Integrative and Comparative Biology
Integrative and Comparative Biology, volume 60, number 5, pp. 1025–1035
doi:10.1093/icb/icaa128
Society for Integrative and Comparative Biology

SYMPOSIUM INTRODUCTION

Introduction to the Symposium: Bio-Inspiration of Quiet Flight of Owls and Other Flying Animals: Recent Advances and Unanswered Questions

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From the symposium "Bio-inspiration of quiet flight of owls and other flying animals: recent advances and unanswered questions" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2020 at Austin, Texas.

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Synopsis Animal wings produce an acoustic signature in flight. Many owls are able to suppress this noise to fly quietly relative to other birds. Instead of silent flight, certain birds have conversely evolved to produce extra sound with their wings for communication. The papers in this symposium synthesize ongoing research in "animal aeroacoustics": the study of how animal flight produces an acoustic signature, its biological context, and possible bio-inspired engineering applications. Three papers present research on flycatchers and doves, highlighting work that continues to uncover new physical mechanisms by which bird wings can make communication sounds. Quiet flight evolves in the context of a predator–prey interaction, either to help predators such as owls hear its prey better, or to prevent the prey from hearing the approaching predator. Two papers present work on hearing in owls and insect prey. Additional papers focus on the sounds produced by wings during flight, and on the fluid mechanics of force production by flapping wings. For instance, there is evidence that birds such as nightbirds, hawks, or falcons may also have quiet flight. Bat flight appears to be quieter than bird flight, for reasons that are not fully explored. Several research avenues remain open, including the role of flapping versus gliding flight or the physical acoustic mechanisms by which flight sounds are reduced. The convergent interest of the biology and engineering communities on quiet owl flight comes at a time of nascent developments in the energy and transportation sectors, where noise and its perception are formidable obstacles.

Introduction

This symposium brings together acoustical engineers and biologists to synthesize ongoing research in "animal aeroacoustics": the study of how animal flight produces an acoustic signature, its biological context, and possible bio-inspired engineering applications. One of the underlying topics is animal flight. Over the past few decades, the Society for Integrative and Comparative Biology (SICB) has experienced dramatic growth in the number of engineers and physicists that attend the annual meeting. One group that has not attended SICB much are aeroacoustical engineers. Acoustical engineers more traditionally interacted with biologists at the biannual Acoustical Society of America (ASA) meetings. The ASA meeting is well attended by bioacousticians (especially bioacousticians studying bats and whales), but not comparative biomechanists studying animal flight. Therefore, one purpose of this symposium was to invite engineers working on questions related to how flying animals produce sound to attend SICB. The other purpose was to synthesize a range of biological questions involving wing sounds (i.e., communication and hunting) by inviting researchers investigating different aspects of animal wing sounds.

Advance Access publication September 10, 2020

Communication

Animals use sound and hearing predominantly in two contexts: for communication, and in predator–prey interactions. Birds, frogs, several insect groups, fish, mammals, and other animals use sound to communicate, usually with other members of their own species. In terrestrial vertebrates, the majority of communication sounds are produced vocally (i.e., with the vocal cords of the throat), hence most research on acoustic communication in this clade has focused on sounds made by the vocal tract. But many animals make "non-vocal" communication sounds with their wings and other parts of their body (Clark 2016). Bostwick and Prum (2003) coined the word "sonation" to refer to non-vocal sounds that serve in communication. A human example of a sonation is the applause at the end of a seminar.

How do sonations evolve? All organisms produce locomotion-induced sound when they move (Clark 2016): human examples include the sounds of footsteps. Most locomotion-induced sounds are adventitious, meaning they do not have communication function; they are simply an inevitable byproduct of animal locomotion. Cues contain information to which a receiver might attend, but were not produced specifically for the receiver, just as you might hear someone's footsteps and therefore know a person is there, irrespective of whether the person making the footsteps was intending to be heard. Sonations (and communication) arise when the sender is advantaged by having the receiver hear the footsteps (Fig. 1). Because the sender is benefitted by having the receiver hear them, they are selected to evolve changes to the locomotion-induced sounds to facilitate communication, such as by making them louder (easier to perceive). That is, over evolutionary time, a positive feedback loop forms between sender and receiver (plus symbol in Fig. 1). The locomotion-induced sounds that were formerly just a byproduct of locomotion become elaborated for communication. For example, human tap-dancing sounds are derived from, but sound a different from, ordinary footsteps. Given enough evolutionary time, the sender often evolves an "instrument", such as loud shoes or modified feathers (Bostwick and Prum 2005; Clark and Feo 2008) that have a functional morphology specifically tied to sound production. Though, note that it is not essential for the animal to have an "instrument": human applause is a sonation and yet human hands do not seem to have any special modifications to produce clapping sounds (Clark 2018). At this point, the sound is no longer a cue, merely a byproduct of locomotion, rather it has become a signal.

Some of the sonations that animals produce that have evolved under this feedback loop are quite loud or distinctive, such as the klaxon-like *breeeeet!* sound made by fluttering wing feathers of *Smithornis* broadbills (Clark et al. 2016a) or the clear, bell-like *tut-tut-tiiiiiiink* sound made by stridulating wing feathers of Club-winged manakins (Bostwick and Prum 2005), both of these sounds carry for some distance through the jungles in which each species

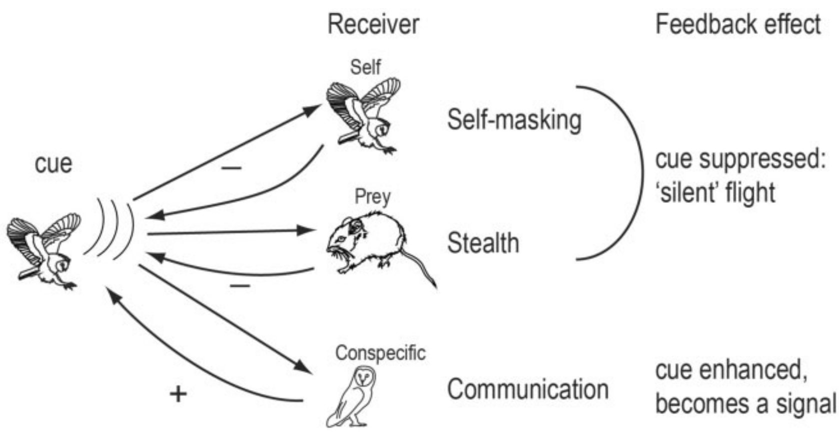

Fig. 1 Potential selection pressures on incidental locomotion-induced sounds (cues) come from detection of those sounds by the animal itself (self), antagonists (such as prey), or from communication partners (usually conspecifics)

Adventitious sounds are selected against when they mask the sender's hearing (self-masking) or when they reveal the sender to the prey (stealth). These selective pressures select against adventitious sound, leading to reduced ("silent") flight sounds. When the receiver responds positively to the sender's sound, they select for the sound to be modified (such as by making it louder, more distinctive, or behaviorally modulated) to enhance its utility in communication. In this case, the enhanced cue becomes a signal, or sonation.

lives. Several clades of birds have high diversity of sonations: hummingbirds, shorebirds (e.g., snipe), manakins, cotingas, nightjars, and new-world flycatchers (Clark and Prum 2015). Of these, the new-world flycatchers (Tyrannidae) are perhaps the least-studied yet might also be the most acoustically diverse clade. Just how many times sonations may have independently evolved in this species-rich clade is completely unclear. In the symposium, Valentina Gomez presented data on how the Fork-tailed Flycatcher (*Tyrannus savanna*) produce sounds with their outer wing feathers, demonstrating that this species produces sound via aeroelastic flutter of their outer wing-feathers (Gómez-Bahamón et al. 2020). This research connects with the paper by Dr Emilio Jordan and his advisor, Dr Ignacio Areta. Dr Areta studies how flycatchers produce sounds with their wings (Areta and Miller 2014). He could not attend the symposium in Austin, but in their paper, they describe the biomechanics of sound production in flycatchers in the genus *Pseudocolopteryx*, a group that, within flycatchers, is distantly related to the genus *Tyrannus* (Jordan and Areta 2020).

There are similarities between the findings of Gómez-Bahamón et al. (2020) and Jordan and Areta (2020); each group of flycatchers produces sounds with multiple fluttering wing feathers, and both Gómez-Bahamón et al. (2020) and Jordan and Areta (2020) for the first time present videos of feathers fluttering in live, wild birds. Previous research on how feathers flutter to produce sound had resorted to eliciting flutter artificially by placing feathers in a wind tunnel (Clark et al. 2011; Clark and Prum 2015; Clark et al. 2016a). One eternal caveat with this type of experiment is that, since most wind tunnels imperfectly replicate flight flow conditions (e.g., it can match the velocity but not the acceleration of the flow), it is never entirely certain whether the flutter elicited in a wind tunnel precisely matches how the feathers flutter in the wild birds. For instance, in a flapping wing, inertial bending of feathers (caused by the wing's acceleration) may affect flutter (Clark et al. 2016a), while in a wind tunnel, all bending prior to flutter is aerodynamic, not inertial. Hummingbirds are very hard to film up close in the field (they are small and fly quickly), which is why there are no videos of feathers fluttering in live hummingbirds. Clark et al. (2016a) filmed displaying *Smithornis* broadbills deep in the dark jungle understory in Uganda. Although *Smithornis* broadbills will perch in one spot and display repeatedly, light was limiting thus the fluttering *Smithornis* wing feathers appear blurry in the videos obtained by Clark et al. (2016a), making it hard to tell what exactly was happening. The flycatchers studied by Gómez-Bahamón et al. (2020) and Jordan and Areta (2020) display in full sun, facilitating acquisition of videos under light conditions that permit visualization of flutter occurring on the bird itself.

Another clade that has evolved sonations repeatedly are pigeons and doves. Dr Robert Niese was also unable to attend the symposium in Austin, but has contributed a paper on wing sounds in ground-doves in the genus *Columbina* (Niese et al. 2020). When birds evolve to produce sounds with their wings, it is most often the outer wing–feathers that are involved, both because these feathers are most likely to collide with other objects, such as the opposite wing in the case of percussive sounds, for example, manakin wing-snaps (Bostwick and Prum 2003; Bodony et al. 2016). Outer primary feathers also tend to be emarginated for flight (Niese and Tobalske 2016), freeing the vane of the emarginated feather from its neighbor, potentially predisposing them to flutter to produce sound. But *Columbina* doves were curious because feathers on the interior of the wing had a subtle modification that was not an emargination, rather it was an extended lobe of the feather vane. *A priori* it was entirely unclear how this shape might make sound, as this morphology did not causes an obvious hole to appear in their wings, as would be needed for a whistle or the previously described ways that feathers flutter. Niese et al. (2020) show that, during the upstroke, a gap between the neighboring primaries permits air to flow between the wing feathers. This occurrence in turn causes this extended feather vane to flutter and collide with the surface of the adjacent feather, producing a buzzing sound rich in harmonics. In short, Niese et al. (2020) have uncovered yet another way that a wing can have rather subtle morphological modifications that cause that wing to produce a fair amount of excess sound.

There are many additional mechanisms that certain species employ, such as manakin wing-snaps, which are percussive (Bodony et al. 2016), wing stridulation in the Club-wing Manakin (Bostwick and Prum 2005; Bostwick et al. 2010; Bostwick et al. 2012), or the swishing sounds Greater sage-grouse make by rubbing their wings against their stiffened tuned breast-feathers (Koch et al. 2015), to name just a few. Some species produce sonations in which the physical acoustic mechanism remains entirely unclear, such as the loud, low-frequency drumming that Ruffed Grouse produce with their wings (Garcia et al. 2012).

What does any of this work on sonations have to do with owls and quiet flight? The work on the physical acoustics of sonations that we have just summarized reveals that there are many different ways that bird wings can make sound in flight. In all of these cases, these sonations did not arise out of nothing; rather, they arose out of sounds that were initially an incidental byproduct of locomotion (Darwin 1871; Prum 1998). What this collective body of work has begun to reveal is just how many different ways bird wings can make sound.

Quiet flight: Biological context

Sonations evolve in the context of animal signaling: the sender evolves to produce more sound with their wings than the underlying adventitious noises of ordinary locomotion (Clark 2016). Comparatively quiet flight also evolves under a feedback loop, but rather than the positive feedback loop of sonations, the feedback loop is negative instead. The sender is a predator that is selected to reduce its noise from locomotion while hunting. This is often called "silent" flight, but applying the word silent must be given proper context, as it is not the case that no sound is produced in flight. Rather, what we really mean is quiet flight: the acoustic signature of the animal or its perception is reduced in some way, rather than that all sound is entirely eliminated (since the only way to entirely eliminate the acoustic signature of locomotion is to freeze in place in still air, ceasing locomotion).

Why does quiet flight evolve? Clark et al. (2020) proposed two hypotheses to describe the evolutionary route toward quiet flight: the stealth ("mouse ear") hypothesis, and the self-masking ("owl ear") hypothesis. According to the stealth hypothesis, the predator (e.g., an owl) reduces its flight sounds to evade detection by the receiver, such as a mouse, until it is too late for the receiver to evade the owl's strike. According to the self-masking hypothesis, the owl evolves quiet flight to avoid blocking (masking) its own sensitive hearing as it listens for prey (Fig. 1). Either selective pressure leads to a negative feedback loop: under either hypothesis, the owl is selected to reduce its acoustic signature in flight, then either the owl or the prey is selected to evolve more sensitive hearing, followed by further selection on the owl to further alter its acoustic signature, and so on. Both the stealth and self-masking hypotheses, which are not mutually exclusive, make predictions about hearing: the stealth hypothesis predicts that the predator (such as an owl) is selected to suppress sounds to which prey are sensitive, while the self-masking hypothesis predicts that owls and other ecologically similar flyers are selected to reduce sounds that they themselves hear (Clark et al. 2020). What the stealth hypothesis makes clear is that the question of quiet flight is in part about psychoacoustics: consideration of how prey may hear an approaching predator is relevant.

Dr Jayne Yack is a neurophysiologist who studies insect hearing, especially in butterflies. Nocturnal insect hearing has been well-studied, especially in the context of the coevolutionary arms race between nocturnal insects and their enemies, bats (Conner and Corcoran 2012; Strauß and Stumpner 2015). In fact, the literature sometimes implies bats are the reason insects have ears (after accounting for the many insects that use hearing for communication). But most butterflies are diurnal, not nocturnal. In her symposium presentation, Dr Yack asked the question: why do butterflies, most of which do not communicate with sound, have ears? Fournier et al. (2013) recorded the wing sounds that two species of passerine birds made in flight, showing that their wing sounds were broadband, including substantial amounts of ultrasound. Moreover, butterfly and moth ears were highly sensitive to these wing sounds, suggesting that butterflies may use hearing as an anti-bird device: they may listen to the wing sounds of birds. In their paper, Yack et al. (2020) take a slightly broader perspective to review the role of hearing in predator avoidance. Many small owls eat insects; it is possible that owls and other birds (especially, nightbirds within Caprimulgiformes, which tend to be insectivorous) have evolved quiet flight under the "butterfly ear" hypothesis: that is, to approach insects more stealthily.

Turning to the self-masking ("owl ear") hypothesis, owls may evolve to reduce their acoustic flight signature in order to better hear their own prey (Clark et al. 2020). Since many owl species hunt at night, many primarily use sound (rather than vision) to locate their prey. Owls have highly sensitive hearing, and neurophysiologists have used Barn Owl (family Tytonidae) hearing as a canonical system in which to study certain aspects of how the brain perceives and processes sound (Volman and Konishi 1990). One well-studied feature of barn owls is their asymmetrical ears (i.e., the left ear canal is not the mirror image of the right), which is an adaptation to better detect the elevation of incoming sound (Payne 1971; Konishi 1973).

This ear asymmetry has evolved more than once within owls (Norberg 1977). An owl species with among the most asymmetrical ears of the Northern Saw-whet Owl (*Aegolius acadicus*), a member of the family Strigidae (i.e., not closely related to the Barn Owl). Dr Megan Gall studies Northern Saw-whet

Owl hearing (Beatini et al. 2018). In her paper, she and her coauthors measured the directional sensitivity of Northern Saw-whet owls, showing that, among other things, sensitivity is reduced to the left and right of the owls' head, that is, in the direction of its own wings and the sounds they produce in flight (de Koning et al. 2020).

Much of the previous research on quiet flight has focused exclusively on owl flight. Yet other nocturnal birds, such as nightbirds (a nocturnal grade within Caprimulgiformes) also have features associated with quiet flight, such as soft feathers and a velvety coating on the dorsal surface of their wing feathers (Mascha 1905). Although nightbirds were once thought to be closely related to owls, modern molecular phylogenies have revealed that owls and nightbirds are distantly related (Hackett et al. 2008; Prum et al. 2015). Thus, quiet flight has convergently evolved. Moreover, some diurnal raptors (such as kites) are reported to have silencing features as well (Negro et al. 2006). Clark et al. (2020) present data showing that at least one species in a fourth bird group, falcons (American Kestrel *Falco sparverius*) has the dorsal velvet, indicating that this trait has evolved at least 4 times within birds. Moreover, among species with the velvet (owls, hawks, nightbirds, and falcons), there is evidence for both the "owl ear" and "mouse ear" hypotheses of the evolution of quiet flight. Finally, Clark et al. (2020) show that fishing owls have velvet on the dorsal aspect of their wing feathers, contrary to the frequently-repeated claim that fishing owls have lost this particular silencing feature present on other owl species (Graham 1934).

Birds are not the only animals that use sound to locate prey while hunting on the wing, and thus may need to fly in silence: bats also fit this description. Dr Arjan Boonman studies both bat wing sounds (Boonman et al. 2014) and owl wing sounds (Boonman et al. 2018). In the latter paper, he and others presented one of the few measurements of the wing sound of an owl taking off (Neuhaus et al. 1973; Thorpe and Griffin 1962), and showed that rodents were sensitive to these sounds. Specifically, Boonman et al. (2018) focused on a type of sound previously ignored by studies of animal flight noise: the low-frequency "Gutin" or "load" sound is the noise due to an aerodynamic force moving through space (e.g., the wind load on a rotating wind turbine rotor) that may also fluctuate in time, as in the case of a flapping wing. Since wing aerodynamic forces vary over the course of the wing beat, the equal, opposite aerodynamic reaction pressure varies in time as well (Gutin 1948), usually manifesting as sound with a fundamental frequency of either the wingbeat, or twice the wingbeat, depending on the kinematics and receiver's location relative to the animal (Bae and Moon 2008). Boonman et al. (2020) recorded the Gutin sound of three species of bat and three species of small passerine bird as they flew in a camera array that tracked their motion, showing the relationship between the sound generated and the wing beat of the bird. They document that the wing sounds of the bats were quieter than the birds for similarly-sized bats and birds.

Quiet flight: Physical acoustics

Above we have covered the function of quiet flight (e.g., stealth vs. self-masking hypotheses). In functional morphology, why a structure evolved is tightly connected to how it works. For instance, is it possible for owls to suppress a single frequency bandwidth, such as the 3–9 kHz band asserted by the self-masking hypothesis, or are all sound suppression mechanisms broadband? Intertwined with the question of why quiet flight has evolved is the question of how owls reduce the noise their wings produce in flight. Graham (1934) proposed what may be referred to as the *three traits* paradigm, which is that there are three wing features possessed by owls that may act to reduce aerodynamic sound: the leading edge comb, the trailing edge fringe, and the dorsal velvet. This paradigm has since been frequently repeated (Kroeger et al. 1972; Lilley 1998), but recent work has made it clear that this paradigm is a bit too simple and neat. Many owl feathers are fringed in locations nowhere near the trailing edge (Bachmann et al. 2012), such as the leading edge of the tail feathers (Clark et al. 2020). Hence Graham's emphasis on the trailing-edge location of this trait may be warranted from the point of view of aerodynamic noise suppression but is incomplete in describing where this trait appears on the owl and its functional implications. It also appears that owl feathers have reduced flexural stiffness relative to other birds (one effect of which is increased wing deformation in the presence of flow: Geyer et al. 2017). Graham's inaccurate assertion that fishing owls lack the velvet might have been a reflection of the stiffer feathers fishing owls have, relative to other owls, rather than the velvet itself (Clark et al. 2020). Moreover, owl feathers have modestly increased air transmissivity relative to feathers of other birds (Müller and Patone 1998; Geyer et al. 2012).

While the leading-edge comb has been subjected to experimental manipulations that test its function (Kroeger et al. 1972; Geyer et al. 2017), similar experiments have not previously been conducted on other wing attributes such as the velvet. Biologists have hypothesized that the velvet reduces frictional sound produced by adjacent feathers rubbing during flapping flight (Lucas and Stettenheim 1972), while engineers have hypothesized that the velvet modifies the dorsal boundary layer during gliding flight (Lilley 1998). To test the first hypothesis, LePiane and Clark (2020) manipulated with hairspray the velvet on inner wing-feathers of live Barn Owls. They found that the hairspray increased broadband sound during flapping flight consistent with frictional noise, and that the greatest increase in sound occurred during the upstroke when the feathers might rub the most. However, their results do not rule out the possibility that presence of the velvet affects both aerodynamic noise and frictional noise. A key test of the frictional noise hypothesis, that hairspraying the velvet on inner wing feathers has *no effect* on the sounds of gliding (since the feathers should not rub during gliding), was not possible because the authors were not able to get the owls they tested to glide in their experiment.

On the engineering side, the structural composition of owl wings has generated interest in how their traits might disrupt standard routes of aerodynamic noise production. Dr Justin Jaworski studies the effects of elasticity, porosity (i.e., transmission of flow or sound waves through the feather or wing), and geometry of owl traits on the reduction of noise from fluid turbulence, which may be present in the air around the owl or generated in the wing boundary layer. Boundary-layer turbulence creates noise that is amplified (weakly) by surface roughness or (strongly) by edges. Clark et al. (2016b) observed that the geometrical structure of the owl dorsal velvet was akin to a perforated canopy that "pushes off" the noisy boundary layer from the rough surface of the wing. To mimic this scenario, the noise produced by a flow passing over a flat wall with sandpaper was measured with and without a canopy of different porous textiles suspended ~1 mm above the rough surface. The best noise reduction observed experimentally occurred for canopy fibers (representing barbules in the dorsal velvet) that were aligned with the flow, which led to the invention of a streamwise-oriented, surface-mounted fin structures termed "finlets" to explore the possibility for greater noise reductions on wings (Clark et al. 2017). These devices reduce noise by both displacing the boundary layer away from the wing surface and by pretreating the boundary layer before it encounters a strong scatterer such as the trailing edge (Clark 2017). Jaworski and Peake (2020) review the physics and investigations to date of the coupled interactions of boundary layers, surface architectures, and noise generation.

Boundary-layer turbulence passing over the wing trailing edge results in the so-called trailing-edge noise, which is a dominant noise source on wind turbines (Oerlemans et al. 2007) and is an unavoidable noise source on flying animals that generate turbulence. Jaworski and Peake (2013) determined that porosity and elasticity of a wing at its trailing edge can weaken turbulence noise generation, and they identified parametric groups in terms of frequency, flexural rigidity, and other such properties to maximize noise reduction from edges. Numerical work based on this model showed that porosity and elasticity are complementary in reducing noise at low and high frequencies, respectively, and can promote broadband noise suppression when used together (Cavalieri et al. 2016). The design of quieter wings using porosity must be balanced by aerodynamic constraints (e.g., required lift). Predictive models have been developed for the steady (Hajian and Jaworski 2017) and unsteady (Baddoo et al. 2019; Hajian and Jaworski 2019) aerodynamics of porous airfoils, where in the latter case porosity may also be used to reject incoming gusts and suppress other unsteady flow disturbances in flight.

Dr Hao Liu is an aerodynamicist who has recently examined how the details of force production (such as formation of a leading-edge vortex) on a wing may interact with mechanisms that affect sound production. For example, the leading-edge comb of owl wings is hypothesized to modify the vorticity generated at the leading edge of the wing; how does this comb affect lift and drag production (Rao et al. 2017)? Computational results were presented for laminar Reynolds numbers, where future work at higher values relevant to owl flight in the turbulent transition regime will help illuminate the role of the leading-edge comb. Rao and Liu (2020) is on this interaction between acoustic and aerodynamic functions of the wing.

Much of the previous aeroacoustics work on owl flight has focused on mathematical models, computational fluid dynamics simulations, or physical models, such as a dried spread owl wing placed in a wind tunnel. These models describe gliding flight, but owls often flap (rather than glide) while hunting, and the sounds of flapping are potentially different from the sounds of gliding. Flapping flight is harder to study, and an open question has been whether or not the acoustic signature of flapping has substantive differences from gliding flight. Dr Roi Gurka has measured the wake of a flying owl (Lawley et al.

2019), suggesting that an owl sheds finer-scale vorticity into its wake during flapping at one particular speed than other species of bird (Krishnan et al. 2020). Finally, Dr Elias Balaras studies the fluid mechanics of turbulent flows. He has modeled how turbulent boundary layers interact with a flexible canopy (Beratlis et al. 2019), inspired by the velvet of owl wings. His contribution to the symposium was further modeling of the aerodynamic interactions between flow and a complex, textured 3D surface that reflects some aspects of the milli- and micro-scale surface texture of bird wings. Together, Dr Gurka and Dr Balaras present in their paper further work on the forces and wake dynamics of an owl (Beratlis et al. 2020).

Fig. 2 The leading-edge comb on a Tawny Frogmouth (*P. strigoides*) 10th primary

UWBM 79150. Field of view: 18 mm, photo courtesy Anand Varma.

Open questions and future directions

The symposium ended with a discussion of open questions in this area. For example, what is the role of wing flapping in the acoustics of flight? Does flapping fundamentally alter the airflow over a wing in a way that changes its acoustic signature? Another question that came up was: how much active control of flow over the wing might owls have? Can owls actively control how much sound they produce in flight? There were multiple anecdotal reports that owls taking off with prey (i.e., carrying a load) flap more loudly than in other flight contexts. Might this simply be caused by the need to produce increased aerodynamic forces when carrying a load? Or might this be the product of the owl, having just secured a meal, abandoning quiet flight as unnecessary? Active control of the wings to suppress sounds in some flight contexts seems theoretically possible. The simplest form of active control is achieved through modulation of the gross kinematics of the wing. For instance, flapping flight is likely louder than gliding flight, so an owl could switch facultatively to gliding when trying to listen for prey. There are at least two more-subtle ways birds may achieve active control of flow conditions over their wings, and hence, suppression of certain sound source types. These approaches are: the repositioning of autonomous wing components, especially the alula (thumb feathers) (Ito et al. 2019); as well as more subtle tuning of wing material properties, such as active muscular tuning of the stiffness of the attachment of wing feather attachments to the wing and tensioning of the ligament that directly attaches adjacent wing feathers (Hieronymus 2016; Matloff et al. 2020). Whether and how owls actively control the flow over their wings, and how such control may affect sound production in flight, is unclear.

More generally, the conversation returned to the same issue multiple times: the single largest gap in the literature is further information about sounds produced by live owls in flight. Experiments such as the flyover experiments of Sarradj et al. (2011) warrant being repeated in environments with less background sound, for instance. How sound levels scale with body size and flight velocity is also of interest.

Moreover, there is interspecific and intraspecific variation in morphologies associated with quiet flight (Weger and Wagner 2016). More data describing this variation, and its effects, would be of use. For instance, Weger and Wagner (2016) present detailed data on the comb of seven owl species, but among owls as a clade there appears to be additional interspecific variation in comb morphology outside the seven species they studied (K. LePiane, personal communication). There are also other birds that have silencing features (Mascha 1905; Negro et al. 2006; Clark et al. 2020). Weger and Wagner (2016) suggested a Caprimulgid, the Tawny Frogmouth (*Podargus strigoides*) lacked a comb (their Fig. 6B), contrary to prior reports Mascha (1905; see their Fig. 25). Clark et al. (2020), when collecting data on the velvet, observed a comb on many of $n=20$ spread wings of *P. strigoides* at the University of Washington Burke Museum (Fig. 2). Among these 20 wings, there was intraspecific variation in comb morphology: the comb was entirely missing on some specimens, possible due to damage or wear to the feather. That is, the comb may be missing in birds that were about to molt their feathers. If Weger and Wagner (2016)'s suggestion that *P. stroigoides* lacks the comb was based on a single worn specimen (sample size is not provided).

Additional data on interspecific (and intraspecific) variation in wing features that apparently promote quiet flight is of strong interest for bioinspiration. Physics-based models and fluid dynamics simulations require the construction of dimensionless parameter groups, including Reynolds number and numerous length-scale ratios (based on wing size, comb length, and spacing, and dorsal velvet geometry), dimensionless frequency (i.e., Helmholtz number, see Cavalieri et al. 2016), as well as dimensionless groups associated with fluid-structural coupling if including the flexibility of certain wing attributes. The sheer number of dimensionless parameters and their ranges of values produce a parametric design space that is unwieldy to explore without guidance from morphological and acoustical measurements to set reasonable bounds on their values. The flight speed of owls is slow enough to not consider Mach (i.e., flow compressibility) effects on the acoustics, although these effects may be important when applying owl-inspired technology to devices that operate outside the parameter space of owl flight. Jaworski and Peake (2020) determine a nominal parameter space based on available morphological data (mostly of the Barn Owl), where interspecific physical and aeroacoustical measurements are called for.

Another topic discussed was the implications of quiet flight for neuroethology and behavioral ecology of hunting. For instance, the observation that Saw-whet Owls have reduced acoustic sensitivity laterally (in the direction of their wings) (de Koning et al. 2020) is predicted by the self-masking hypothesis, that is, it is consistent with Saw-whet Owls listening for prey sounds while flying toward that prey. There appears to be interspecific variation in how owls hunt. Many owls are sit-and-wait predators (they sit on a perch, waiting until a potential prey item reveals itself below) and thus are not flying when prey is first detected. Other owls (such as Short-eared Owl, *Asio flammeus*) hunt by "coursing", flying back and forth low over an open (usually grassy) area, listening for prey on the wing (Wiggins et al. 2006). These different hunting strategies likely influence how self-masking is expressed, because the time at which wing sounds are produced during the entire timecourse of the predator–prey interactions (i.e., from initial prey detection through to the conclusion of the strike on prey) will be different for these two hunting styles (Clark et al. 2020).

The precise nature of a given owl species's acoustic acuity is likely a product of the hunting strategy it employs, and likely coevolves with the anatomy of the silencing features. For instance, Volman and Konishi (1990) present data on the sound localization abilities of four owl species, two of which had symmetrical ears and two of which had asymmetrical ears. This difference in ear asymmetry produces a major difference in foraging strategy, since asymmetrical ears permit decoupling of interaural intensity differences from interaural time differences cues, which in turn allows owls with asymmetrical ears to disambiguate between elevation and azimuth of incoming sounds. This asymmetry is presumably correlated with substantial differences in their acoustic foraging ecology. We suggest that interspecific differences in hunting style (with variation in the timecourse of wing-sound production) may also select for more subtle interspecific differences in silencing features.

Another topic broached was that we do not yet have aeroacoustic models that make actual predictions of the sound levels that live owls might make in flight. Producing such a model would require enumeration of all of the mechanisms that generate substantial levels of sound in ordinary bird flight. This brings us back to the topic of sonations: as described above, our model for how sonations evolve is that they arise out of the adventitious sounds produced during ordinary flight, the same adventitious sounds that owls and other quiet fliers suppress. Given the diversity of physical acoustic mechanisms by which sonations are produced seems both broad and incompletely explored, it seems likely that future research will uncover a number of additional new ways that birds can produce biologically salient sounds.

The convergent interest of the biology and engineering communities on quiet owl flight comes at a time of nascent developments in the energy and transportation sectors, where noise and its perception are formidable obstacles. Commercial aircraft are continuously pushed toward lower fuel burn rates, greater aerodynamic efficiency, and lower noise levels, which must meet specific performance targets (e.g., Flightpath 2050 for European aircraft) and abide by local noise regulations near airports. Emergent small craft, such as regional sky taxis (Seeley 2015), and other vehicles pursued within the urban air mobility paradigm seeking to alleviate traffic congestion in densely-populated areas must also overcome local noise regulations and develop novel technological approaches to decrease noise from low-speed rotors. Quadcopters and similar unmanned air vehicles that have emerged for product delivery and reconnaissance tasks create a distinctive acoustic signature (Intaratep et al. 2016), where technological leaps in noise reduction inspired by noise suppression mechanisms of owls or other means promise to give a commercial competitive advantage.

A final general conclusion was that there was surprisingly little data on sounds that bat wings make, a gap that begins to be addressed by the data presented in Boonman et al. (2020). Whether bats have evolved silencing features, or if any produce communication sounds with their wings, would both be fascinating research topics.

Acknowledgments

We thank Susan Williams and Jake Socha for coordinating the symposium; Arjan Boonman, Jayne Yack, Megan Gall, Krista LePiane, Roi Gurka, Elias Balaras, Robert Niese, and Nacho Areta for participating in the symposium, and SICB and the Company of Biologists for funding the symposium; and Anand Varma for use of a photo. J.W.J. acknowledges the support of the National Science Foundation under award 1805692 to participate in this symposium. The authors declare no conflicts of interest.

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