Invited Ideas

Fitness costs as well as benefits are important when considering responses to anthropogenic noise

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Trade-offs lie at the heart of behavioral ecology, with our ultimate understanding of many behaviors reliant on an assessment of both fitness benefits and costs. However, the rapidly expanding research literature on the impacts of anthropogenic noise (a recently recognized global pollutant) tends to focus on the benefits likely to be accrued by any resulting behavioral adaptations or plasticity. In particular, although studies investigating acoustic communication (the topic receiving the most attention to date) invariably discuss, and occasionally attempt to measure, the perceived benefits in terms of reduced masking that might arise from vocal adjustments by signalers, only rarely are the potential fitness costs even mentioned. The bias toward benefits prevents a full understanding of the consequences of anthropogenic noise, including the implications for population viability and community structure. Here, we argue for a greater consideration of fitness costs, outline a number of specific examples (reduced transmission distances, increased risk of predation/parasitism, altered energy budgets, loss of vital information), make suggestions about how to move forward, and showcase why a balanced view is as crucial in this field as any other aspect of behavioral ecology.

Key words: **acoustic communication, anthropogenic noise, costs and benefits, fitness, trade-offs, vocalizations.**

INTRODUCTION

Noise-generating human activities, such as urban development, transportation, and the exploitation of energy sources, increased considerably in the last century and have led to substantial changes in the acoustic landscape in both terrestrial and aquatic ecosystems (e.g., McDonald et al. 2006; Watts et al. 2007). A burgeoning number of studies have demonstrated that anthropogenic (man-made) noise can affect animals in various ways (see Tyack 2008; Barber et al. 2009; Slabbekoorn et al. 2010; Kight and Swaddle 2011); however, the topic receiving by far the greatest attention has been acoustic communication (Radford et al. 2012; Morley EL, Jones G, Radford AN, unpublished data). The possibility that signalers might alter their acoustic output as a consequence of anthropogenic noise has been suggested by correlational studies on a variety of taxa (e.g., birds: Slabbekoorn and Peet 2003; marine mammals: Parks et al. 2011; anurans: Vargas-Salinas and Amezquita 2013; fish: Picciulin et al. 2012; invertebrates: Lampe et al. 2012), with the strongest body of experimental evidence coming from avian research (e.g., Halfwerk, Bot, et al. 2011; Halfwerk, Holleman, et al. 2011; McLaughlin and Kunc 2013; Montague et al. 2013); here, we focus on bird vocalizations to illustrate our argument.

The most obvious way in which anthropogenic noise can disrupt acoustic communication is through masking, whereby there is an increase in the threshold for detection or discrimination of one sound in the presence of another (Brumm and Slabbekoorn 2005). Loss of clear and efficient transmission of acoustic information can create potential fitness costs, including those related to mate attraction and territory defense if song is masked (e.g., Halfwerk, Bot, et al. 2011), increased predation risk if detection of alarm calls is impaired (Lowry et al. 2012), and reduced reproductive success if parent–offspring or parent–parent communication is disrupted (Halfwerk et al. 2012; Leonard and Horn 2012). Consequently, adjustments resulting from both evolutionary adaptation (e.g., Luther and Baptista 2010) and behavioral plasticity (e.g., Gross et al. 2010) have been indicated in studies on a variety of avian species (Ortega 2012). For instance, evidence exists for anthropogenic noise–induced changes in vocal timing (Fuller et al. 2007), temporal structure (Halfwerk and Slabbekoorn 2009), amplitude (see Brumm and Zollinger 2011), frequency (see Slabbekoorn 2013), and complexity (Montague et al. 2013), and birds may also attempt to improve signal detection and discrimination by altering their choice of perch from which to vocalize (Halfwerk et al. 2012).

These vocal adjustments have often been described as adaptive in terms of a release from masking (Slabbekoorn and Ripmeester 2008), although there is some debate with respect to frequency

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shifts (Nemeth and Brumm 2010). More recent work has begun to test these perceived *benefits*, by calculating the increases in potential communication distances (e.g., Nemeth and Brumm 2009) and assessing reproductive output (Halfwerk, Bot, et al. 2011). Although direct evidence of fitness benefits remains scarce (Slabbekoorn 2013), less attention has been paid to the potential fitness *costs* arising from vocal adjustments made in response to anthropogenic noise. This issue was raised by Patricelli and Blickley (2006), but the majority of the 50 studies investigating the impacts of anthropogenic noise on bird vocal communication published since then (unpublished data) do not even mention the possibility of costs (see Nemeth and Brumm 2010; Halfwerk, Bot, et al. 2011; Halfwerk, Holleman, et al. 2011; Luther and Derryberry 2012; Proppe et al. 2012 for exceptions). We argue that both sides of the trade-off need careful consideration if the true effects of noise are to be determined.

POTENTIAL FITNESS COSTS

Vocal adjustments could result in many direct or indirect fitness costs; we highlight 4 general examples here.

Reduced transmission distances

Signals are shaped over time by the acoustic environment in which they are emitted, the "acoustic adaptation hypothesis" (Morton 1975). Changes in vocal parameters may therefore affect the level of attenuation and degradation, potentially reducing transmission through vegetation or into and out of a nest (Slabbekoorn 2004). As a specific example, high-frequency signals—favored in urban areas (e.g., Slabbekoorn and Peet 2003)—attenuate faster and are degraded more easily than low-frequency signals (Wiley and Richards 1982). Adjustments in the timing of when vocalizations are produced may also come at a cost to transmission distances. For instance, because sound transmits further and more reliably at dawn than at other times of the day, due to lower wind noise and fewer atmospheric fluctuations (e.g., Brown and Handford 2003), birds that shift their singing away from the dawn chorus may suffer by communicating to a more localized audience.

Increased risk of predation or parasitism

The alarm calls of small passerines are often suggested to utilize high frequencies because this renders the signaler more difficult to detect or locate by birds of prey (Marler 1955; Klump and Shalter 1984). Changes in frequency may therefore result in the caller being more at risk; ultimately, this could lead to selection for a reduction in alarm calling, with consequences for subsequent generations that learn to give and utilize alarm calls from experienced adults (Hollén and Radford 2009). For all vocalizations, an increase in amplitude and the duration of vocalizing will make the signaler more conspicuous and potentially more vulnerable to predators. Similarly, noise-driven changes in perch choice, such as vocalizing from higher or more exposed positions (see Halfwerk et al. 2012), could increase predation risk. More time spent vocalizing and louder sound production could also enhance the likelihood of brood parasitism if host vocal activity is used as a cue by parasites to locate nests (see Banks and Martin 2001).

Altered energy budgets

There is some evidence that it is metabolically costly to vocalize for longer (Gillooly and Ophir 2010), to produce high-amplitude songs

compared with those of lower amplitude (Oberweger and Goller 2001), and to shift songs to higher frequencies (Lambrechts 1996). Although the energy required for such vocal adjustments may not be as great as first assumed (see Ward et al. 2004; Zollinger et al. 2011), there could be consequences for growth, survival, and reproductive success if compensation does not occur. Moreover, spending more time foraging to compensate for increased energy consumption may itself increase predation risk (Lima and Dill 1990), enhance the likelihood of foraging errors (see Purser and Radford 2011), and reduce opportunities for other important activities such as preening (Tieleman and Williams 2002). If insectivorous birds sing at dawn because prey are hardest to detect at times of low light intensities and reduced invertebrate activity (Kacelnik and Krebs 1983), then a diel shift in singing may also result in foraging at less optimum times.

Loss of vital information

The auditory sensitivity of a species is often tightly tuned to the frequencies used in communication (e.g., Okanoya and Dooling 1988), and thus the efficacy of perception by receivers may be impaired by noise-induced vocal changes. Moreover, because mate choice and male–male competition are often based on assessments of song characteristics, with higher quality indicated by such aspects as high amplitude (Brumm and Ritschard 2011; but see Nemeth et al. 2012), low frequency (Halfwerk, Bot, et al. 2011; but see Eens et al. 2012), broad bandwidth (Ballentine et al. 2004), and large repertoire size (Krebs et al. 1978), changes to acoustic structure and output could have direct consequences for reproductive success. Alterations in one song component in response to changes in the acoustic environment could also restrict the elaboration of other characteristics, which are preferred by females (Gross et al. 2010), thus indirectly impacting fitness. For instance, singing more loudly may compromise the ability to generate a high song rate and longer song duration (Wasserman and Cigliano 1991), whereas an increase in minimum frequency could constrain song complexity (Montague et al. 2013). Misjudging quality during mate choice may result in rejection of high-quality mates and less time spent raising the offspring, with impacts on their success, if a low-quality mate is selected (Halfwerk, Holleman, et al. 2011). In male–male competition, signalers may be attacked more often if perceived as less aggressive, and receivers may mistakenly attack males that are stronger or have a higher motivation to fight than anticipated (Ripmeester et al. 2007). Song matching may also be an important aggressive signal in male–male competition (Krebs et al. 1981), and a male that drops low-frequency songs from his repertoire may not possess the song types required to match conspecific rivals.

These fitness costs introduce a series of trade-offs for individuals. For example, although low-frequency songs might be favored by sexual selection, anthropogenic noise could exert a natural selection pressure for high-frequency songs; there may be a choice between being heard by many or being perceived as high quality by a few (Halfwerk, Bot, et al. 2011). The preference could be molded by the fundamental need of females to mate, with a signal that is heard being at a selective advantage compared with one that is not heard, even if the quality communicated is lower. Other methods of assessment could then be developed, or other existing signals relied on to a greater extent, to restore the element of choice in the future.

POPULATION AND COMMUNITY CONSEQUENCES

All members of a population are unlikely to suffer the same costs associated with vocal adjustments. For instance, alterations that are energetically costly may be more easily borne by higher quality individuals (Zahavi 1975), which might give them further advantages in terms of female choice and male–male competition. However, if anthropogenic noise results in the loss of certain acoustic features that are used as honest indicators of quality, such as low-frequency song elements, then discrimination between different males becomes harder and lower quality males may be less easily dismissed. Ultimately, the exact nature of the cost will also depend on whether, and how quickly, a corresponding shift in assessment and preference by receivers occurs. Because females often have a preference for songs similar to those of their father or that were heard frequently during a learning period (Catchpole and Slater 2008), it is feasible that preference in this context at least could shift passively over a few generations simply through subadult experience.

In general, the effect of vocal adjustment on fitness will differ between species depending on 1) inherent vocal characteristics that vary the amount of adjustment needed, 2) the relevant sexual signals used that could be disrupted by adjustment, 3) the plasticity of song learning and corresponding plasticity in assessment, and 4) the inherent suitability of a species to persist in urban environments. For instance, there is a positive relationship between the existing vocal frequency range of a species and its response to noise (Hu and Cardoso 2010; Francis et al. 2011), and it is likely that naturally loud vocalizations also convey an advantage. Moreover, only a relatively small percentage of bird species are thought to be urban-adaptable (Johnston 2001). The different costs and benefits faced by different species in relation to anthropogenic noise will have consequences for community structure and functioning (Francis et al. 2009).

MOVING FORWARD

Ultimately, the assessment of fitness consequences requires measurement of reproductive success and survival. These are logistically challenging to determine, especially if the specific impact of a particular response, in this case vocal adjustments, is targeted. However, studies focusing on other, but related, questions have assessed such variables as pairing success (Habib et al. 2007; Gross et al. 2010), clutch size and fledging success (Francis et al. 2009; Halfwerk, Holleman, et al. 2011), and female fidelity (Halfwerk et al. 2012); care is needed to ensure that such effects are not the result of differential use of areas by individuals of different qualities (see Slabbekoorn 2013). Using playbacks at nests, or perhaps presentation of models, also offer opportunities to assess how different vocalizations affect predation or parasitism rates (see Haff and Magrath 2011).

If the fitness benefits and costs of responses to anthropogenic noise are to be determined, studies need to include several key elements (see also Slabbekoorn 2013). First, potential confounding factors must be ruled out; correlational work comparing, for instance, rural and urban areas or habitats at different distances from roads, cannot isolate noise as the reason for any differences found. Instead, naturally matched areas where only the noise differs (see Francis et al. 2009, 2011) or experimental manipulations (e.g., Halfwerk, Bot, et al. 2011; Halfwerk, Holleman, et al. 2011; McLaughlin and Kunc 2013; Montague et al. 2013) are required. Second, to assess cumulative effects and consider the possibility that responses

change due to processes such as habituation, tolerance, and sensitization (Bejder et al. 2009), experiments over an extended period of time should ideally be conducted (e.g., Blickley et al. 2012), although they are more difficult to implement than short-term, acute exposures. Third, proper levels of replication are required; if strong conclusions are to be drawn about population-level consequences, then data from multiple sites, as well as multiple individuals, are needed (see Slabbekoorn 2013). In addition, to maximize the usefulness of studies investigating the impact of anthropogenic noise, the noise source should be characterized as fully as possible (reporting, for instance, dB, any weighting function, integration time and temporal variation, along with power spectra and spectrograms) and utilize equipment that best reflects the auditory capabilities of the study animal (see Schaub et al. 2009).

CONCLUSIONS

The human population is projected to increase by 2.3 billion between 2011 and 2050, with urban areas likely to absorb most of this growth (United Nations 2011). Noise pollution is thus both a pressing issue and one of ever-increasing concern. Ultimately, we need assessments of how anthropogenic noise affects individual fitness, population viability, and community structure. As with any aspect of behavioral ecology, this will only be possible if we consider both the benefits and costs arising from adjustments made in response to noise. Our aim is to stimulate a more balanced approach with respect to this trade-off; although we have illustrated our argument with reference to vocal signaling in birds, the principles apply across taxonomic groups and are relevant to all noise-induced behavioral changes.

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REFERENCES

Ballentine B, Hyman J, Nowicki S. 2004. Vocal performance influences female response to male bird song: an experimental test. Behav Ecol. 15:163–168.

Banks AJ, Martin TE. 2001. Host activity and the risk of nest parasitism by brown-headed cowbirds. Behav Ecol. 12:31–40.

Barber JR, Crooks KR, Fristrup KM. 2009. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol Evol. 25:180–189.

Bejder L, Samuels A, Whitehead H, Finn H, Allen S. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Mar Ecol Prog Ser. 395:177–185.

Blickley JL, Blackwood D, Patricelli GL. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of Greater Sage-Grouse at leks. Conserv Biol. 26:461–471.

Brown TJ, Handford P. 2003. Why birds sing at dawn: the role of consistent song transmission. Ibis. 145:120–129.

Brumm H, Ritschard M. 2011. Song amplitude affects territorial aggression of male receivers in chaffinches. Behav Ecol. 22:310–316.

Brumm H, Slabbekoorn H. 2005. Acoustic communication in noise. Adv Study Behav. 35:151–209.

Brumm H, Zollinger SA. 2011. The evolution of the Lombard effect: 100 years of psychoacoustic research. Behaviour. 148:1173–1198.

Catchpole CK, Slater PJB. 2008. Bird song: biological themes and variations. Cambridge (MA): Cambridge University Press.

Eens M, Rivera-Gutierrez HF, Pinxten R. 2012. Are low-frequency songs sexually selected, and do they lose their potency in male–female interactions under noisy conditions? Proc Natl Acad Sci USA. 109:208.

Francis CD, Ortega CP, Cruz A. 2009. Noise pollution changes avian communities and species interactions. Curr Biol. 19:1415–1419.

Francis CD, Ortega CP, Cruz A. 2011. Noise pollution filters bird communities based on vocal frequency. PLoS One. 6:e27052.

Fuller RA, Warren PH, Gaston KJ. 2007. Daytime noise predicts nocturnal singing in urban robins. Biol Lett. 3:368–370.

Gillooly JF, Ophir AG. 2010. The energetic basis of acoustic communication. Proc R Soc Lond B. 277:1325–1331.

Gross K, Pasinelli G, Kunc HP. 2010. Behavioral plasticity allows short-term adjustment to a novel environment. Am Nat. 176:456–464.

Habib L, Bayne EM, Boutin S. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. J Appl Ecol. 44:176–184.

Haff TM, Magrath RD. 2011. Calling at a cost: elevated nestling calling attracts predators to active nests. Biol Lett. 7:493–495.

Halfwerk W, Bot S, Buikx J, van der Velde M, Komdeur J, ten Cate C, Slabbekoorn H. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proc Natl Acad Sci USA. 35:14549–14554.

Halfwerk W, Bot S, Slabbekoorn H. 2012. Male great tit song perch selection in response to noise-dependent female feedback. Func Ecol. 26:1339–1347.

Halfwerk W, Holleman LJM, Lessells CM, Slabbekoorn H. 2011. Negative impact of traffic noise on avian reproductive success. J Appl Ecol. 28:210–219.

Halfwerk W, Slabbekoorn H. 2009. A behavioral mechanism explaining noise-dependent frequency use in urban birdsong. Anim Behav. 78:1301–1307.

Hollén LI, Radford AN. 2009. The development of alarm call behaviour in mammals and birds. Anim Behav. 78:791–800.

Hu Y, Cardoso GC. 2010. Which birds adjust the frequency of vocalizations in urban noise? Anim Behav. 79:863–867.

Johnston RF. 2001. Synanthropic birds of North America. In: Marzluff JM, Bowman R, Donnelly R, editors. Avian ecology in an urbanizing world. Norwell (MA): Kluwer Academic Publishers. p. 49–67.

Kacelnik A, Krebs JR. 1983. The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. Behaviour. 83:287–309.

Kight CR, Swaddle JP. 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecol Lett. 14:1052–1061.

Klump GM, Shalter MD. 1984. Acoustic behaviour of birds and mammals in the predator context: I. Factors affecting the structure of alarm signals. II. The functional significance of alarm signals and their evolution. Z Tierpsychol. 66:189–226.

Krebs JR, Ashcroft R, Van Orsdol K. 1981. Song matching in the great tit *Parus major*. Anim Behav. 29:918–923.

Krebs JR, Ashcroft R, Webber MI. 1978. Song repertoires and territory defence. Nature. 271:539–542.

Lambrechts MM. 1996. Organisation of birdsong and constraints on performance. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 305–320.

Lampe U, Schmoll T, Franzke A, Reinhold K. 2012. Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. Funct Ecol. 26:1348–1354.

Leonard ML, Horn AG. 2012. Ambient noise increases missed detections in nestling birds. Biol Lett. 8:530–532.

Lima SL, Dill LM. 1990. Behavioural decisions made under the risk of predation—a review and prospectus. Can J Zool. 68:619–640.

Lowry H, Lill A, Wong BBM. 2012. How noisy does a noisy miner have to be? Amplitude adjustments of alarm calls in an avian urban 'adapter'. PLoS One. 7:e29960.

Luther D, Baptista L. 2010. Urban noise and the cultural evolution of bird songs. Proc R Soc Lond B. 277:469–473.

Luther DA, Derryberry EP. 2012. Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication. Anim Behav. 83:1059–1066.

Marler P. 1955. Characteristics of some animal calls. Nature. 176:68.

McDonald MA, Hildebrand JA, Wiggins SM. 2006. Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California. J Acoust Soc Am. 120:711–718.

McLaughlin KE, Kunc HP. 2013. Experimentally increased noise levels change spatial and singing behaviour. Biol Lett. 9:20120771.

Montague MJ, Danek-Gontard M, Kunc HP. 2013. Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. Behav Ecol. 24:343–348.

Morton ES. 1975. Ecological sources of selection on avian sounds. Am Nat. 109:17–34.

Nemeth E, Brumm H. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? Anim Behav. 78:637–641.

Nemeth E, Brumm H. 2010. Birds and anthropogenic noise: are urban songs adaptive? Am Nat. 176:465–475.

Nemeth E, Kempenaers B, Matessi G, Brumm H. 2012. Rock sparrow song reflects male age and reproductive success. PLoS One. 7:e43259.

Oberweger K, Goller F. 2001. The metabolic cost of birdsong production. J Exp Biol. 204:3379–3388.

Okanoya K, Dooling RJ. 1988. Hearing in the swamp sparrow *Melospiza georgiana*, and the song sparrow *Meospiza melodia*. Anim Behav. 36:726–732.

Ortega CP. 2012. Effects of noise pollution on birds: a brief review of our knowledge. Ornith Monogr. 74:6–22.

Parks SE, Johnson M, Nowacek D, Tyack PL. 2011. Individual right whales call louder in increased environmental noise. Biol Lett. 7:33–35.

Patricelli GL, Blickley JL. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk. 123:639–649.

Picciulin M, Sebastianutto L, Codarin A, Calcagno G, Ferrero EA. 2012. Brown meagre vocalization rate increases during repetitive boat noise exposures: a possible case of vocal compensation. J Acoust Soc Am. 132:3118–3124.

Proppe DS, Avey MT, Hoeschele M, Moscicki MK, Farrell T, St Clair CC, Sturdy CB. 2012. Black-capped chickadees *Poecile atriapillus* sing at higher pitches with elevated anthropogenic noise, but not with decreasing canopy cover. J Avian Biol. 43:325–332.

Purser J, Radford AN. 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). PLoS One. 6:e17478.

Radford AN, Morley EL, Jones G. 2012. The effects of noise on biodiversity. Defra Report NO0235 [cited 2013 September 19]. Available from: http://randd.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=None&Completed=O&ProjectID=18136.

Ripmeester EAP, Vries AM, Slabbekoorn H. 2007. Do blackbirds signal motivation to fight with their song? Ethology. 113:1021–1028.

Schaub A, Ostwald J, Siemers BM. 2009. Foraging bats avoid noise. J Exp Biol. 211:3174–3180.

Slabbekoorn H. 2004. Singing in the wild: the ecology of birdsong. In: Marler P, Slabbekoorn H, editors. Nature's music—the science of birdsong. San Diego (CA): Elsevier Academic Press. p. 178–205.

Slabbekoorn H. 2013. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim Behav. 85:1089–1099.

Slabbekoorn H, Bouton N, van Opzeeland I, Coers A, ten Cate C, Popper AN. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol Evol. 25:419–427.

Slabbekoorn H, Peet M. 2003. Birds sing at a higher pitch in urban noise. Nature. 424:267.

Slabbekoorn H, Ripmeester EAP. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Mol Ecol. 17:72–83.

Tieleman BI, Williams JB. 2002. Effects of food supplementation on behavioural decisions of hoopoe-larks in the Arabian Desert: balancing water, energy and thermoregulation. Anim Behav. 63:519–529.

Tyack PL. 2008. Implications for marine mammals of large-scale changes in the marine acoustic environment. J Mamm. 89:549–558.

United Nations. 2011. World urbanization prospects: the 2011 revision. New York: United Nations [cited 2013 September 19]. Available from: http://esa.un.org/unup/pdf/WUP2011_Highlights.pdf.

Vargas-Salinas F, Amezquita A. 2013. Traffic noise correlates with calling time but not spatial distribution in the threatened poison frog *Andinobates bombetes*. Behaviour. 150:569–584.

Ward S, Lampe HM, Slater PJB. 2004. Singing is not energetically demanding for pied flycatchers, *Ficedula hypoleuca*. Behav Ecol. 15:477–484.

Wasserman FE, Cigliano JA. 1991. Song output and stimulation of the female in white-throated sparrows. Behav Ecol Sociobiol. 29:55–59.

Watts RD, Compton RW, McCammon JH, Rich CL, Wright SM, Owens T, Ouren DS. 2007. Roadless space of the conterminous United States. Science. 316:736–738.

Wiley RH, Richards DG. 1982. Adaptations for acoustic communication in birds: sound propagation and signal detection. In: Kroodsma DE, Miller EH, editors. Acoustic communication in birds. Vol. 1. New York: Academic Press. p. 131–181.

Zahavi A. 1975. Mate selection: selection for a handicap. J Theor Biol. 53:205–214.

Zollinger SA, Goller F, Brumm H. 2011. Metabolic and respiratory costs of increasing song amplitude in zebra finches. PLoS One. 6:e23198.