What Can Birds Hear?

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ABSTRACT: For birds, hearing is second in importance only to vision for monitoring the world around them. Avian hearing is most sensitive to sounds from about 1 to 4 kHz, although they can hear higher and lower frequencies. No species of bird has shown sensitivity to ultrasonic frequencies (>20 kHz). Sensitivity to frequencies below 20 Hz (infrasound) has not received much attention; however, pigeons and a few other species have shown behavioral and physiological responses to these low frequencies. In general, frequency discrimination in birds is only about one-half or one-third as good it is for humans within the 1 - 4 kHz range. A problem that birds suffer that is similar to humans is damage to the auditory receptors (hair cells) from loud noises. The sound intensity that produces damage and the amount of damage produced differs depending on the species. Birds residing in the active areas of airports might be constantly subjected to sound pressure levels that damage their hearing. Thus, to effectively disperse birds using sound, auditory alerts must be at frequencies that can be detected by the damaged auditory receptors. Although some if not all species of birds have the ability to repair damaged hair cells, continued exposure to loud noises would prevent recovery of their hearing. In this paper I review what is known about avian hearing and compare that to the operational characteristics (frequencies, intensities, duration) of techniques and devices to disperse birds.

KEY WORDS: birds, deterrents, hearing, infrasound, sound, ultrasound

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INTRODUCTION

Birds present a hazard to aviation and depredate many crops. Although lethal control is necessary in many situations, it is often more desirable to use nonlethal techniques to disperse or deter birds from selected locations, for a variety of reasons. One category of deterrent/dispersal techniques is sound. To maximize their effectiveness, the sounds that are used must:

1. be loud enough to be audible to the birds,
2. be within the frequency range the birds' ears can detect, and
3. provide a biologically relevant message such that the birds depart.

Given this knowledge, we can compare the operational characteristics of sound dispersal devices that are available on the market and make some predictions about their efficacies.

AVIAN HEARING

Avian ears and hearing differ from those of humans and other mammals in several ways, some obvious and some not. The first, obvious difference is that birds lack an external ear or pinna. Terrestrial mammals use the pinna and external ear canal to concentrate sound and increase the sensitivity of the ear. The sound travels down the auditory canal to the eardrum (tympanic membrane) where it produces vibrations in the fluid-filled inner ear. Transmission of vibrations from the eardrum to the inner ear, where sound information becomes encoded in the nervous system, is mediated by the ear ossicles (bony elements). Birds have a single ossicle, the columella, compared to three in mammals. The theoretical amplification for a single element is about 20-fold from the tympanum to the fluid of the inner ear. The inner ear of birds serves two functions: equilibrium and hearing. Hearing takes place in the cochlea. Unlike the coiled mammalian cochlea, the avian cochlea is a straight or slightly curved tube whose length differs among species. In pigeons (*Columba livia*) it is about 5 mm long but over 1 cm in the barn owl (*Tyto alba*) (Schwartzkopff 1968, Smith 1985). The differences in length, both among avian species and between birds and mammals, probably reflect differences in the range of frequencies that the species can detect. Longer cochlea allow for more auditory receptors and better sensitivity to either a wider range of frequencies or better resolution among frequencies.

The auditory sensory receptors are the hair cells, which are similar in form and function to those of other vertebrates. These cells are equipped with cilia that are stimulated by the vibrations in the fluid of the cochlea. Because of the differences in cilia lengths and the locations of the cells along the basilar membrane, individual cells are most sensitive to specific frequencies; i.e., they are tuned to a narrow band of frequencies. Consequently, the information sent to the brain contains encoded frequency information. As might be expected, species differ in their sensitivities and range of sensitivities to frequencies of sound (Table 1). Different species of birds have the greatest sensitivity to sounds within a relatively narrow range. For most avian species this is around 1 - 4 kHz, but some species are sensitive to lower or higher frequencies (Konishi 1970, Hienz et al. 1977). Pigeons are most sensitive to sound between 1 - 2 kHz, with an absolute upper limit of about 10 kHz (Goerdel-Leich and Schwartzkopff 1984). None of the avian species that have been examined has shown sensitivity to frequencies above 20 kHz (ultrasound) (Schwartzkopff 1973) and generally the upper threshold is about 10 kHz (Hamershock 1992, Necker 2000).

Sensitivity to infrasound (less than 20 Hz) has been observed in the pigeon and in some other species but not in all species tested (Yodlowski et al. 1977, Kreithen and

Table 1. Species-specific sensitivities to frequencies, peak sensitivity, and range of sensitivities.

Species	Lower Limit (HZ)	Most Sensitive (kHz)	Upper Limit (kHz)	Reference
Black-footed Penguin (*Spheniscus demersus*)	100	0.6-4	15	Wever et al. 1969
Mallard (*Anas platyrhynchos*)	300	2-3	8	Trainer 1946
Canvasback (*Aythya valisineria*)	190		5.2	Edwards 1943
American Kestrel (*Falco sparverius*)	300	2	10	Trainer 1946
Ring-necked Pheasant (*Phasianus colchicus*)	250		10.5	Stewart 1955
Turkey (*Meleagris gallopavo*)			6.6	Maiorana and Schleidt 1972
Gull (*Larus ridibundus?*)	100	3	10	Beuter and Weiss 1986
Ring-billed Gull (*Larus delawarensis*)	100	0.5-0.8	3	Schwartzkopff 1973
Rock Dove (*Columba livia*)	50	1.8-2.4	11.5	Wever and Bray 1936
	200		7.5	Brand and Kellog 1939a
	300	1-4		Heise 1953
[Infrasound]	300	1-2		Trainer 1946
	0.05			Kreithen and Quine 1979
Budgerigar (*Mellopsittacus undulatus*)	40	2	14	Knecht 1940
Barn Owl (*Tyto alba*)			12.5	Konishi 1973
Eagle Owl (*Bubo bubo*)	60	1	8	Trainer 1946
Great Horned Owl (*Bubo virginianus*)	60		7	Edwards 1943
Long-eared Owl (*Asio otus*)	100	6	18	Schwartzkopff 1955
Tawny Owl (*Strix aluco*)	100	3-6	21	Schwartzkopff 1955
Horned Lark (*Eremophila alpestris*)	350		7.6	Edwards 1943
European Robin (*Erithacus rubecula*)			21	Granit 1941
American Crow (*Corvus brachyrhynchos*)	300	1-2	8	Trainer 1946
Black-billed Magpie (*Pica pica*)	100	0.8-1.6	21	Schwartzkopff 1955
Blue Jay (*Cyanocitta cristata*)			7.8	Cohen et al. 1978
Red-winged Blackbird (*Agelaius phoniceus*)			9.6	Heinz et al. 1977
Brown-headed Cowbird (*Molothrus ater*)			9.7	Heinz et al. 1977
European Starling (*Sturnus vulgaris*)	700		15	Brand and Kellogg 1939a
		2000		Trainer 1946
			8.7	Dooling 1982
House Sparrow (*Passer domesticus*)	675		11.5	Brand and Kellog 1939a
			18	Granit 1941
Chaffinch (*Fringilla coelebs*)	200	3.2	29	Schwartzkopff 1955
Greenfinch (*Chloris chloris*)			20	Granit 1941
Canary (*Serinus canaria*)	1100		10	Brand and Kellogg 1939b
	250	2.8	10	Dooling et al. 1971
Bullfinch (*Pyrrhula pyrrhula*)	200	3.2	20-25	Schwartzkopff 1952
			21	Granit 1941
Field Sparrow (*Spizella pusilla*)			11	Dooling et al. 1979
House Finch (*Carpodacus mexicanus*)			7.2	Dooling et al. 1978
Red Crossbill (*Loxia curvirostra*)			20	Knecht 1940
Snow Bunting (*Plectrophenax nivalis*)	400		7.2	Edwards 1943

Quine 1979, Theurich et al. 1984). One problem with infrasound and other low frequencies, especially for birds, is determination of the direction of the sound source. Because their ears are close together, mechanisms that function at higher frequencies are not usable. One technique birds could use to locate a sound source would be to fly in a circle and use the doppler shifts to determine direction (Quine and Kreithen 1981, Hagstrum 2000). Although this technique would be usable for birds seeking another bird or for navigation, it is not suitable for dispersing birds from an airfield because the circling might bring the bird into conflict with aircraft. Thus, infrasound by itself might be used to disperse birds but it would not be directional and could result in birds flying in many directions, not just away from the source.

The sensitivity to sound intensity (loudness) is influenced by the frequency of the sound. In general, birds have higher thresholds (are less sensitive) to a specific frequency (pitch) than humans (Smith 1985). This means that if a human can hear a faint sound, birds at the same location might not be able to hear it. This can be compensated for by using louder sounds, moving closer to the birds, or using highly directional speakers. Overall, birds hear well over a limited frequency range, but not as well as humans. Large, nocturnal owls are the exception in that they can hear well over a wide frequency range (Konishi 1973).

Two problems that birds face, along with humans working in environments with loud noises, are damage to the hair cell receptors of the auditory system caused by overstimulation, and hearing signals above the background noise. These problems can have a synergistic relationship in that reduced sensitivity caused by damage requires a louder signal to be effective, which in turn can cause more damage. The amount and type of damage birds suffer after acoustic overstimulation differs among species (Ryals et al. 1999). Unlike humans, birds show recovery of sensitivity and hair cell receptors but the rates differ among species (Stone and Rubel 2000). Repeated exposure, as occurs around airfields, would continuously counter any recovery, however. Birds show behavioral responses in their vocalizations to noisy environments, singing or calling more loudly (Pytte et al. 2003) or at higher pitches (Slabbekoorn and Peet 2003). Such behavioral responses to noise must be taken into consideration when using acoustic deterrents on birds.

ACOUSTIC DEVICES

Our objective in using acoustic devices is to displace birds through communication or through annoyance. The three conditions listed above must be met for an acoustic signal to be an effective avian deterrent: detectable, audible, and relevant. These conditions are useful for initial evaluations of proposed devices. If either of the first two conditions is not met, the birds will not hear the transmitted signal; if the third condition is not met, the birds might ignore the signal.

There are several devices on the market that produce only ultrasonic frequencies (see Table 2 for some examples). Because no species of bird has shown behavioral or neurophysiological responses to ultrasonic frequencies (Schwartzkopff 1973, Hamershock 1992, Necker 2000), such devices theoretically are ineffective at communicating with birds. In their reviews of published research on ultrasonic deterrents, Hamershock (1992) and Bomford and O'Brien (1990) reported that there was no evidence that ultrasonic devices had any effect on avian behavior, including dispersal.

Signals produced by sonic devices can be categorized as biologically relevant or biologically irrelevant. Biologically irrelevant signals include constant signals and modulated signals. Constant signals can be tones or broadband noise, but they do not change frequency or intensity. Such signals can be annoying but are not threatening, and animals, including humans, become habituated to them. Consequently, although they might be effective for a short time, such signals rapidly will be ignored by the birds. Modulated signals vary in frequency, amplitude, or both. In some cases, the modulation is random, but constant in other cases. Birds quickly habituate to and ignore modulated signals, because they provide no information. Bomford and O'Brien (1990) reported that there were no data to indicate that pure or modulated tones are aversive to birds. Starlings initially reacted to white noise, but they habituated rapidly (Thompson et al. 1979, Cole et al. 1983, Johnson et al. 1985).

Biologically relevant signals are those signals that have meaning to the bird. They include sounds made by members of their same species, other avian species, and predators. Conspecific and heterospecific sounds that are used to disperse or repel birds are typically distress and alarm calls. Although birds responded more strongly to such sounds than to tones when tested, the effects were short term. All species of birds become habituated to nearly all the sounds that have been tested when the sounds are used by themselves (Bomford and O'Brien 1990).

Another group of biologically relevant sounds are those made by predators. Although we usually don't think of it in this way, humans are predators of birds. Whether a bird is killed by a fox, hawk, or shotgun, it is removed from the breeding population. At least one manufacturer of sonic broadcast devices uses prerecorded predator vocalizations in its equipment. Pyrotechnics, including bangers, poppers, screamers, etc., are biologi-

Table 2. Characteristics of selected sonic avian repellent devices. The characteristics and information are based on a search of the Internet.

Device Company	Frequency Range	Sound Level	Comments
BirdXPeller Pro Super BirdXPeller Pro Bird-X	3-5 kHz	105-110 dB @ 1 m	distress calls
BroadBand Pro Bird-X	3-5 kHz 15-25 kHz	105-110 dB @ 1 m 92-102 dB @ 1 m	audible and ultrasonic
Transonic IX-L Bird-X	20-50 kHz 10-50 kHz 1-50 kHz	116 dB @ 0.5 m	
Critter Blaster Bird-X	2-10 kHz	105-110 dB @ 1 m	
Quadrablaster QB-4 Bird-X	20 kHz 20-30 kHz		warble
Goosebuster Bird-X	500-1500 Hz	110 dB @ 1 m	alert and alarm calls
YardGuard Bird-X	15-26 kHz	114 dB @ 1 m	
MFG DiBro (NZ) Mfg Ltd.	NA	NA	random frequencies
Sonic BirdChaser Krupps	NA	NA	predator calls
Silent Bird Scarer Pestoff	17-65 kHz	NA	
Bird Scarer Pestoff	3-25 kHz	NA	predator calls
Ultrasound Ceiling Device U-Spray	22 kHz	112 dB @ 1 m	
Yard Team	15-25 kHz	114 dB @ 1 m	

NA = not available

cally relevant sounds because they provide the acoustic information generated by a (human) predator without the actual predatory attack. I will categorize both prerecorded predator calls and pyrotechnics as acoustic mimics of predators. The effects of using acoustic mimics alone are almost always short term (Bomford and O'Brien 1990). When such sounds are reinforced by a shooting or another real threat, the behavioral avoidance lasts much longer (Dolbeer et al. 2003). There are many mimic-model systems in nature. We have only to examine them to understand how unreinforced warnings come to be ignored. In nature, the general rule is that the model must be much more common than the mimic for the mimic to be regarded in the same perspective as the model. Otherwise, the animals learn to associate the characteristics of the mimic with the stimulus rather than those of the model; this is exactly the opposite of what is desired. In order to be effective, predator sounds must be associated regularly with predation; i.e., birds must be killed or suffer pain to reinforce the message of the acoustic signal.

CONCLUSIONS

Avian hearing encompasses a narrower range of frequencies than human hearing; within that range, avian hearing is less sensitive than human hearing. Birds cannot hear ultrasound (>20,000 Hz), but some can hear infrasound (<20 Hz).

By themselves, acoustic devices are ineffective or effective only for a short time at dispersing birds. To be useful, acoustic devices must be combined with other control techniques in an integrated management program. The most effective use of acoustic signals is when they are reinforced with activities that produce death or a painful experience to some members of the population. Such reinforcement will prevent birds from habituating to the auditory stimulus. Future research should be focused on determining the relative contributions of visual, acoustic, and lethal or painful experiences to deter birds when used in an integrated management program.

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