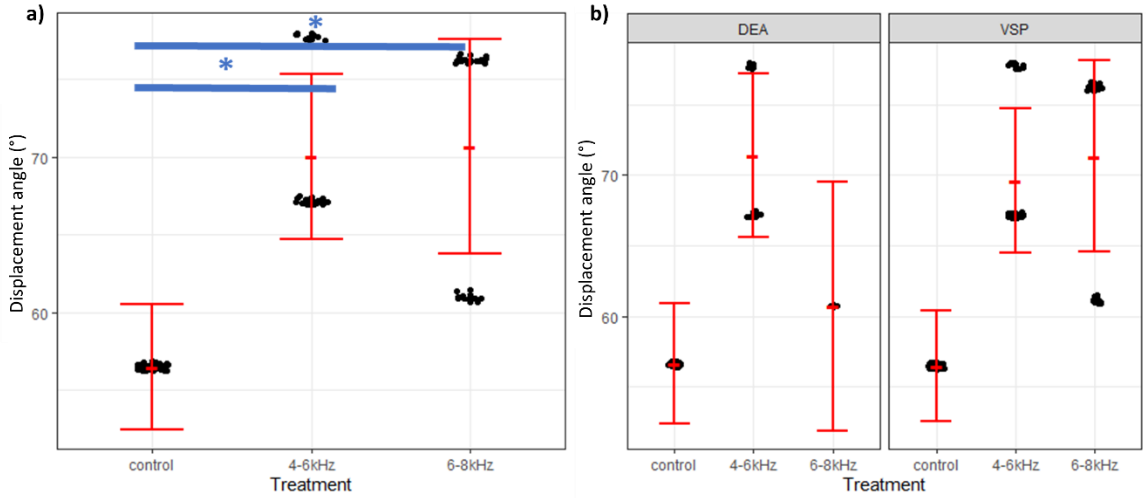


Figure 8. Overall median angle of displacement from tower by treatment condition and tower site location. Panel a) shows the overall median tower angle from tower by treatment condition. Panel b) shows the overall median tower angle from tower by treatment condition within each tower site. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Blue asterisks indicate statistically significant influence of model-averaged parameter estimates according to 95% confidence intervals.

Flight behavior metrics: Within-flight change in distance from towers

Neither the 4-6 kHz nor the 6-8 kHz treatment conditions significantly influenced the within-flight change in distance from towers, based on 95% confidence intervals overlapping zero (Table 12). The statistically non-significant 4-6 kHz treatment condition parameter was related to an estimated 2.84 m increase in the change in median distance compared to control conditions. With all estimates of change in distance being negative, an increase in change in distance means that bird flights remained further away from towers during 4-6 kHz conditions compared to control conditions. The statistically non-significant 6-8 kHz treatment condition parameter was related to an estimated 4.4 m increase in the change in median distance compared to control conditions. This again indicates that bird flights remained further away from towers during 6-8 kHz conditions compared to control conditions. The interaction term between VSP site and 6-8 kHz treatment condition significantly influenced change in median distance, with the 95% confidence interval not overlapping zero (Table 12). The effect size of the VSP site and 6-8 kHz interaction parameter was related to an estimated 11.4 m increase in the change in median distance compared to reference levels. The interaction term between small bird size and 6-8 kHz treatment condition significantly influenced change in median distance, with the 95% confidence interval not overlapping zero (Table 12). The effect size of the small bird size and 6-8 kHz interaction parameter was related to an estimated 7.5 m decrease in the change in median distance compared to reference levels.

Parameter	beta coefficient	2.5% C.I.	97.5% C.I.
(Intercept)	-9.17	-12.1	-6.26
treatment4-6kHz	2.84	-1.83	7.51
treatment6-8kHz	4.40	-4.88	13.7
siteVSP	-1.66	-5.20	1.87
siteVSP:treatment4-6kHz	1.06	-4.70	6.81
siteVSP:treatment6-8kHz	11.4	1.72	21.1
bird_sizesmall	0.556	-2.79	3.90
bird_sizesmall:treatment4-6kHz	3.00	-2.43	8.42
bird_sizesmall:treatment6-8kHz	-7.55	-13.2	-1.88

Table 12. Change in median distance model-averaged parameter estimates. Subset of all model-averaged parameter estimates based on a-priori interest and estimated parameter importance. Parameter estimates with 95% confidence intervals not overlapping zero are highlighted in dark gray. Parameter estimates with 95% confidence intervals marginally overlapping zero are highlighted in light gray.

Table 13 presents the results of the candidate models fit to the change in median distance outcome variable, ordered by delta AICc value and derived model weight. The relative contribution of individual parameters to the final averaged model are listed in Table 14. Treatment condition was the top-performing parameter of importance in the averaged overall median distance model. Bird size and the interaction between bird size and treatment condition were the second and third most important parameters in the averaged model, respectively.

Model	ΔAICc	weight
treatment + bird_size + treatment * bird_size	0	0.587
treatment + date + treatment * date	4.539	0.061
treatment + date	4.638	0.058
treatment + site + treatment * site	5.113	0.046
treatment	5.247	0.043
treatment + site + date + treatment * site	5.491	0.038
treatment + site	6.601	0.022
treatment + site + date + treatment * site + treatment * date	6.66	0.021
treatment + site + date	6.729	0.02
treatment + site + date + treatment * date	6.81	0.019
treatment + bird_group	7.279	0.015
treatment + bird_size	7.31	0.015
treatment + site + date + bird_size	7.844	0.012
treatment + bird_group + treatment * bird_group	8.189	0.01
treatment + site + bird_size	8.474	0.008
treatment + site + bird_group	8.651	0.008
date	8.869	0.007
treatment + site + date + bird_group	8.981	0.007
site + date	11.148	0.002
site	12.321	0.001
treatment + site + date + site * date	12.606	0.001

Table 13. Change in median distance model selection table. AICc weight was used to rank model suitability. Models performing worse than the null model were excluded from subsequent analyses.

	treat	Bird_ size	bird_size: treatment	date	site	site: treatment	date: treatment	bird_ group
Sum of weights:	0.99	0.62	0.59	0.25	0.2	0.1	0.1	0.04
N containing models:	19	4	1	13	15	4	4	4

Table 14. Change in median distance model-averaged parameter importance. AICc weights are summed for each model containing the parameter of interest to indicate the relative importance of individual parameters within the averaged model. Shown are parameters with sum of weights >0.01

The averaged model was used to generate model-based estimates of the outcome variable. Figure 9 plots these model-based estimates of change in median distance against treatment conditions (Figure 9a) and against treatment conditions within site (Figure 9b).

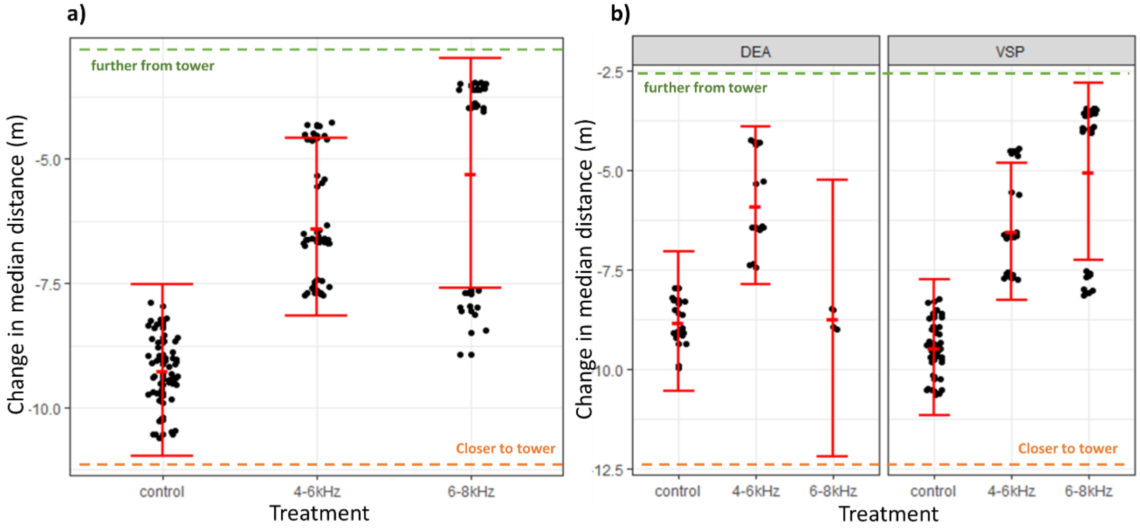


Figure 9. Change in median distance by treatment condition and tower site location. Panel a) shows the change in median distance by treatment condition. Panel b) shows the change in median distance by treatment condition within each tower site. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Green dotted line indicates the level of change in distance when flights are further from the tower; orange dotted line indicates the level of change in distance when flights are closer to the tower.

Flight behavior metrics: Within-flight change in velocity

The 4-6 kHz treatment condition significantly influenced change in median velocity, with the 95% confidence interval not overlapping zero (Table 15). The effect size of the 4-6 kHz parameter was related to an estimated -1.03 m/s decrease in the mean change in velocity compared to control conditions.

Changes in velocity all had positive estimates, indicating increases in speed through flights. A smaller change in velocity, therefore, means that bird flights increased speed less during 4-6 kHz conditions compared to control conditions. The statistically non-significant 6-8 kHz treatment condition parameter was related to an estimated -0.78 m/s decrease in the mean outcome of the change in median velocity, compared to control conditions (Table 15). Again, this means that bird flights increased speed less during 6-8 kHz conditions compared to control conditions. The interaction term between VSP site and 6-8 kHz treatment condition significantly influenced change in median velocity, with the 95% confidence interval not overlapping zero (Table 15). The effect size of the VSP site and 6-8 kHz interaction parameter was related to an estimated -2.93 m/s decrease in the mean change in velocity compared to reference levels.

Parameter	beta coefficient	2.5% C.I.	97.5% C.I.
(Intercept)	1.58	0.828	2.34
treatment4-6kHz	-1.03	-1.95	-0.116
treatment6-8kHz	-0.783	-2.69	1.13
siteVSP	0.386	-0.568	1.34
siteVSP:treatment4-6kHz	-0.764	-2.42	0.892
siteVSP:treatment6-8kHz	-2.93	-5.73	-0.131
bird_sizesmall	0.447	-0.393	1.29
bird_sizesmall:treatment4-6kHz	0.167	-1.42	1.76
bird_sizesmall:treatment6-8kHz	1.39	-0.274	3.04

Table 15. Change in median velocity model-averaged parameter estimates. Subset of all model-averaged parameter estimates based on a-priori interest and estimated parameter importance. Parameter estimates with 95% confidence intervals not overlapping zero are highlighted in dark gray. Parameter estimates with 95% confidence intervals marginally overlapping zero are highlighted in light gray.

Table 16 presents the results of the candidate models fit to the change in median velocity outcome variable, ordered by delta AICc value and derived model weight. The relative contribution of individual parameters to the final averaged model are listed in Table 17. Treatment condition was the top-performing parameter of importance in the averaged change in median velocity model. Bird size and tower site were the second and third most important parameters in the averaged model, respectively.

Model	ΔAICc	weight
treatment + bird_size	0	0.247
treatment	0.284	0.214
treatment + site + bird_size	1.425	0.121
treatment + bird_size + treatment * bird_size	1.434	0.12
treatment + site + treatment * site	2.061	0.088
treatment + site	2.252	0.08
treatment + bird_group	2.396	0.074
treatment + site + bird_group	4.406	0.027
treatment + bird_group + treatment * bird_group	5.967	0.012
treatment + date	7.816	0.005
site	8.104	0.004
treatment + site + date + bird_size	9.348	0.002
treatment + site + date + treatment * site	9.727	0.002
treatment + site + date	9.908	0.002
treatment + site + date + bird_group	12.307	0.001

Table 16. Change in median velocity model selection table. AICc weight was used to rank model suitability. Models performing worse than the null model were excluded from subsequent analyses.

	treat	Bird _size	site	bird_size: treatment	Bird _group	site: treatment
Sum of weights:	1	0.49	0.33	0.12	0.11	0.09
N containing models:	19	4	15	1	4	4

Table 17. Change in median velocity model-averaged parameter importance. AICc weights are summed for each model containing the parameter of interest to indicate the relative importance of individual parameters within the averaged model. Shown are parameters with sum of weights >0.01

The averaged model was used to generate model-based estimates of the outcome variable. Figure 10 plots these model-based estimates of change in median velocity against treatment conditions (Figure 10a) and against treatment conditions within site (Figure 10b).

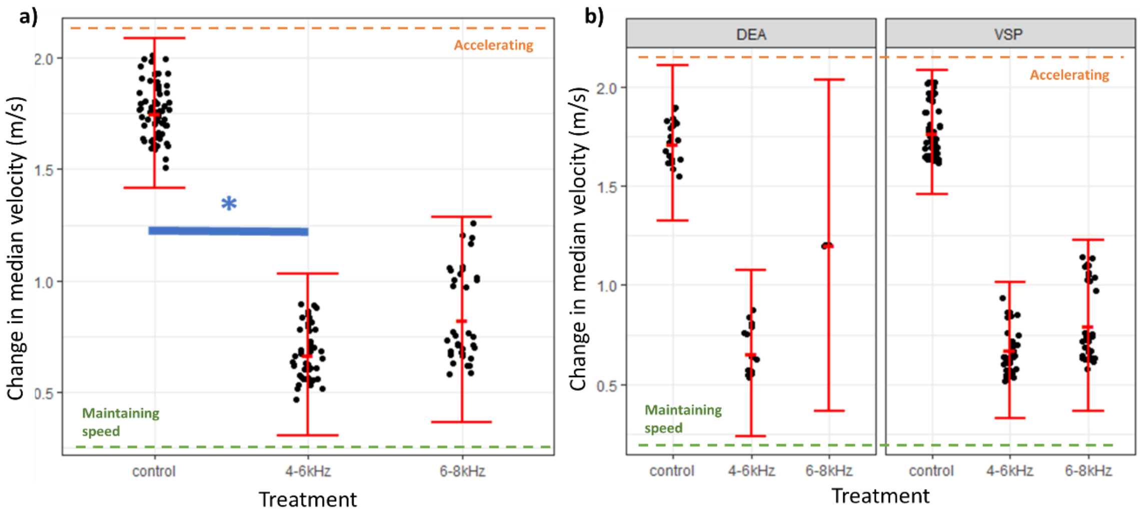


Figure 10. Change in median velocity by treatment condition and tower site location. Panel a) shows the change in median velocity by treatment condition. Panel b) shows the change in median velocity by treatment condition within each tower site. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Blue asterisks indicate statistically significant influence of model-averaged parameter estimates according to 95% confidence intervals.

Flight behavior metrics: Within-flight change in angle of displacement from tower

Neither the 4-6 kHz nor the 6-8 kHz treatment conditions significantly influenced change in median angle of tower avoidance, based on 95% confidence intervals overlapping zero (Table 18). The statistically non-significant 4-6 kHz treatment condition parameter was related to an estimated 0.14° increase in the mean change in angle of tower avoidance compared to control conditions. The statistically non-significant 6-8 kHz treatment condition parameter was related to an estimated 11.6° increase in the mean change in angle of tower avoidance compared to control conditions. The influence of sampling date on the change in angle of tower avoidance was notable, with multiple dates indicating significant differences compared to the randomly assigned reference date (Table 18). This indicates an influence of sampling date variation on the change in angle of tower avoidance.

Parameter	beta coefficient	2.5% C.I.	97.5% C.I.
(Intercept)	41.0	19.2	62.8
treatment4-6kHz	0.139	-14.3	14.6
treatment6-8kHz	11.6	-7.18	30.4
siteVSP	-8.09	-20.7	4.49
siteVSP:treatment4-6kHz	-0.654	-25.9	24.6
siteVSP:treatment6-8kHz	-7.26	-49.7	35.2
date100119	-21.1	-40.1	-2.18
date110319	-8.19	-27.6	11.2
date110419	-19.2	-36.9	-1.46
date92419	-17.6	-35.8	0.737
date93019	-5.44	-26.5	15.6
bird_groupsingle	-8.50	-23.1	6.14

Table 18. Change in median angle of displacement from tower model-averaged parameter estimates. Subset of all model-averaged parameter estimates based on a-priori interest and estimated parameter importance. Parameter estimates with 95% confidence intervals not overlapping zero are highlighted in dark gray. Parameter estimates with 95% confidence intervals marginally overlapping zero are highlighted in light gray.

Table 19 presents the results of the candidate models fit to the change in median angle of displacement from tower outcome variable, ordered by delta AICc value and derived model weight. The relative contribution of individual parameters to the final averaged model are listed in Table 20. Treatment condition was the top-performing parameter of importance in the averaged change in median angle of displacement from tower model. Tower site and sampling date were the second and third most important parameters in the averaged model, respectively.

Model	ΔAICc	weight
treatment + site + date + bird_group	0	0.134
date	0.387	0.111
treatment	0.615	0.099
treatment + site	0.735	0.093
site	1.179	0.075
site + date	1.208	0.074
treatment + site + date	1.525	0.063
treatment + date	1.564	0.062
treatment + bird_group	1.588	0.061
treatment + site + bird_group	1.799	0.055
treatment + bird_group + treatment * bird_group	2.065	0.048
treatment + site + bird_size	2.481	0.039
treatment + bird_size	2.702	0.035
treatment + site + date + bird_size	3.799	0.02
treatment + site + treatment * site	5.04	0.011
treatment + bird_size + treatment * bird_size	6.038	0.007
treatment + site + date + treatment * site	6.261	0.006
site + date + site * date	7.353	0.003
treatment + site + date + site * date	7.742	0.003
treatment + site + date + treatment * date	8.641	0.002
treatment + date + treatment * date	8.787	0.002

Table 19. Change in median angle of displacement from tower model selection table. AICc weight was used to rank model suitability. Models performing worse than the null model were excluded from subsequent analyses.

	treat	site	date	Bird _group	Bird _size	bird_group: treatment	site: treatment
Sum of weights:	0.74	0.58	0.48	0.3	0.1	0.05	0.02
N containing models:	19	15	13	4	4	1	4

Table 20. Change in median angle of displacement from tower model-averaged parameter importance. AICc weights are summed for each model containing the parameter of interest to indicate the relative importance of individual parameters within the averaged model. Shown are parameters with sum of weights >0.01

The averaged model was used to generate model-based estimates of the outcome variable. Figure 11 plots these model-based estimates of change in median angle of tower avoidance against treatment conditions (Figure 11a) and against treatment conditions within site (Figure 11b).

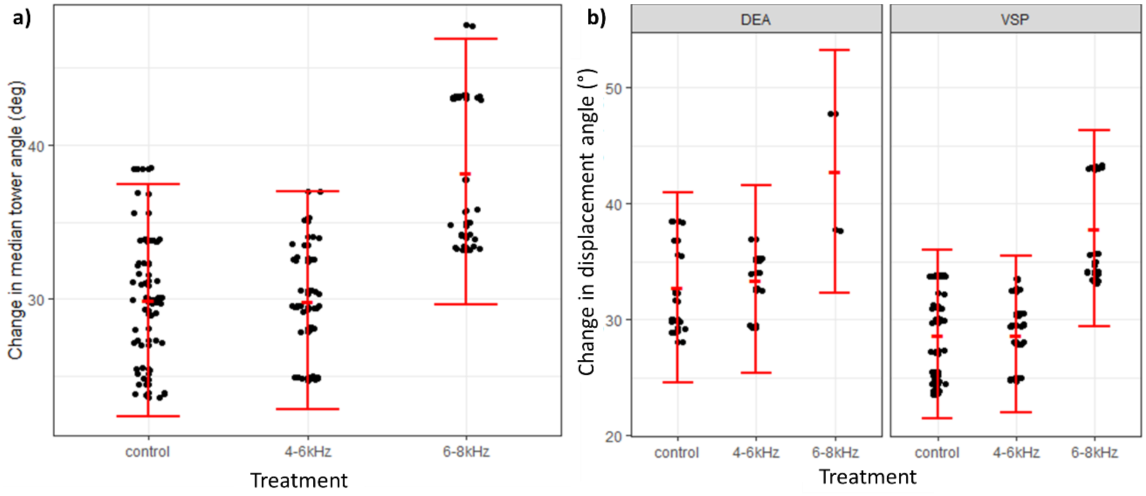


Figure 11. Change in median angle of displacement from tower by treatment condition and tower site location. Panel a) shows the change in median tower angle by treatment condition. Panel b) shows the change in median tower angle by treatment condition within each tower site. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean.

Discussion

Bird activity rates around towers were lowest during 4-6 kHz sound treatment conditions, intermediate during 6-8 kHz sound treatment conditions and highest during control conditions (Figure 5). While these differences in activity rate do not measure flight behaviors at the towers themselves, they may still indicate an effect of the treatment on bird activity in the general area surrounding towers and if general activity is lower, this could arguably already decrease the overall risk of collisions at the towers.

When exposed to a 4-6 kHz sound, estimates showed that birds flew 1.5 m/s slower and 5 m further away from the towers, on a heading that was an additional 10.7° away from the tower, relative to flights in control conditions (Figures 6, 7 and 8). Collectively, these observations indicate that birds experiencing the 4-6 kHz were at less risk of collision with the towers, in agreement with our predictions. Birds flying at greater distance from towers, with greater displacement angles relative to towers, and at slower velocities around towers are arguably more likely to detect and avoid potential collision hazards. Furthermore, augmenting the detectable range of hazards extends both the spatial and temporal dimensions in which at-risk birds can take evasive action, thereby lowering the risk of collision (Blackwell et al., 2009).

Through the course of flight trajectories, estimates showed that birds exposed to a 4-6 kHz sound had slower accelerations, by 1.2 m/s, and remained an additional 2.9 m further away from towers, relative to control conditions. Thus, within-flight behavioral responses during 4-6 kHz treatment conditions also supported some of our predictions. Though not robustly statistically supported, flights during 4-6 kHz treatment conditions had a smaller decrease in distance from towers during their flight trajectories, compared to control conditions (Figure 9). This smaller decrease indicates that through the course of flight paths, birds did not on average draw as close to towers compared to control conditions. This change in distance should be interpreted alongside the overall median distance measures, which characterized bird flights as being further away from towers overall during 4-6 kHz treatments compared to control treatments. During control conditions, flights showed significantly greater accelerations through the course of flight trajectories compared to 4-6 kHz conditions (Figure 10). Again taken alongside overall flight measures, this can be interpreted as birds maintaining an already slower flight speed (overall velocity was significantly lower in 4-6 kHz treatments compared to controls) during 4-6 kHz conditions, compared to birds accelerating upon an already faster flight speed in control conditions, as they approach towers. The change in displacement angle from towers throughout flight trajectories did not differ noticeably between control and 4-6 kHz conditions (Figure 11). However, with overall greater distances from towers and overall greater displacement angles from towers, it is possible that deflective movements away from towers occurred in the temporally earlier portions of flight trajectories during 4-6 kHz conditions.

When exposed to a 6-8 kHz sound, estimates showed that birds flew faster, at greater displacement angles from towers and at similar distances from towers, compared to control conditions. Collectively, these observations do not uniformly meet our predictions and offer less evidence that the 6-8 kHz sound reduced the risk of collision. The overall median distance of birds did not differ noticeably between control flights and 6-8 kHz flights (Figure 6). The overall median velocity of 6-8 kHz flights was significantly greater than control flights by an estimated 1.89 m/s (Figure 7). And the overall median displacement angle from towers was significantly greater, by an estimated 19.4°, during 6-8kHz treatments compared with control flights (Figure 8). Greater angles relative to towers are consistent with predicting a decreased collision risk. However, faster velocities would presumably render birds more susceptible to collisions, and it appears as though birds flew on average as close to towers during 6-8 kHz conditions as during control conditions.

Within-flight behavioral metrics may provide some clarity on the effect of 6-8 kHz treatments and flight behavior responses. Though not statistically significant, flights during 6-8 kHz treatment conditions had a smaller decrease in distance from towers during their flight trajectories, compared to control conditions (Figure 9). As in 4-6 kHz conditions, this smaller decrease indicates that through the course of flight paths, birds did not on average draw as close to towers during 6-8 kHz conditions compared to control conditions. While also not statistically significant, flights showed greater accelerations through the course of flight trajectories during control periods compared to 6-8 kHz conditions (Figure 10). Once again, taken alongside overall flight measures, this indicates birds maintaining an already slower flight speed (overall velocity lower in 6-8kHz compared to control) during 6-8 kHz conditions, compared to birds accelerating upon an already faster flight speed in control conditions, as they approach towers. Lastly, and once again though not statistically significant, 6-8 kHz flights showed a greater positive change in displacement angle from towers through the course of flight trajectories compared to control conditions (Figure 11). Furthermore, 6-8kHz flights showed a greater positive change in displacement angle from towers compared to control flights than 4-6 kHz flights compared to control flights. Thus, differences in metrics between 6-8 kHz and control conditions which were less apparent in overall measures may be more apparent in within-flight measures.

It is possible that, during 6-8 kHz flights, there was a delay in collision avoidance behavior and the expression of such behavior occurred closer to the towers, compared to 4-6kHz, though still further than in control flights. If there is indeed a delayed response in evasive flight behavior during 6-8 kHz conditions, it could be because 6-8 kHz signals are less detectable to flying birds compared with 4-6 kHz signals. This would be consistent with established understanding of avian auditory sensitivity (peaking in general closer to 4-6 kHz than 6-8 kHz) (Gill, 2007; McGee et al., 2019). This is illustrated most convincingly by comparisons of overall flight metrics and within-flight metrics as regards to distances form towers and angles of avoidance: Overall, 6-8 kHz flights came as close to towers on average as control flights, while 4-6 kHz flights stayed significantly further away from towers. Overall angles of avoidance were significantly larger in both 4-6 kHz and 6-8 kHz flights, compared to control flights. Change in angle of tower avoidance, however, was lower and more similar to control flights in 4-6 kHz flights but greater in 6-8 kHz flights. This could well indicate that, during 6-8 kHz flights, evasive flight behavior was expressed closer to towers compared to 4-6 kHz flights. However, with statistical significance lacking, these hypotheses should be further investigated.

We initially proposed testing the use of higher frequency signals so as to minimize potential masking by lower frequency background noise (Wiley & Richards, 1978b). However, we provide here at least preliminary evidence that lower frequency signals, which more closely target the known peak auditory sensitivities of most birds, propagate with suitable detectability through open airspace for flying birds. It may be worthwhile for future studies to test the use of even lower frequency signals, such as those in the 2-4 kHz range, which would target the most sensitive portions of the general avian auditory sensitivity spectrum (Gill, 2007) and which would also propagate generally further with less attenuation through open air (Wiley & Richards, 1978b). Lower frequency signals may, however, be at increased risk to masking by background noise. In addition to exploring the frequency-dependent nature of warning signals, future work may also aim to characterize effective signals in terms of temporal modulations. Modulations to signals may help increase their detectability in amongst background noise, so these considerations might be particularly appropriate for lower frequency signals, when background noise masking is a concern.

Overall, there appears to be a significant influence of 4-6 kHz acoustic signals and a non-significant but discernable influence of 6-8 kHz acoustic signals on flight behaviors interpretable as lowering collision risk. The use of acoustic signals in mitigating collisions in open airspace thus merits further exploration in an applied context. In particular, work should further investigate increasingly diverse spatial and temporal contexts, prioritizing known patterns of collision incidence. We believe that behavioral methods, similar to those employed here, will be particularly useful in continued assessment of collision incidence and mitigation approaches in diverse contexts.

We provide evidence of the benefits of a behavioral framework in assessing collision mitigation techniques. A robust sample size was generated with relative ease over a short data collection period, enabling the detection of statistically significant effect sizes, and allowing for the interpretation of a collision mitigation approach. The advantages of behavioral methods could help address some of the shortcomings of current assessment methods, such as mortality surveys. Behavioral methods could increase sampling effort, allowing collision assessments to cover broader temporal scales and to generate larger sample sizes. Behavioral methods also offer a nuanced perspective on collision risk. Not all collisions are fatal and hazardous structures may present other, non-lethal, challenges to birds. For example, avoiding hazards may increase energetic expenditure which could prove costly, particularly for migratory species (Lennox et al., 2016). Behavioral methods could seek to quantitatively measure such impacts. A more refined interpretation of the responses of birds to hazards will also help in understanding threats specific to certain taxa, locations or other environmental contexts.

Although we did not achieve species-level identification in this study, the general size of birds was a notable predictor variable in some of our modeled behaviors (Tables 11, 14, 17). Differences in flight behavior between bird sizes are most likely determined by flight kinematics, as smaller birds are generally more able to readily adjust their flight behaviors compared to larger birds (Gill, 2007a). This is generally the pattern we see in our results, with smaller birds showing mostly greater changes in flight behavior metrics through the course of flight trajectories (Appendix Figures A1, A2, A3). Interestingly, there appears to be some interaction between stimulus type and bird size such that differences in behaviors by bird size appear to be more pronounced during 6-8 kHz treatment conditions compared to 4-6 kHz signal. However, these differences are also most obvious in the within-flight metrics, and not as much in the overall metrics. Therefore, it is possible that, during 6-8 kHz conditions, birds in general had less space and time to respond to these potentially less conspicuous signals and small birds were more able to respond under these constraints than larger birds. This would maintain a flight kinematics explanation for this trend, but future work should ask whether any differences in auditory sensitivity between taxa could contribute to differential flight behaviors in response of acoustic signals.

The date of data collection was also notable predictor variable in some of our modeled behaviors (Tables 5, 8, 20). Differences in flight behavior between sampling dates may be attributable to a multitude of factors. We measured the weather variables of temperature, precipitation and cloud cover on each sampling date (Appendix Table A1) but did not find any strong association between these weather variables and flight behaviors (Appendix Figures A4, A5, A6). Therefore, there are likely other factors that we did not measure which influenced behavior by date. These could include other weather variables, such as wind speed and direction, or perhaps bird-specific differences, due to different species moving through on different dates, as is known with migrations.

We sampled two tower locations and, unsurprisingly, location was a notable predictor variable in a number of our flight behavior models. There are many local factors which could influence the flight behaviors of birds around towers, such as surrounding landcover type and the taxonomic makeup of local birds, particularly resident individuals. However, the influence of treatment condition on flight behaviors mostly did not interact with tower location (Figures 6 - 11). On the occasions when treatment condition and tower location did notably interact, it was the 6-8 kHz condition which differed from control conditions at one tower location but not the other. In some scenarios, this may be attributable to a lower sample size of bird flights during the 6-8 kHz condition at the DEA site, which had overall lower bird activity rates. However, it is possible that other location-associated factors interact with the 6-8 kHz treatment condition to produce variable behavioral responses. Of particular interest would be whether resident individuals differed in their behavioral responses to sound stimuli from non-resident individuals. We were unable to test this in the current study, but future work should explore this potential source of variation further, as it could begin to address whether birds may habituate to acoustic warning signals associated with collision hazards.

The implementation of acoustic deterrence methods in open-air contexts may be relatively accessible. For example, sound sources may be mounted on or near structures, using highly directional sound fields to minimize potential noise pollution, as was done in our study. Future work should also investigate any differential influence of the placement of the sound source relative to the hazardous structure. Our study, due to logistical constraints, placed directional speakers at the base of towers. However, previous work has illustrated the prevalence of ecologically referential signals in nature. For example, studies have shown that signal receivers direct attention in a spatially appropriate manner in response to certain types of alarm calls, such as directing visual attention upwards in response to alarm signals specific to aerial predators (Dawson Pell et al., 2018; Gill & Bierema, 2013). Other research has shown, more generally, the tendency of multiple species to orient visual attention based partly on simple signal characteristics such as frequency (Ratcliffe et al., 2015). Collision mitigation approaches could co-opt such natural tendencies in the behaviors of at-risk birds, to help elicit collision avoidance. Conversely, however, there could be unintended consequences of using signals familiar to wildlife, such as attraction to rather than deterrence from hazards. In such instances, novel and unfamiliar signals may prove more effective.

In general, the use of acoustic signals in mitigating collisions with open-air hazards may be more appropriate in some settings over others. Given the similarities between avian and human auditory sensitivities (Gill, 2007), the use of acoustic signals in areas close to humans may result in unwanted noise pollution. Acoustic warning signals could also present challenges to other wildlife, through masking of communication signals or by increasing stress through a variety of mechanism (Kight and Swaddle, 2011). Some geographical areas may be more suitable than others based on their community composition and any implementation of acoustic warning methods should pay careful attention to the makeup of and potential impacts on local wildlife populations. To generally reduce any unintended negative consequences of acoustic warning signals, context-dependent intermittent use may be compelling solution. For example, signals may only be projected during higher risk periods such as at times of peak migration or under certain weather conditions that have been associated with elevated collision risk. As with any mitigation approach, the use of acoustic warning signals should be tailored to the context of a given hazard, including its location and surrounding ecological communities, the predominant environmental conditions of the area, and the characteristics of any at-risk bird populations.

Appendix

A.1 Figures

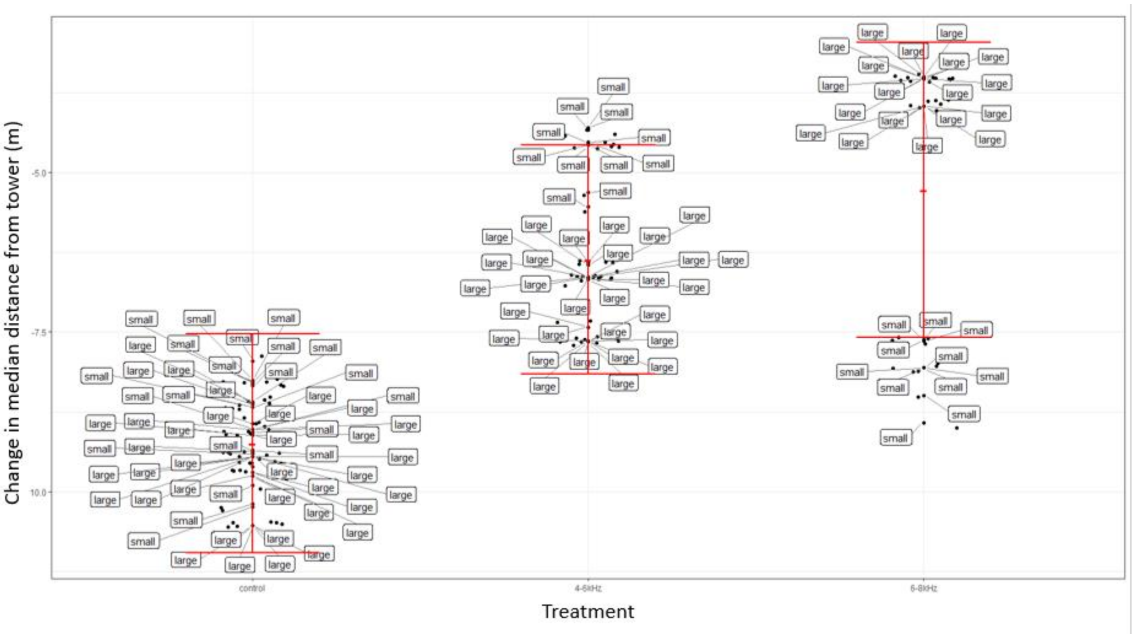


Figure A1. Change in median distance from tower by treatment condition and bird size. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Each data point is labeled with the attribute of bird size.

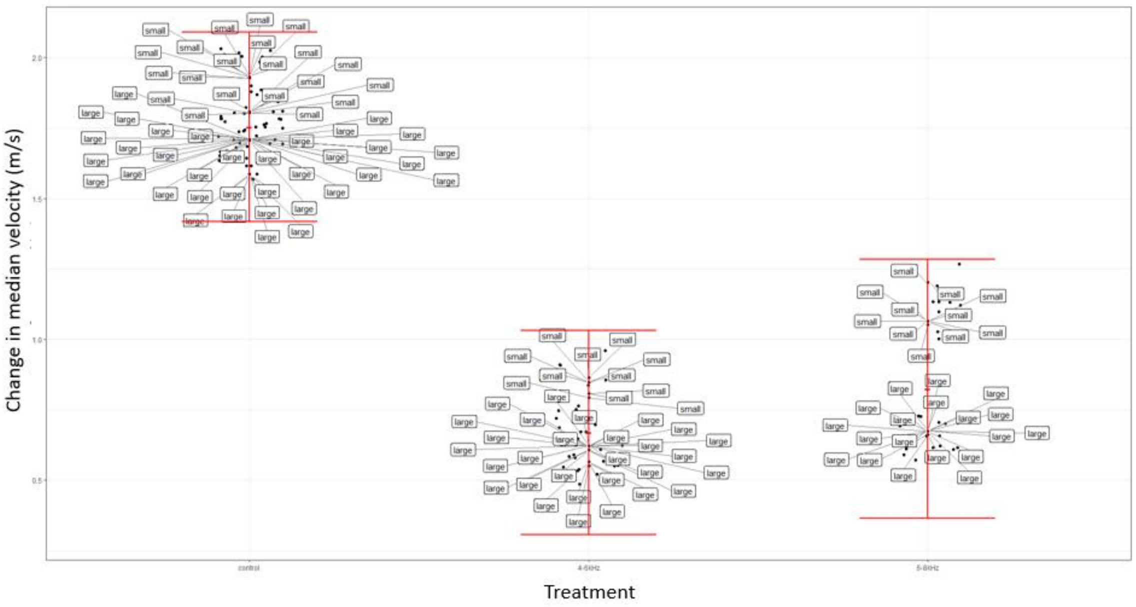


Figure A2. Change in median velocity by treatment condition and bird size. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Each data point is labeled with the attribute of bird size.

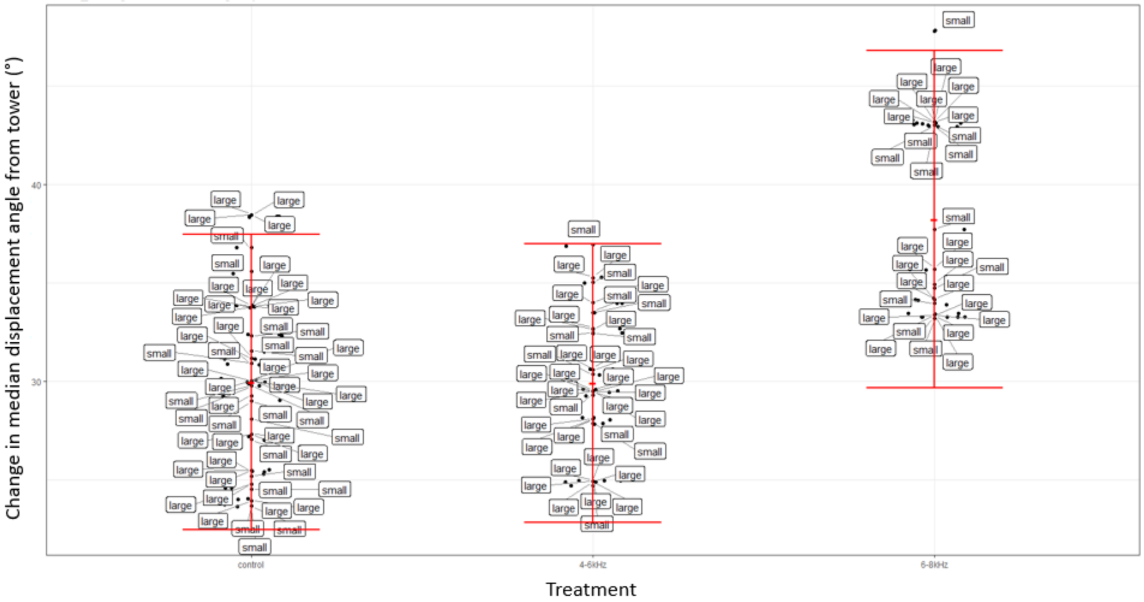


Figure A3. Change in median displacement angle from tower by treatment condition and bird size. Solid red dots and error bars represent model-averaged mean of outcome variable ± standard error of the mean. Each data point is labeled with the attribute of bird size.

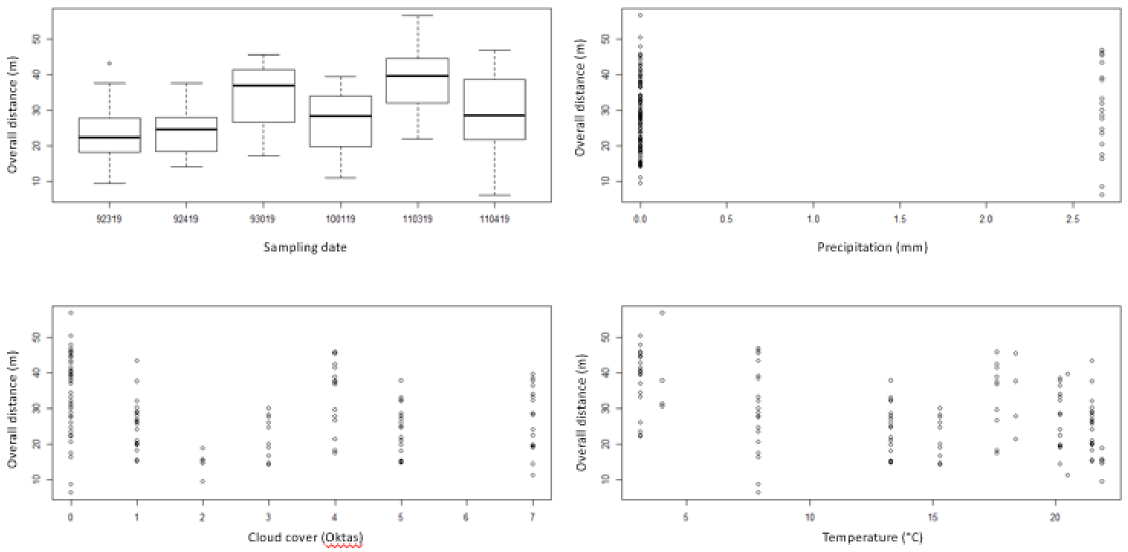


Figure A4. Overall median distance from towers by date and weather conditions. Sampling date, precipitation (mm), mean temperature (°C) and cloud cover (oktas) are reported.

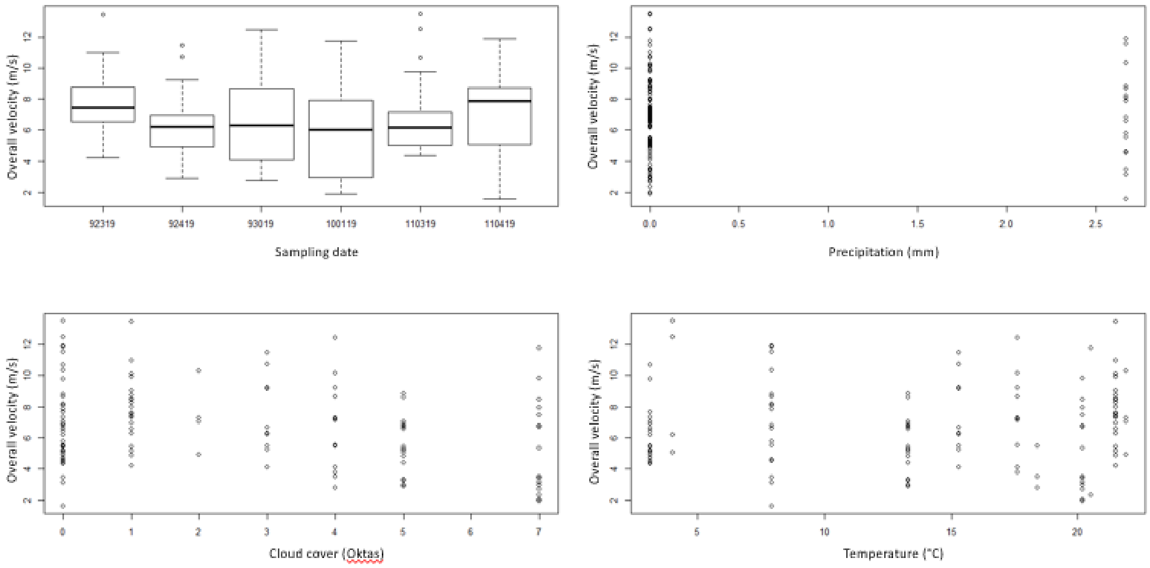


Figure A5. Overall median velocity by date and weather conditions. Sampling date, precipitation (mm), mean temperature (°C) and cloud cover (oktas) are reported.

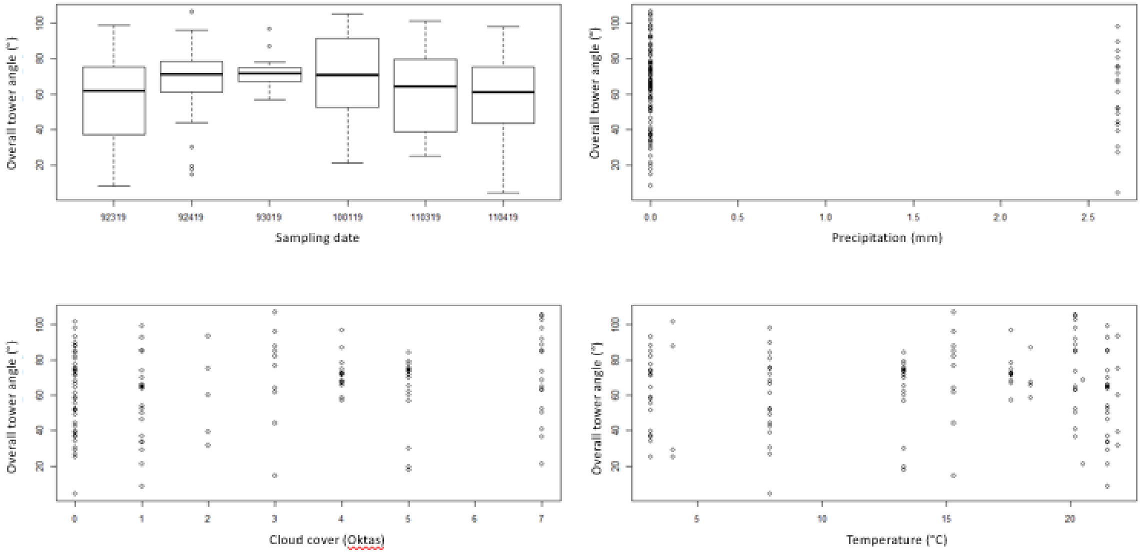


Figure A6. Overall median displacement angle from tower by date and weather conditions. Sampling date, precipitation (mm), mean temperature (°C) and cloud cover (oktas) are reported.

A.2 Tables

Date	ppt (mm)	tmean (degrees C)	cloudcover (oktas)
9/24/2019	0	25.9	2
9/25/2019	0	21.1	1
10/1/2019	0	21.8	3
10/2/2019	0	23.1	5
10/10/2019	0.99	16.8	4
10/11/2019	0	17.6	7
10/19/2019	0	11.5	8
10/20/2019	5.95	14.8	6
10/29/2019	0	17.4	7
10/30/2019	0	16.9	2
11/4/2019	0	8.7	1
11/5/2019	2.67	12.6	0

Table A1. Weather variables across sampling dates. Precipitation (mm), mean temperature (°C) and cloud cover (oktas) are reported. Average daily estimates of weather variables were extracted from the PRISM Climate Group gridded dataset (Oregon State University).

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