

The emerging significance of bioacoustics in animal species conservation

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ABSTRACT

This review reports on the effects of human activities on animal acoustic signals published in the literature from 1970 to 2009. Almost 5% of the studies on variation in animal communication tested or hypothesized on human impacts, and showed that habitat fragmentation, direct human disturbance, introduced diseases, urbanization, hunting, chemical and noise pollution may challenge animal acoustic behaviour. Although acoustic adaptations to anthropogenic habitats have been documented, human impacts have most often generated neutral variation or potential maladaptive responses. Negative impacts have been postulated in the sexual signals of fishes, amphibians, birds, and mammals; these are concerning as any maladaptive alteration of sexual behaviour may have direct bearings on breeding success and ultimately population growth rate. Acoustic communication also facilitates other vital behaviours influenced by human-driven perturbations. Bat and cetacean echolocation, for instance, is disrupted by noise pollution, whereas bird and mammal alarming is also affected by introduced diseases and hunting. Mammal social signals are sensitive to noise pollution and hunting, and birds selecting habitats by means of acoustic cues are especially vulnerable to habitat loss. Anthropogenic intervention in these cases may have a negative impact on individual survival, recruitment and group cohesion, limiting rescue effects and triggering Allee effects. Published evidence shows that acoustic variation may be used as an early-warning indicator of perturbations even when not directly affecting individual fitness. Acoustic signalling can be studied in a broad range of ecosystems, can be recorded, analyzed, synthesised and played back with relative ease and limited economic budget, and is sensitive to many types of impacts, thus can have great conservation significance.

Key-words: Conservation bioacoustics, animal behaviour, mating systems, calls, sexual selection, small populations

1. Introduction

Communication, the way organisms convey information to each other, is the gel that holds animal societies together: it facilitates reproduction, provides information on individual identity, status, mood and intentions (Bradbury and Vehrencamp 1998). As it includes a substantial proportion of the behavioural repertoire of animal species, communication behaviour can become an important driver of several aspects of species biology, affecting the evolution of life histories and genes.

Along with several other animals, humans share the use of sounds as the principal means of exchanging information. Many vertebrates (bony fishes, amphibians, reptiles, birds, mammals) and invertebrates (insects, spiders, crustaceans, nematodes) make sounds (or vibrations) for a variety of reasons, mostly for courtship and agonistic behaviours, but also for more complex social communication (Hauser 1997, Owings et al. 1998). Many birds (oscines, some sub-oscines, trochilids and psittacines) and some mammals (cetaceans, primates, bats) may acquire important components of their acoustic repertoires by copying others, while this behaviour is thought to be innate in the other taxonomic groups (Kroodsma and Baylis 1982, Janik and Slater 1997). As an example, birdsong was the first ‘cultural’ trait (i.e. acquired through social learning) to be described in non-human animals, based on evidence dating back to Aristotle (Laland and Galef 2009).

Acoustic signals are particularly well suited for studying the evolution of animal communication because of the relative ease with which sounds can be recorded and analyzed, synthesised and played back with efficiency (Gerhardt and Huber 2002). Animal sounds have indeed served as models to address essential evolutionary questions, such as the way sexual selection operates and intervenes in speciation processes and the way natural selection shapes animal interactions (Kroodsma and Miller 1996). In spite of being the target of many evolutionary studies, the role of animal vocalizations has been less significant in applied ecological research (Terry et al. 2005). Until the last decade, their use has been limited to

acoustic surveys and censuses to detect vocal species of birds, mammals, amphibians and insects. Bioacoustics has also been used to generate basic demographic variables through the vocal identification of individuals, or estimate species occurrence and richness in those cryptic taxa characterized by species-specific acoustic signals (see also Caro (1998), Vaughan et al. (1997), Gaunt and McCallum (2004)).

More recently, bioacousticians have begun to tackle the questions of how human activities challenge the communication systems of animal species, what are the stochastic or deterministic mechanisms involved (natural, sexual or social selection processes), and what information of conservation significance can be derived by studying animal sounds (Rabin and Greene 2002, Slabbekoorn & Ripmeester 2008, Laiolo et al. 2008). A similar drive determined the development of '*Conservation Behaviour*', a discipline that combines applied and baseline research to address the behavioural mechanisms that influence the fate of populations and species (Curio 1996, Buchholz 2007, Caro 2007).

The aim of this review is to collect recent literature on the impact of human activities on animal communication, and provide an overview of the potential of bioacoustics in conservation science. Based on published evidence, I discuss the type of information that could be extracted from animal sounds which may be relevant to species conservation and population ecology, and highlight a series of troublesome cases, in which acoustic variation may cause conservation problems and affects population persistence. Finally, I discuss how acoustic signals can be used in conservation studies as early-warning indicators of ongoing human-driven perturbations or to monitor population processes.

2. Bibliographic Search

The overview is based on a Thompson's ISI Web of Science search of journals within the subject categories of 'Zoology', 'Ecology', 'Multidisciplinary Sciences', 'Behavioural Science', 'Acoustics', 'Biology', 'Marine and Freshwater Biology', 'Evolutionary Biology',

‘Ornithology’, and ‘Environmental Science’ from 1970 to 2009. As a variety of human impacts has been proven to affect animal communication and no single search term could define them, I started with a broad search of the terms CALL or SONG or VOCAL* or ACOUST* and VARIATION, and refined the search to the subject categories mentioned above. I checked 1711 papers on acoustic communication variation, and identified those titles and abstracts with conservation relevance (see also Results).

By checking literature, I classified human-driven effects according to the potential consequences for individual fitness or population persistence, on the basis of the conclusions of the authors themselves. I found that some species deal well with anthropogenic change and adapt their communication system to the novel conditions imposed by humans. In contrast, other species respond maladaptively, with deleterious consequences for individual fitness (such as reduced survival or mating success). In other cases, human driven variation is neutral, e.g. differentiation does not affect individual fitness.

3. Results

I found that 53 papers explicitly focused on human-driven alterations (excluding review papers). For simplicity, I refer to these studies as ‘Conservation Bioacoustics’ papers. In the remaining titles of the search, I paid special attention to those of a more descriptive nature, which dealt with intra-specific acoustic variation. I searched here for inadvertent comparisons among natural and anthropogenic habitats, populations separated by anthropogenic barriers or differently affected by human impact. I found that 23 of the 406 descriptive papers read (5.7%) speculated on some anthropogenic causes to explain the patterns of acoustic variation found, as an alternative to other ecological or evolutionary hypotheses. Although these studies do not directly address conservation issues in the title, nor sometimes in the abstract, they do testify to the pervasiveness of human impact even in many behavioural study fields, which in theory tends to restrict the sources of variation to those of evolutionary significance.

The number of papers testing or hypothesising on human impact was therefore 76, less than 5% of the studies on variation in animal communication behaviour. Literature is summarized in Table 1, which reports the type of anthropogenic impact, the underlying mechanisms (internal mechanisms, demographic processes, etc.), the taxon affected, and the potential problems derived from acoustic variation. The types of impact were diverse: noise pollution (47.3% of papers), habitat fragmentation and degradation (40.8% of papers), direct human disturbance (2.6%), hunting (2.6%), chemical pollution (2.6%), introduced diseases (1.3%) and food supplementation (1.3%). Overall, 55 species were affected, mostly birds (66% of species) and mammals (24%) and, less frequently, arthropods, amphibians and fishes. Some species responded to multiple impacts, such the Great Tit *Parus major*, whose song structure proved to vary in response to both urban noise and chemical pollution (Gorissen et al. 2005, Slabbekoorn & den Boer-Visser 2007).

Adaptive variation to counteract human impact was recorded in 27.6% of the 76 papers considered, and was mostly described in noise pollution cases. Deleterious or neutral effects for individuals or populations were advocated in 28.9% and 43.4 % of cases, respectively. A few studies only detailed adverse consequences using an experimental approach, and in most of the study cases evidence was correlative (Markman et al. 2008, Schaub et al. 2008).

Species that learn to vocalize through imitation and do not depend solely on innate signals, such as some birds and mammals, provided the most examples of plastic acoustic shifts and adaptive responses. Luther & Baptista (2009) in their study on the urban white crowned sparrow *Zonotrichia leucophrys* showed that acoustic responses to habitat alteration can occur over very short times (30 years), a lag that is shorter than that proposed for the evolution of heritable traits under anthropogenic pressure (a few hundred generations, Stockwell et al. 2003). Notably, maladaptive responses have also been recorded in species of mammals and birds that learn their vocalizations, and groups whose signals are innate were

also capable of adaptive shifts, suggesting that cultural transmission alone is not a prerequisite for successful adaptations to human altered environments.

The number of conservation bioacoustics papers (i.e. studies specifically addressing a conservation problem) increased greatly in the years 2000-2003; it is in this period that Slabbekoorn & Peet (2003) published in *Nature* a study on Great Tit song shifts to avoid city masking noise (Fig. 1). In the following years more than 60% of the conservation bioacoustics papers addressed man-made noise in terrestrial systems. The 23 papers hypothesising human-driven acoustic variation without explicitly focusing on human impact were significantly older (median year 2000 *versus* 2006 of Conservation Bioacoustics studies, Mann Whitney U-test, $U = 349$, $P = 0.004$). They most frequently dealt with acoustic variation following anthropogenic separation (or mixing) of once interconnected populations (69% of the 23 papers).

4. Discussion

In the following sections (4.1-4.7) I consider each anthropogenic vector of acoustic change and discuss the consequences for individuals and populations. When the species response (or lack of response) critically affects the fate of populations living in human-transformed ecosystems, the acoustic shift has great conservation significance. When human-driven acoustic variation is not directly affecting individual fitness or population viability, it could still serve in a conservation context, as it may provide evidence of anthropogenic changes underway. Studies in which sounds have been used to monitor populations or as indicators of human-driven perturbations are illustrated in Section 4.8.

4.1 Acoustic signals and noise pollution

Anthropogenic noise is the impact that most directly disrupts and affects the acoustic modality of communication. Sounds produced by urban traffic, motorways, wind farms, etc. in terrestrial habitats, and boats, whale watching, military sonar, etc. in marine habitats have been shown to interfere with the detection and discrimination of crucial signals among

individuals (Richardson et al. 1995, Barber et al. 2009). Passerine birds and marine mammals were the target of the first studies and numerous reviews and updates have already been published on the subject (Myrberg 1990, Richardson et al. 1995, Katti and Warren 2004, Brumm and Slabbekoorn 2005, Patricelli and Blickley 2006, Warren et al. 2006, Nowacek et al. 2007, Slabbekoorn and Ripmeester 2008, Hu and Cardoso 2009). Recently, evidence has also been gathered for other groups, such as terrestrial mammals, frogs and bony fishes (Barber et al. 2009).

Terrestrial and freshwater habitats

The acoustic behaviour of urban-dwelling birds is an example of the adaptation of wildlife to urban habitats: to avoid masking traffic noise, a number of bird species have shifted song frequencies, duration, amplitudes and timing of singing (references quoted in Table 1). These adjustments represent adaptive responses to the evolutionary novel habitat represented by cities, and probably depend upon the learning process itself and the plasticity of singing behaviour, although microevolutionary (genetic) changes may be occurring as well (Brumm 2006).

It has been suggested that song switches in urban habitats may lead to trade-offs between natural selection, which determines signal-habitat acoustic matching, and sexual selection for 'attractive' signals (Slabbekoorn and Ripmeester 2008). This problem may arise when high-pitched sounds broadcast better in noisy environments, but low-pitched sounds better advertise individual quality to competitors and potential mates, as they signal a large body size (Ryan and Brenowitz 1985). Frequency shifts in the noisiest environments can make males less attractive to mates or less effective in avoiding territorial intrusions, with negative consequences in terms of individual fitness (Slabbekoorn and Ripmeester 2008).

Not all passerines can change their signals to communicate in noisy habitats, especially large birds that face constraints in producing higher pitched vocalizations, and avoid patches that are characterized by high levels of anthropogenic noise (Rheindt 2003, Bayne et al. 2008,

Hu & Cardoso 2009). Other species do settle but pay fitness costs because they are unable to communicate properly in noisy conditions (Habib et al. 2007). Swaddle and Page (2007), by studying zebra finches *Taeniopygia guttata*, found that pair bonds may become weaker and extra-pair behaviour increases in noisy environments because noise masks pair-bond calls. Interpreted from a population ecology perspective, noise may contribute to the creation of ecological traps in habitats otherwise suitable for feeding or nesting.

In the few cases reported for amphibians, some species have been found to adjust their temporal or frequency call structure to increase the efficiency of information transfer in noisy habitats (Tab. 1; Kaiser and Hammers 2009, Parris et al. 2009). As in the case of birds, frogs calling at higher pitches in traffic noise may face trade-offs between audibility (achieved through high frequencies) and attractiveness to potential mates (attained by giving lower frequencies calls) (Parris et al. 2009). The Tree frog (*Hyla arborea*), the Taipei frog (*Rana taipehensis*) and the Lusitanian toadfish (*Halobatrachus didactylus*) showed no acoustic adaptation but rather reduced sound emission in noisy environments (Sun & Narins 2005, Vasconcelos et al. 2007, Lengagne 2008). Although the fitness costs of reduced activity have not been analysed in detail, some effects on mate choice, territory defence and ultimately reproductive success can be expected, given that the affected species mostly relies on acoustic signals for pair formation and antagonistic disputes (Lengagne 2008).

Apart from affecting sexual signalling, noise also influences foraging and anti-predator acoustic behaviours. Traffic noise can mask rustling sounds made by moving arthropods, eventually reducing the foraging efficiency of bats, which depend on echolocation for feeding (echolocation is a form of acoustic auto-communication; Schaub et al. 2008). On the other hand, wind farm noise has been shown to affect acoustic alarming and vigilance in the California ground squirrel (Rabin et al. 2006).

Marine environment

Even in large areas of the oceans where there are no nearby sources of human-made noise, background noise levels are several decibels above preindustrial levels (Richardson et al. 1995). This makes noise pollution one of the most serious concerns in the conservation of cetacean species, which depend almost exclusively on acoustic information for communication, feeding and orientation (Zacharias and Gregr 2005). As for birds, some marine mammals have responded to noise disturbance by changing the type or timing of vocalizations relative to the noise source; these are mostly whales whose communication channel overlaps with low-frequency human-made noise (see Table 1 for literature). The response of dolphins and pinniped species varies from hearing damage to shifts in surfacing, diving and heading patterns, or displacement to less noisy areas (Nowacek et al. 2007). In the long run, the repeated disturbance of vital activities such as breeding, communicating and feeding may severely affect individuals and generate population-level problems (Myrberg 1990).

4.2 Acoustic signals and habitat fragmentation

Habitat isolation, habitat loss, and changes in the composition of the habitat matrix are just some of the patterns in habitat fragmentation that can determine demographic processes, by separating individuals, conditioning population size, determining inbreeding, altering age class distribution and affecting dispersal and recruitment (MacNally et al. 2000, Fahrig 2001). These processes can indirectly promote differentiation in the way organisms communicate to each other, as shown by the study cases documented below.

Habitat isolation

Isolation is an important driver of sound variation, especially when cultural evolution shapes animal communication (Laiolo and Tella 2006). When two or more populations become isolated and signals follow a cultural transmission pattern, the acoustic behaviours of isolated nuclei can differentiate because of learning mistakes or innovations within the repertoire of each local population, a phenomenon that may be determined either by deterministic (natural

selection) or stochastic processes (Rendell and Whitehead 2003, Podos and Warren 2008). Bird ‘dialects’ are an example of such a process: they represent marked local song differences among populations separated by some type of barrier. Natural barriers are of course a common cause of differentiation, but anthropogenic barriers and gradients can play some role, as shown in Table 1. In Australia, North and South America, populations of woodland passerines have differentiated their repertoires possibly as a result of habitat clearance occurring before or after the arrival of the Europeans (see Table 1 for literature). In general, the affected species are characterized by stable dialects, high site fidelity or limited dispersal, conditions under which the effects of isolation are not overshadowed by the homogenizing effect of cultural flow and the rapid turnover of dynamic repertoires.

Dialects are claimed as a classical example of neutral variation, because they often represent an incidental by-product of the stochastic evolution of isolated nuclei (Slater 1986, Whitehead et al. 2004). In some instances, however, dialects can speed up the isolation of local pools, for instance when population-level song preferences exist and home dialects are favoured by females over foreign dialects (Grant and Grant 1996). Acoustic differentiation in these cases may contribute to the formation of reproductive barriers, with consequences for genetic diversity and gene flow. This argument is controversial and largely debated in evolutionary biology (Patten et al. 2004), but it is a worthy challenge also from a conservation point-of-view, to ascertain the role played by acoustic differentiation in the connectivity of meta-populations.

I found no evidence of isolation-driven variation in the communication behaviour of species that do not learn sounds (insects, fishes, amphibians, etc.), despite its being able to vary geographically under natural conditions.

Habitat loss

When habitats become fragmented, total habitat area is reduced in size and the remaining habitat becomes restricted to smaller patches, inhabited by small local populations (Bender et

al. 1998). Laiolo and Tella (2007) have shown that bird population decline can result in a drop in the diversity of syllables or song type pools through cultural erosion driven by anthropogenic habitat loss. Just as genetic drift, bottlenecks and inbreeding can lead to a loss in genetic variation in small populations, cultural drift, bottlenecks and the reduced possibility of learning from models may determine the loss of acoustic diversity in species that learn their vocalizations (Thielcke 1972; Mundinger 1980).

Signal variation in small populations can result as a by-product of ongoing genetic processes. In the field cricket *Teleogryllus commodus*, for instance, inbreeding depression can directly affect sound production and the acoustic properties of signals (Drayton et al. 2007). In other species, it is social selection that mediates the population size-acoustic behaviour relationship: a reduction of daily signalling activities can be observed in small populations where male-male competition and individual interactions are reduced (Osiejuk et al. 2007). In small populations of the wolf spider *Hygrolycosa rubrofasciata* the rate of courtship drumming (a form of sound transmission through the soil) dropped (Ahitiainen et al. 2004), whereas in those of the Dupont's lark *Chersophilus duponti* it was the daily vocal effort that declined considerably (Laiolo and Tella 2008). The same pattern was described in the populations of howler monkeys *Alouatta pigra* decimated by hurricanes (Pavelka et al. 2003).

Many of the signals mentioned above are important for ensuring breeding, thus any variation in their functional significance may have direct bearings on individual fitness and population growth rate. In small populations with poor signalling males, female choice under strong sexual selection may determine an exponential drop in the number of males that are regarded as appealing and acceptable as mates, determining the decline of the effective population size (N_e) (Blumstein 1998; Anthony and Blumstein 2000). On the other hand, if sexual selection is weak, mates may no longer be chosen on the basis of their signals, and the probability of fixing deleterious new mutations increases, eventually posing a threat to the population's genetic integrity (Whitlock 2000, Laiolo et al. 2008). In both conditions, a

variation in sexual signals that is not followed by a parallel shift in female choice may eventually bolster Allee effects.

Apart from their prime role in reproduction, many acoustic signals are also inadvertent cues that help dispersing individuals to locate good habitat patches. Sounds are used in this context by several bird species during territory or colony establishment to reduce search and settlement costs (Reed and Dobson 1993, Fletcher 2008). If conspecific attraction occurs and acoustic performance reflects habitat availability and suitability, dispersing individuals may avoid those populations where acoustic activities are depressed. Such behavioral mechanisms may have population-level consequences as they reduce rescue effects in small nuclei (Fletcher 2007, Laiolo and Tella 2008).

Transformation of the habitat matrix and edge effects

Habitat conversion and degradation often interact synergically in many rural landscapes (Laiolo 2005) and are here treated together. These transformations can lead to changes in species distribution or may alter demographic processes, in some cases impacting acoustic signals. Dialectal shifts or disappearance of dialect units have been documented in various farmland passerines as a consequence of large-scale displacement associated with agricultural rotations (see literature in Table 1). Smith et al. (2003) reported an effect of habitat matrix conversion on the dominant call frequency of the sunset frog *Spicospina flammocaerulea* populations. In this case, it was burning activities that induced changes in recruitment and age class distribution of populations, in turn affecting signal frequencies (*via* their allometry with body size and age; Ryan and Brenowitz 1985).

Shifts can also be induced by new selection pressures arising in novel habitats. Transformations like clear-cutting or abrupt rotations, by drastically altering vegetation structure, can disrupt the acoustic properties of the medium and challenge the communication systems of species that persist through disturbance. Successful adaptations or mismatches

were described in birds by Rabin and Greene (2002), Ljtnaer and Tubaro (2007), Wright et al. (2008).

The proliferation of edges is another consequence of habitat fragmentation, and a study on Dupont's lark shows that it can affect singing behaviour (Laiolo and Tella 2005). In this species, edges diminish the magnitude of aggressive interactions among individuals separated by small habitat barriers, and song copying decreases between males located at opposite sides of a barrier. This drop does not depend on the number of neighbours interacting, as suggested by Catchpole and Slater (2008) as an alternative explanation for this phenomenon.

4.3 Acoustic signals and chemical pollution

The exposure to and continued interaction with toxins affects brain development early in life and energy allocation in adults, two key processes that ultimately influence communication behaviour (Buchanan 2000). The effects of exposure to pollutants were analyzed on bird communication only, and appear to vary depending on the type of toxin and physiological mechanisms involved. Gorissen et al. (2005) have shown that Great Tits from areas polluted with heavy metals had smaller repertoires and sang less than birds from less polluted sites. In the European starling *Sturnus vulgaris*, Markman et al. (2008) studied the effects of the so-called 'endocrine disruptive chemicals' (EDCs), ubiquitous chemicals that include DDT and other organochlorine insecticides. These compounds are estrogen mimics, and when experimentally supplied to male starlings, determined the production of longer and more complex songs compared to control males, a volumetric increase of the brain nucleus associated with song production (HVC) and, ultimately, immunosuppression. In spite of their poor health, exposed males were preferred by females because of their complex songs, a paradox for the sexual selection theory centred on the honesty of sexual signals. Female choice in this case is maladaptive, given that their reproductive output may drop because poor condition mates are less efficient in caring for young. This study represents an example of

trade-offs between sexual and natural selection processes, and shows that polluted areas can turn into ecological traps for females of farmland bird populations.

4.4 Acoustic signals and direct human disturbance

Gutzwiller et al. (1994, 1997) and Bergen and Abs (1997) found out that human intrusion during breeding reduced the timing of male song in forest passerines. Because of the link between the timing of singing activities and that of territory establishment, pair formation and egg laying, Gutzwiller et al. (1994) hypothesised that intrusion may have detrimental effects on individual breeding success.

4.5 Acoustic signals and hunting

Wild animal populations have long been regulated through hunting by removing the oldest individuals, supposedly because they contribute less to population growth (Swenson 2003). In complex animal societies, however, old individuals may be the reservoir of cultural traditions (including social calls) that serve purposes for group recognition, breeding and survival. As an example, elephant families maintaining old matriarchs had greater reproductive success than families that did not, since among other factors, these old individuals preserved the entire tradition of social calls (McComb et al. 2001). Hence, poaching, by removing the oldest individuals, can severely compromise group breeding success due to the erosion of social traditions. Another example is provided by Slobodchikoff et al. (1998), who studied Gunnison's prairie dogs *Cynomys gunnisoni* from various geographic locations in the United States. The authors found that the alarms of this species may vary as a consequence of the different hunting pressures experienced by the colonies.

4.6 Acoustic signals and introduced diseases

The human-induced spread and infection of pox virus determined by contact with domestic fowls has been associated with changes in the acoustic structure of lesser short-toed lark *Calandrella rufescens* distress calls in the Canary Islands. Infection affected the condition-

dependent nature of these calls, which are used in an anti-predator context (Laiolo et al. 2004, Laiolo et al. 2007a).

4.7 Acoustic signals and food supplementation

Zanette et al. (2009) found that young Song Sparrows *Melospiza melodia* fed by food-supplemented parents sang less diverse songs than young from unfed parents, and discussed the possible negative effects of food-supplementing wild populations for conservation purposes. Supplemented parents laid larger clutches and lighter eggs, thus their young had to accelerate their growth more than control birds, at the detriment of their learning abilities and song output once they become adults.

4.8 Bioacoustics as a tool in conservation science

The studies documented above showed that acoustic variation can bring to light perturbations that are difficult to detect via other indicators. This information can be used by conservation biologists as a complement to other indirect indicators that have become popular in conservation issues, such as neutral genetic markers, which have no relationship to organism fitness or population persistence but are widely used as proxies of adaptive variation (Laiolo and Tella 2006). As an example, Ahitainen et al. (2004) and Laiolo et al. (2008) found an association between acoustic sexual performance and indices of population viability in vertebrate and invertebrate taxa. Long-term monitoring programmes and extensive studies (capture-recapture schemes, individual trapping, etc.) represent classic alternatives to obtaining viability estimates, but are often unaffordable when studying rare and cryptic species.

In Table 2 other examples of the potential uses of bioacoustics in conservation studies are provided, along with information on their applicability and potential limitations. A common application is the use of acoustic information to obtain basic demographic parameters in species difficult to observe or mark. Acoustic monitoring, for instance, can be used to track inter-population movements in geographically structured populations in bird species that

learn their vocalizations before dispersal, i.e. when individuals carry with them the natal acoustic repertoire during recruitment. Several behavioural studies have provided evidence of inter-patch movements by using this approach (see Table 2 for literature), an opportunity that could be seized by population ecologists to obtain baseline demographic information (Laiolo and Tella 2008). More specifically, individual recognition by means of the acoustic features of vocalizations can be achieved in several animal taxa, from frogs to mammals and birds, and is one of the best examples of the application of acoustic analysis to population monitoring (see Terry et al. 2005, and Gaunt and McCallun 2004 for a review). The identification of individual-specific acoustic features can permit the use of ‘acoustic signatures’ as an alternative to physical marks (rings, tags, etc.) in studies on dispersal distance, site fidelity, survival and abundance (Gilbert et al. 2002, Tripp and Otter 2006, Laiolo et al. 2007b, Vögeli et al. 2008). Recent years have seen the continuous implementation of bioacoustics technology for large-scale automated monitoring programs, to identify individuals or species for use in population ecology / biodiversity studies, or in wildlife management (Dawson and Efford 2009, Efford et al. 2009).

Ultimately, playbacks of acoustic cues have been successfully employed in bird species management plans, to attract individuals and promote territory establishment in suitable but empty habitat patches through the exploitation of conspecific attraction behaviour (Ward and Schlossberg 2004, Alhering et al. 2006, Hahn and Silverman 2007, Fletcher 2008; see also section 4.2).

5. Conclusions

A variety of human impacts can affect animal communication systems by triggering stochastic or deterministic forces of evolutionary or ecological change. The findings of this overview show that communication may become a mechanism that negatively affects population persistence in some instances, resulting in a conservation dilemma. All acoustic

traits associated with (or mediating) aspects of reproductive success, survivorship and/or recruitment can indirectly affect population growth rates and are therefore relevant for population persistence and conservation. Sexual signals (like birdsong, frog calling, spider drumming) may have direct bearings on reproduction as they primarily mediate sexual interactions. These sounds, taking part in mate competition/attraction, are often costly to produce and can impose substantial fitness costs at the individual level. When humans alter natural processes, the selection load generated by the evolution of mating signals via sexual selection may rise above natural levels and may impact population viability, increasing the risk of extinctions (Tanaka 1996, Morrow and Pitcher 2003). Examples provided above show that sexual selection in some circumstances may slow adaptation processes to novel environmental conditions (Slabbekoorn and Ripmeester 2008, Parris et al. 2009), bolster behaviourally-mediated Allee effects when population size declines (Laiolo et al. 2008), and maintain poorly viable wild populations in degraded areas (Markman et al. 2008).

Apart from breeding, acoustic communication also facilitates other vital behaviours, such as foraging and orientation (echolocation), anti-predator defence (alarming), habitat selection and settlement decisions through acoustic social information. By disrupting signals that facilitate these activities, anthropogenic intervention can eventually generate population-level problems by reducing individual survival (Rabin et al. 2006, Laiolo et al. 2007), limiting rescue-effects and metapopulation connectivity or populations' ability to withstand environmental degradation (Laiolo & Tella 2008).

Studies reported in Section 4.8 and Table 2 demonstrate that bioacoustics have also begun to define a methodology for the use of conservation biologists and wildlife managers, renovating its traditional evolutionary perspective to serve as a potential tool in conservation science. Although the contributions of bioacoustics to conservation are recently growing (Fig. 1), they are still limited when compared to other well-established conservation approaches (Conservation Genetics, Conservation Physiology, etc.). The use of bioacoustics is indeed

restricted to animals communicating through sounds, and it is only indirectly linked with habitats and ecosystems, features more openly relevant to wildlife managers and legislation. However, the target behaviour (acoustic signalling) is often conspicuous, and can be studied in a broad range of terrestrial and marine ecosystems around the world, may have a popular/educational appeal and is sensitive to many types of environmental disturbance (Laiolo and Jovani 2007). Some researchers have begun to appraise the value of behavioural diversity or peculiarity when dealing with reserve plans or reintroduction schemes of birds and mammals (Baker et al. 2006, Saranathan et al. 2007, Kidjo 2008, Laiolo 2008), a conservation problem traditionally dealt with by addressing neutral genetic variation. Bioacoustics can therefore add fresh input to conservation biology, and provide principles and a methodology of conservation significance. On the other hand, it could become a promising branch of the *Conservation Behaviour* discipline, which often lacks precise information on the behaviours we should be concerned about (Anthony and Blumstein 2000).

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References

- Adkisson, C.S. 1981. Geographic variation in vocalizations and evolution of North American Pine Grosbeaks. *Condor* 83, 277-288.
- Ahlering, M.A., Faarborg, J. 2006. Avian habitat management meets conspecific attraction: if you built it, will they come? *The Auk* 123, 201-312.
- Ahtiainen J.J., Alatalo R.V., Mappes J., Vertainen L. 2004. Decreased sexual signalling reveals reduced viability in small populations of the drumming wolf spider *Hygrolycosa rubrofasciata*. *Proc R Soc London B* 271: 1839-1845

- Anthony, L.L. , Blumstein, D.T .2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce Ne. *Biological Conservation* 95, 303-315
- Avery, M., Oring, L.W. 1977. Song dialects in the Bobolink (*Dolichonyx oryzivorus*). *The Condor* 79, 113-118.
- Baker, M.C. 2000. Cultural diversification in the flight call of the ringneck parrot in western Australia. *The Condor* 102, 905-910
- Baker, M.C., Baker, M.S.A., Tilghman, L.M. 2006. Differing effects of isolation on evolution of bird songs: examples from an island-mainland comparison of three species. *Biological Journal of the Linnean Society* 89, 331-342.
- Barber, J.R., Crooks, K.R., Fristrup, K.M. 2009. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology and Evolution*, in press.
- Bayne, E.M., Habib, L., Boutin, S. 2008. Impacts of Chronic Anthropogenic Noise from Energy-Sector Activity on Abundance of Songbirds in the Boreal Forest. *Conservation Biology* 22,1186-1193.
- Bender, D.J, Contreras, T.A., Fahrig, L. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*79, 517-533.
- Bergen, F., Abs, M. 1997. Etho-ecological study of the singing activity of the blue tit (*Parus caeruleus*) great tit (*Parus major*), and chaffinch (*Fringilla coelebs*). *Jurnal für Ornithologie* 138, 451-467.
- Bergmann, H.H. 1993. *Der Buchfink: Neues über einen bekannten Sänger. -Wiesbaden.*
- Bermúdez-Cuamatzin, E., Ríos-Chelén, A.A.; Gil D.; Garcia , Macías D. 2009. Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use? *Behaviour* 146: 1269-1286
- Blumstein, D.T. 1998. Female Preferences and Effective Population Size. *Animal Conservation* 1, 173-177

- Bradbury, J.W., Vehrencamp, S.L. 1998 Principles of Animal Communication. Sinauer Associates Sunderland, MA.
- Bretagnolle, V, and McGregor, PK. 2006. Using bird vocalisations as individual tags: Prospects for the conservation of threatened species in counts, survival rates and population structure. *Journal of Ornithology* 147 suppl 1, 66
- Briefer, E., Osiejuk, T.S., Rybak, F., Aubin, T. 2009. Are bird song complexity and sharing shaped by habitat structure? An information theory and statistical approach. *Journal of theoretical Biology* in press, DOI:10.1016/j.jtbi.2009.09.020
- Brumm, H. 2006. Animal Communication: City Birds Have Changed Their Tune. *Current Biology* 16, R1003 - R1004
- Brumm, H. and Slabbekoorn, H. 2005. Acoustic communication in noise. *Adv. Stud. Behav.* 35, 151-209
- Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* 73, 434–440.
- Buchanan, K.L. 2000. Stress and the evolution of condition-dependent signals. *Trends in Ecology and Evolution* 15, 156-160.
- Buchholz, R. 2007. Behavioural biology: an effective and relevant conservation tool. *Trends in Ecology and Evolution* 22, 401-407
- Buckstaff, K.C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 20, 709-725.
- Cadena, C.D., Lopez-Lanus, B., Bates, J.M., Krabbe, N., Rice N.H., Stiles F.G., Palacio J.D., Salaman P. 2007. A rare case of interspecific hybridization in the tracheophone suboscines: Chestnut-naped Antpitta *Grallaria nuchalis* x Chestnut-crowned Antpitta *G. ruficapilla* in a fragmented Andean landscape. *Ibis* 149, 814-825.

- Caro, T.M. 2007. Behavior and conservation: a bridge too far? *Trends in Ecology & Evolution* 22, 394-400.
- Catchpole, C.K., Slater, P.J.B. 2008. *Bird Song: Biological Themes and Variations*. Second Edition. Cambridge University Press, Cambridge.
- Chilton, G. and Lein, M.R. 1996. Long-term changes in songs and song dialect boundaries of Puget sound white crowned sparrows. *Condor* 98, 567-580.
- Cunningham, M.A., Baker, M.C., Boardman, T.J. 1987. Microgeographic song variation in the Nuttall's white-crowned sparrow. *Condor* 89, 261-275.
- Curio, E. 1996. Conservation needs ethology. *Trends in Ecology & Evolution* 11: 260-263.
- Currie, D., Valkama, J. 2000. Population density and the intensity of paternity assurance behaviour in a monogamous wader: the Curlew *Numenius arquata*. *Ibis* 142, 372 -381.
- Dahlheim, M. E., 1987. Bio-acoustics of the gray whale (*Eschrichtius robustus*). Ph. D. Dissertation. Department of Zoology, University of British Columbia
- Dawson, D.K., Efford, M.G. 2009. Bird population density estimated from acoustic signals. *Journal of Applied Ecology* 46, 1201-1209.
- Drayton, J.M, Hunt J., Brooks, R., Jennions, M.D. 2007 Sounds different: inbreeding depression in sexually selected traits in the cricket *Teleogryllus commodus*. *J. Evol. Biol.* 20, 1138-1147.
- Efford, M.G., Dawson, D.K., Borchers, D.L. 2009. Population density estimated from locations of individuals on a passive detector array. *Ecology* 90, 2676-2682.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.
- Fernández-Juricic, E., Poston, R., De Collibus, K, Morgan, T., Bastain, B., Martin, C., Jones, K, Treminio, R. 2005. Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the Western U.S. *Urban Habitats* 3, 49-69

- Fletcher, R.J. Jr. 2008. Social information and community dynamics: nontarget effects from simulating social cues for management. *Ecological Applications* 18,1764-1773
- Fletcher, R.J. Jr. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* 76, 598-606.
- Foote, A.D., Osborne, R.W., Hoelzel, A.R., 2004. Whale-call response to masking boat noise. *Nature* 428, 910
- Förschler, M.I., Kalko, E.K.V. 2008. Vocal types in crossbill populations (*Loxia* spp.) of Southern Europe. - *Journal of Ornithology*. *Journal of Ornithology* 150, 17-27
- Fristrup, K.M., Hatch, L.T., Clark, C.W. 2003 Variation in humpback whale (*Megaptera novaengliae*) song length in relation to low-frequency sound broadcasts. *Journal of the Acoustical Society of America* 113, 3411–3424
- Fuller, R.A., Warren, P.H., Gaston, K.J. 2007. Daytime noise predicts nocturnal singing in urban robins. *Biology Letters* 3, 368–70
- Fuller, R.A., Warren, P.H., Gaston, K.J. 2007. Daytime noise predicts nocturnal singing in urban robins. *Biology Letters* 3, 368–70
- Gammon, D.E., Backer, M.C., Topton, J.R. 2005. Cultural divergence within novel song in the black-capped chickadee (*Poecile atricapillus*). *The Auk* 122, 853-871.
- Gaunt, S. L. L., D. A. McCallum. 2004. Birdsong and conservation. In: Marler, P., Slabbekoorn, H (Eds.) *Nature's music: The science of birdsong*. Academic Press.
- Gerhardt H.C., Huber F. 2002. *Acoustic Communication in Insects and Anurans*. Chicago University Press.
- Gilbert, G., Tyler, G.A., Smith, K.W. 2002. Local annual survival of booming male Great Bittern *Botaurus stellaris* in Britain, in the period 1990-1999. *Ibis* 144, 51-61
- Goold, J.C. 1996 Acoustic assessment of populations of common dolphin *Delphinus delphis* in conjunction with seismic surveying. *Journal of the Marine Biological Association of the United Kingdom* 76, 811–820.

- Goold, J.C., Fish, P.J. 1998 Broadband spectra of seismic survey air-gun emissions, with reference to dolphin auditory thresholds. *Journal of the Acoustical Society of America* 103, 2177–2184.
- Gorissen, L., Snocijs, T., Van Duyse, E., Eens, M. 2005. Heavy metal pollution affects dawn singing behaviour in a small passerine bird. *Oecologia* 145, 504-509.
- Grant, P.R., Grant, B.R.. 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution* 50, 2471–2487.
- Gutzwiller, K.J., Kroese, E.A. Anderson, S.H., Wilkins, C.A 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? *The Auk* 114, 55-65.
- Gutzwiller, K.J., Wiedenmann, E.A., Clements, K.L., Anderson, S.H. 1994. Effects of human intrusion on song occurrence and singing consistency in subalpine birds. *The Auk* 111, 28-37.
- Habib, L., Bayne, E.M., Boutin, S. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology* 44,176 - 184
- Hahn, B.A., Silverman, E.D. 2007. Managing breeding forest songbirds with conspecific song playbacks. *Animal Conservation* 10, 436-441
- Hauser MD 1997. *The evolution of communication*. MIT press.
- Holland, J., McGregor, P.K., Rowe, C.L. 1996. Changes in microgeographic song variation of the Corn Bunting *Miliaria calandra*. *Journal of Avian Biology* 27, 47-55.
- Hu, Y.H., Cardoso, G.C. 2009. Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? *Behavioural Ecology* 20, 1268-1273.
- Janik, V.M., Slater, P.B. 1997 Vocal learning in mammals. *Adv. Stud. Behav.* 26, 59-99
- Kaiser, K., Hammers, J.L 2009. The effect of anthropogenic noise on male advertisement call rate in the neotropical treefrog, *Dendropsophus triangulum*. *Behaviour* 146, 1053-1069

- Katti, M., Warren, P.S. 2004. Tits, noise, and urban bioacoustics. *Trends in Ecology and Evolution* 19, 109-110.
- Kidjo, N., Cargnelutti, B., Charlton, B.D., Wilson, C., Reby, D. 2008. Vocal behaviour in the endangered Corsican deer: description and phylogenetic implications. *Bioacoustics* 18, 159-181
- Kroodsma, D.E., Miller, E.H. 1996. Ecology and evolution of acoustic communication in birds. Cornell Univ. Press, Ithaca, NY.
- Kroodsma, D.E. 1989. Two North American song populations of the marsh wren reach distributional limits in the Central Great Plains. *The Condor* 91, 332-340
- Kroodsma, D.E., Baylis, J.R. 1982. A world survey of evidence for vocal learning in birds. In: Kroodsma, D.E., Miller, E.H. (Eds.). *Acoustic communication in birds*. Vol. 2, pp. 311-337, Academic Press, New York
- Kroodsma, D.E., Byers, B.E., Halkin, S.L., Hill, C., Minis, D., Bolsinger, J.R., Dawson, J., Donelan, E., Farrington, J., Gill, F.B., Houlihan, P., Innes, D., Keller, G., Macaulay, L., Matantz, C.A., Ortiz, J., Stoddart, P.K., Wilda, K. 1999. Geographic variation in black-capped chickadee songs and singing behavior. *The Auk* 116, 387-482.
- Laiolo, P. 2005. Spatial and seasonal patterns of bird communities in Italian agroecosystems. *Conservation Biology* 19, 1547-1556.
- Laiolo, P., Jovani, R. 2007. The emergence of animal culture conservation. *Trends in Ecology & Evolution* 22, 5
- Laiolo, P., Tella, J.L., Carrete, M., Serrano, D., Lopez, G. 2004. Distress calls may honestly signal bird quality to predators. *Proc. R. Soc. London B* 271, S513 - S515
- Laiolo, P. 2008. Characterizing the spatial structure of songbird cultures. *Ecological Applications* 18, 1174-1780.
- Laiolo, P., Tella, J.L. 2005. Habitat fragmentation affects culture transmission: patterns of song matching in Dupont's lark. *Journal of Applied Ecology* 42, 1183-1193.

- Laiolo, P., Tella, J.L. 2006. Landscape bioacoustics allows detection of the effects of habitat patchiness on population structure. *Ecology* 87, 1203-1214
- Laiolo, P., Tella, J.L. 2007a. Erosion of animal cultures in fragmented landscapes. *Frontiers in Ecology and the Environment* 5, 68-72.
- Laiolo, P., Tella, J.L. 2007b. Vocal diversity patterns – Reply. *Frontiers in Ecology and Environment* 8, 406-407.
- Laiolo, P., Tella, J.L. 2008. Social determinants of songbird vocal activity and implications for the persistence of small populations. *Animal Conservation* 11, 433-441.
- Laiolo, P., Serrano, D., Tella, J.L., Carrete, M., Lopez, G. and Navarro, C. 2007a. Effects of pox-virus infection on the distress calls of lesser short-toed lark *Calandrella rufescens*. *Behavioral Ecology* 18, 507-512
- Laiolo, P., Vögeli, M., Serrano, D. and Tella, J.L.. 2008. Song diversity predicts the viability of fragmented bird populations. *PLoS-ONE* 3, e1822.
- Laiolo, P., Vögeli, M., Serrano, D., Tella, J.L. 2007b. Testing acoustic versus physical marking: two complementary methods for individual-based monitoring of elusive species. *Journal of Avian Biology* 38, 672-681.
- Laland, K.N., Galef, BG. 2009. *The Question of Animal Culture*. Cambridge, Mass.: Harvard University Press.
- Leader, N., Wright, J., Yom-Tov, Y. 2000. Microgeographic song dialects in the orange-tufted sunbird (*Nectarinia osea*). *Behaviour* 137, 1613-1627
- Lengagne, T. 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation* 141, 2023-2031
- Lesage, V., Barrette, C., Kingsley, M. C. S. and Sjare, B. 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River Estuary, Canada. *Mar. Mamm. Sci.* 15, 65-84

- Lijtmaer, D.A., Tubaro, P.L. 2007. A reversed pattern of association between song dialects and habitat in the rufous-collared sparrow. *The Condor* 109, 658-667.
- Lougheed, S.C., Lougheed, A.J., Rae M, Handford, P. 1989. Analysis of a dialect boundary in chaco vegetation in the rufous-collared sparrow. *The Condor* 91, 1002-1003.
- Luther, D., Baptista, L. 2009. Urban noise and the cultural evolution of bird songs. *Proceedings of The Royal Society B*, in press
- MacNally, R., Bennett, A.F., Horrocks, G. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation* 95: 7-29.
- Markman, S., Leitner, S., Catchpole, C., Barnsley, S. Muller, C.T., Pascoe, D., Buchanan, K.L. 2008. Pollutants Increase song complexity and the volume of the brain area HVC in a Songbird. *PLoS-ONE* 3, e1674.
- May-Collado, L.J., Wartzok, D. 2008. A comparison of bottlenose dolphin whistles in the atlantic ocean: factors promoting whistle variation. *Journal of Mammalogy* 89, 1229-1240
- McComb, K., Moss, C., Durant, S., Baker, L., Sayialel, S.. 2001. Matriarchs act as repositories of social knowledge in African elephants. *Science* 292, 491-494.
- McGuire, M. 1996. Dialects of the Chowchilla *Orthonyx spaldingii* in Upland Rainforest of North-eastern Australia. *Emu* 96, 174-180.
- Miller, P.J.O., Biasson, N., Samuels, A., Tyack, P.L. 2000. Whale songs lengthen in response to sonar. *Nature* 405, 903.
- Mockford, E.J., Marshall, R.C. 2009. Effects of urban noise on song and response behaviour in great tits. *Proceedings of the Royal Society B* 276, 2979-2985
- Morrow, E.H., Pitcher, T.E. 2003. Sexual selection and the risk of extinction in birds. *Proc. R. Soc. Lon. B* 270, 1793-1799.

- Mundinger, P.C. 1980. Animal cultures and a general theory of cultural evolution. *Ethology and Sociobiology* 1, 183–223
- Myrberg, A. A. 1990. The effects of man-made noise on the behavior of marine animals. *Environ. Int.* 16, 575-586.
- Nemeth, E., Brumm, H. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *Animal Behaviour* 78: 637-641.
- Nowacek, D.P., Thorne, L.H., Johnston, D.W., Tyack, P.L. 2007 Responses of cetaceans to anthropogenic noise. *Mammalian Review* 37, 81-115.
- Osiejuk, T.S., Grzybek, J., Tryjanowski, P. 2007 Song structure and repertoire sharing of the Tawny Pipit *Anthus campestris* in Poland. *Acta Ornithol.* 42: 157-165.
- Osiejuk, T.S., Ratynska, K. 2003. Song repertoire and microgeographic variation in song types distribution in the corn bunting *Miliaria calandra* from Poland. *Folia Zoologica* 52, 275-286
- Owings, H., Beecher, M.D., Thompson, N.S. 1998. Perspectives in Ethology: Communication. Plenum Press, NY.
- Parris, K.M., Velik-Lord, M., North, J.M.A. 2009. Frogs call at a higher pitch in traffic noise. *Ecology and Society* 14: 25
- Patricelli, G.L., Blickley, J.L. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. *The Auk* 123, 639–649.
- Patten, M.A., Rotenberry, J.T., Zuk, M. 2004. Habitat selection, acoustic adaptation, and the evolution of reproductive isolation. *Evolution* 58, 2144–2155
- Pavelka, M.S.M., Brusselers, O.T., Nowak, D., Behie, A.M. 2003. Population Reduction and Social Disorganization in *Alouatta pigra* Following a Hurricane. *International Journal of Primatology* 24, 1037.
- Podos, J., Warren, P.S. 2008. The Evolution of Geographic Variation in Birdsong. *Advances in the Study of Behaviour* 37, 403-458.

- Pohl, N.U., Slabbekoorn, H., Klump, G.M., Langemann, U. 2009. Effects of signal features and environmental noise on signal detection in the great tit, *Parus major*. *Animal Behaviour* 78, 1293-1300
- Rabin, L.A., Greene, C.M. 2002. Changes to acoustic communication systems in human-altered environments. *Journal of Comparative Psychology* 116, 137-141
- Rabin, L.A., Coss, R.G., Owings, D.H. 2006. The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). *Biological Conservation* 131, 410-420.
- Reed, J.M., Dobson, A.P. 1993. Behavioural constraints and conservation biology: Conspecific attraction and recruitment. *Trends in Ecology and Evolution* 8, 253-256.
- Rendell, L.E., Whitehead, H. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society B* 270, 225-31
- Rheindt, F.E. 2003. The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? *Journal fur Ornithologie* 144, 295-306
- Rich, T. 1981. Microgeographic variation in the song of the sage sparrow. *The Condor* 83, 113-119.
- Richardson, W.J., Greene, C.R., Malme, C.I., Thomson, D.H. 1995. *Marine Mammals and Noise*. Academic Press, San Diego, CA.
- Rogers, D.J. 2003. Geographic song variation within and between populations and subspecies of the rufous bristlebird, *Dasyornis broadbenti*. *Australian Journal of Zoology* 51, 1-14
- Ryan, M.J., Brenowitz, E.A. 1985. The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *American Naturalist* 126, 87-100.
- Saranathan, V., Hamilton, D., Powell, G.V.N., Kroodsma, D.W.E., Prum, R.O. 2007. Genetic evidence supports song learning in the three-wattled bellbird *Procnia stricarunculata* (Cotingidae). *Molecular Ecology* 16, 3689-3702

- Schaub, A., Ostwald, J., Siemers, B.M. 2008. Foraging bats avoid noise. *J. Exp. Biol.* 211, 3174–3180.
- Seibt, U., Wickler, W., Kleindienst, H.U., Sonnenschein, E. 2002 Structure, geography and origin of dialects in the traditive song of forest weaver *Ploceus bicolor sclateri* in Natal S. Africa. *Behaviour* 139, 1237-1269
- Sewall, K.B. 2009. Limited adult vocal learning maintains call dialects but permits pair-distinctive calls in red crossbills. *Animal Behaviour* 77, 1303-1311
- Slabbekoorn, H., Ripmeester, E.A.P. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology* 17, 72-83.
- Slabbekoorn, H., den Boer-Visser, A. 2006. Cities Change the Songs of Birds. *Current Biology* 16, 2326–2331.
- Slabbekoorn, H., Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature* 424, 267.
- Slabbekoorn, H., Yeh, P. Hunt, K. 2007. Sound transmission and song divergence: a comparison of urban and forest acoustics. *Condor* 109, 67-78
- Slater, P.J.B. 1986. The cultural transmission of bird song. *Trends in Ecology & Evolution* 1, 94–97
- Slobodchikoff, C.N., Ackers, S.H., Van Ert, M. 1998. Geographic variation in alarm calls of Gunnison's prairie dogs. *Journal of Mammalogy* 79, 1265-1272
- Smith, M.J., Smith, J. D., Roberts, T., Hammond, J., Davis, R.A. 2003. Intraspecific Variation in the Advertisement Call of the Sunset Frog *Spicospina flammocaerulea* (Anura: Myobatrachidae): a Frog with a Limited Geographic Distribution. *Journal of Herpetology* 37, 285-291.
- Smith, T.B., Mila, B., Grether, G.F., Slabbekoorn, H., Sepil, I. Buermann, W., Saatchi, S., Pollinger, J.P. 2008. Evolutionary consequences of human disturbance in a rainforest bird species from Central Africa. *Molecular Ecology* 17, 58-71

- Soha, J.A., Nelson, D.A., Parker, P.G. 2004. Genetic analysis of song dialect populations in Puget sound white-crowned sparrows. *Behavioral Ecology* 15, 636-646.
- Stockwell C.A., Hendry, A.P., Kinnison, M.T. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution* 18, 94-101.
- Sun, J.W.C., Narins, P.M. 2005. Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation* 121, 419–427
- Swaddle, L.C., Page, J.P. 2007. High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. *Animal Behaviour* 74, 363-368
- Swenson, J.E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. In: Festa-Bianchet, M. and Apollonio, M. (Eds). *Animal Behavior and Wildlife Conservation*. Island Press. Pp 171-190.
- Tanaka, Y. 1996. Sexual selection enhances population extinction in a changing environment. *J. Theor. Biol.* 180, 197–206
- Terry, A.M.R., Peake, T.M., McGregor, P.K. 2005. The role of vocal individuality in conservation. *Frontiers in Zoology* 2,10
- Thielcke, G. 1972. On the origin of divergence of learned signals (songs) in isolated populations. *Ibis* 115, 511–16.
- Trainer, J.M 1983. Changes in song dialect distributions and microgeographic variation in song of white-crowned sparrows (*Zonotrichia leucophrys nuttalli*). *The Auk* 100, 568-582.
- Tripp, T., Otter, K.A. 2006. Vocal individuality as a potential long-term monitoring tool for adult male Western Screech Owls. *Canadian Journal of Zoology* 84, 744-753
- Tubaro, P.L., Segura, E.T., Handford, P. 1993. Geographic variation in the song of the rufous-collared sparrow in Eastern Argentina. *The Condor* 95, 588-595.

- Valderrama, S.V., Parra, J.E., Mennill, D.J. 2007. Species differences in the songs of the critically endangered Niceforo's wren and the related rufous-and white wren. *The Condor* 109, 870-877.
- Vasconcelos, R.O., Amorim, M.C., Ladich F. 2007. Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. *The Journal of Experimental Biology* 210, 2104-2112.
- Vaughan, N, Jones, G., Harris, S. 1997. Habitat Use by Bats (Chiroptera) Assessed by Means of a Broad-Band Acoustic Method. *Journal of Applied Ecology* 34, 716-730
- Vögeli, M., Laiolo, P., Serrano, D., Tella, J.L. 2008. Who are we sampling? Apparent survival differs between methods in a secretive species. *Oikos* 117, 1816 -1823
- Ward, M.P., Schlossberg, S. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* 18, 519-525.
- Warren, P.W. 2003. Winter dialects in the bronzed cowbird and their relationship to breeding-season dialects. *Animal Behaviour* 65, 1169-1178.
- Warren, P.S., Katti, M., Ermann, M., Brazel, A. 2006. Urban bioacoustics: it's not just noise. *Animal Behaviour* 71,491-502.
- Watkins, W.A. Schevill, W.E. 1975. Sperm whales (*Physeter catodon*) react to pingers. *Deep-Sea Res.* 22, 123-129.
- Watkins, W.A., Daher, M.A., Fristrup, K.M., Howald, T.J., Notarbartolo Di Sciara, G. 1993 Sperm whales tagged with transponders and tracked underwater by sonar. *Mar. Mamm. Sci.* 9, 55-67.
- Weilgart, L.S. 2007. The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Can. J. Zool.* 85, 1091-1116.
- Westcott, D.A., Kroon, F.J. 2002. Geographic song variation and its consequences in the golden bowerbird. *Condor* 104, 750-60.

- White, F.W.G. 1985. Microgeographic variation in the song of the Olive Whistler in Kosciusko National park. *Emu* 85,181-187.
- White, F.W.G. 1987. Macrogeographic variation in the song of the Olive Whistler in Australia. *Emu* 87,14-25.
- Whitehead, H., Rendell, L., Osborne, R.W., Würsig, B. 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biological Conservation* 120, 427-437.
- Whitlock, M.C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution* 54, 1855-1861.
- Wood, W.E., Yezerinac, S.M. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk* 123, 650–659.
- Wright, T.F., Dahlin, C.R., Salinas-Melgoza, A. 2008. Stability and change in vocal dialects of the yellow-naped amazon. *Animal Behaviour* 76, 1017-1027.
- Zacharias, M.A., Gregr, E. 2005. Sensitivity and vulnerability in marine environments: A value-stress approach to identifying Vulnerable Marine Areas. *Conservation Biology* 19, 86-97.
- Zanette, L., Clinchy, M., Sung, H.C. 2009. Food-supplementing parents reduces their sons' song repertoire size. *Proceedings of the Royal Society B* 276, 2855-2860

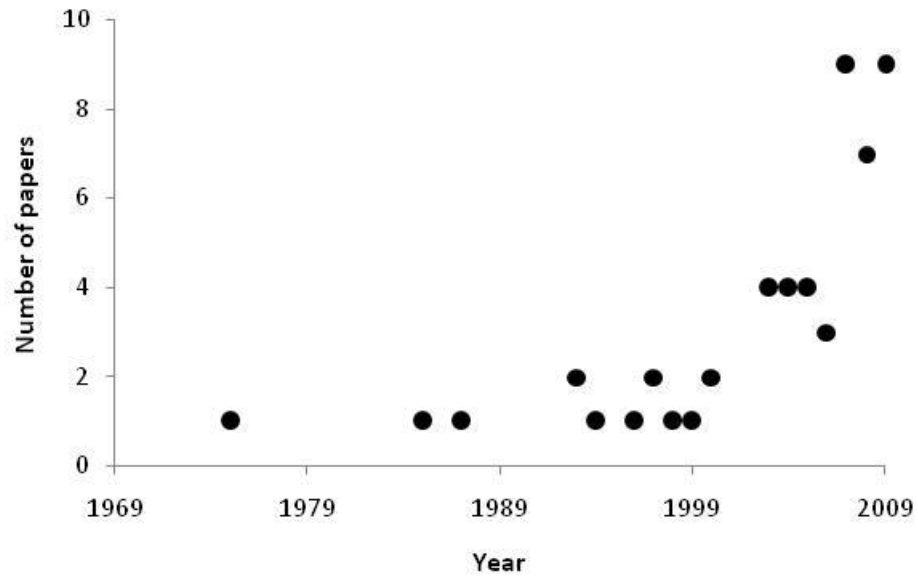


Fig. 1. The total number of papers on animal communication that studied variation in relation to anthropogenic impact ('Conservation Bioacoustics' studies) increased exponentially since the year 2000.

Table 1. Studies that have evoked some kind of human intervention to explain acoustic variation.

Anthropogenic effect	Environmental, demographic or physiological mechanism	Taxonomic groups and species affected	Potential Consequences
Noise pollution	Impediment to communication and masking natural sounds	BONY FISHES: Lusitanian toadfish <i>Halobatrachus didactylus</i> (Vasconcelos et al. 2007)*	DELETERIOUS (<i>Reduced territory defense and mating</i>)
		AMPHIBIANS: Taipei frog <i>Rana taipehensis</i> (Sun & Narins 2005)* European tree frog <i>Hyla arborea</i> (Lengagne 2008)*	ADAPTIVE VARIATION: Frequency or temporal switch to permit communication in noisy environment
		Southern brown tree frog <i>Litoria ewingii</i> (Parris et al. 2009)* Amazonian treefrog <i>Dendrophsophus triangulum</i> (Kaiser & Hammers 2009)*	ADAPTIVE VARIATION: Time, amplitude and frequency switches to permit communications in noisy environments
		BIRDS: Common chaffinch <i>Fringilla coelebs</i> (Bergmann 1993 in Rheindt 2003)* Great tit <i>Parus major</i> (Slabbekoorn & Peet 2003, Slabbekoorn & den Boer-Visser 2007, Pohl et al. 2009, Halfwerk et al. 2009, Mockford & Marshall 2009)* Dark-eyed Juncos <i>Junco hyemalis</i> (Slabbekoorn et al.2007) * Common nightingale <i>Luscinia megarhynchos</i> (Brumm 2004)* House finch <i>Carpodacus mexicanus</i> (Fernández-Juricic et al. 2005, Bermúdez-Cuamatzin et al. 2009)* Song sparrow <i>Melospiza melodia</i> (Wood & Yezerinac 2006)* European robin <i>Erithacus rubecula</i> (Fuller et al. 2007)* Blackbird <i>Turdus merula</i> (Nemeth & Brumm 2009)* White –crowned sparrow <i>Zonotrichia leucophrys</i> (Luther & Baptista 2009) Ovenbird <i>Seiurus aurocapilla</i> (Habib et al. 2007)*	DELETERIOUS EFFECTS (<i>Reduced breeding success</i>)
MARINE MAMMALS: Bottle-nosed dolphin <i>Tursiops truncatus</i> (Buckstaff 2004)* Common dolphin <i>Delphinus delphis</i> (Goold 1996)* Long-beaked common dolphin <i>Delphinus capensis</i> (Goold & Fish 1998)* Sperm whale <i>Physeter macrocephalus</i> (Watkins & Schevill 1975, Watkins et al. 1993)* Bottle-nosed dolphin <i>Tursiops truncates</i> (May-Collado & Wartzok 2008) Humpback whale <i>Megaptera novaeangliae</i> (Miller et al. 2000, Fristrup et al. 2003)* Beluga whale <i>Delphinapterus leucas</i> (Lesage et al. 1999)* Killer whale <i>Orcinus orca</i> (Foote et al. 2004)* Beaked whales (family Hyperoodontidae) (Weilgart 2007)* Gray whale <i>Eschrichtius robustus</i> (Dahlheim 1987)*	NEUTRAL or DELETERIOUS (<i>Reduced foraging efficiency</i>)		
TERRESTRIAL MAMMALS: Greater mouse-eared bats <i>Myotis myotis</i> (Schaub et al. 2008)*	ADAPTIVE VARIATION: Adjustment of sound structure to compensate for anthropogenic noise DELETERIOUS: The lack of adaptation		

		California ground squirrels <i>Spermophilus beecheyi</i> (Rabin et al. 2006)*	results in reduced foraging efficiency DELETERIOUS (<i>Reduced survival</i>)
Habitat isolation	Reduced dispersal and patch connectivity	BIRDS: Dupont's lark <i>Chersophilus duponti</i> (Laiolo & Tella 2006, 2007a,b 2008)* Skylark <i>Alauda arvensis</i> (Briefer et al. 2009)* Rufous bristlebird <i>Dasyornis broadbenti</i> (Rogers 2003)* Black-capped chickadee <i>Poecile atricapillus</i> (Kroodsma et al. 1999, Gammon et al 2005) Golden bowerbird <i>Prionodura newtonia</i> (Westcott & Kroon 2002) Niceforo's Wren <i>Thryothorus nicefori</i> (Valderrama et al 2007) Olive whistler <i>Pachycephala olivacea</i> (White 1985, 1987) Forest weaver <i>Ploceus bicolor sclateri</i> (Seibt et al. 2002)	NEUTRAL or DELETERIOUS (<i>Gene flow reduction</i>)
Habitat loss	Reduced population size	SPIDERS: Wolf spider <i>Hygrolycosa rubrofasciata</i> (Ahitainen et al. 2004)*	NEUTRAL or DELETERIOUS (<i>Genetic or demographic effects</i>)
	Reduced population size, dear-enemy effects (1)	BIRDS: Dupont's lark <i>Chersophilus duponti</i> (Laiolo & Tella 2007a, 2008, Laiolo 2008)* Black-capped chickadee <i>Poecile atricapillus</i> (Kroodsma et al 1999, Gammon et al 2005) Forest weaver <i>Ploceus bicolor sclateri</i> (Seibt et al. 2002) Chestnut-naped and Chestnut-crowned Antpitta <i>Grallaria nuchalis</i> and <i>G. ruficapilla</i> (Cadena et al. 2007)	
Transformation of the habitat matrix (logging, agricultural rotation and fire)	Constraints to recruitment, alteration of age-classes distribution, density variations	AMPHIBIANS: Sunset frog <i>Spicospina flammocaerulea</i> (Smith et al. 2003)	NEUTRAL ADAPTIVE VARIATION: Acoustic switches permit communication in novel habitats NEUTRAL
	Changes in habitat structure and acoustics	BIRDS: Curlew <i>Numenius arquata</i> (Currie & Valkama 2000)	
	Extinction and /or colonization processes	BIRDS: Little greenbul <i>Andropadus virens</i> (Smith et al. 2008) * BIRDS: Corn bunting <i>Miliaria calandra</i> (Holland et al 1996) White-crowned sparrows <i>Zonotrichia leucophrys nuttalli</i> (Trainer 1983) Rufous-collared sparrow <i>Zonotrichia capensis</i> (Lougheed et al 1989, Tubaro et al 1993, Lijtmaer & Tubaro 2007) Australian / Port Lincoln Ringneck parrot <i>Barnardius zonarius</i> (Baker 2000) Sage sparrow <i>Amphispiza belli</i> (Rich 1981) Bobolink <i>Dolichonyx oryzivorus</i> (Avery & Oring 1977) European crossbills <i>Loxia</i> spp. (Förschler & Kalko 2009) Puget Sound white-crowned sparrows <i>Zonotrichia leucophrys pugetensis</i> (Chilton & Lein 1996) Orange-tufted sunbird <i>Nectarinia osea</i> (Leader et al. 2000)*	
Hedge proliferation	Relaxed neighbor interactions	BIRDS: Dupont's lark <i>Chersophilus duponti</i> (Laiolo & Tella 2005)*	NEUTRAL
Hunting	Change in age class	TERRESTRIAL MAMMALS: African elephant <i>Loxodonta africana</i> (McComb et al. 2001)	NEUTRAL or DELETERIOUS (<i>Reduced</i>)

	distribution, population size reduction	Gunnison's prairie dog <i>Cynomys gunnisoni</i> (Slobodchikoff et al 1998)	<i>breeding success</i>
Environmental pollution	Disruption of neuronal/hormonal circuits of sound production	BIRDS: Great tit <i>Parus major</i> (Gorissen et al 2005)* European starling <i>Sturnus vulgaris</i> (Markman et al. 2008) *	NEUTRAL or DELETERIOUS (<i>Reduced breeding success, ecological traps</i>)
Introduced diseases	Health problems	BIRDS: Lesser short-toed lark <i>Calandrella rufescens polatzeki</i> (Laiolo et al. 2007a)*	DELETERIOUS (<i>Reduced survival</i>)
Human intrusion	Switch in territory establishment	BIRDS: Ruby-crowned kinglet <i>Regulus calendula</i> (Gutzwiller et al 1997)* Yellow-rumped warblers <i>Dendroica coronata</i> (Gutzwiller et al. 1994, 1997)* Hermit thrush <i>Catharus guttatus</i> (Gutzwiller et al. 1994, 1997)* Common chaffinch <i>Fringilla coelebs</i> (Bergen & Abs 1997)*	NEUTRAL or DELETERIOUS (<i>Reduced breeding success</i>)
Food supplementation	Trade-offs between compensatory growth and learning	BIRDS: Song sparrows <i>Melospiza melodia</i> (Zanette et al. 2009)	DELETERIOUS (<i>Reduced fitness of young reared with supplemental food</i>)

(1) Dear-enemy effect defines the lower levels of aggression shown by territorial males toward known neighbors in their usual territories than toward unfamiliar individuals (Fisher, 1954)

(*) Studies that explicitly test for anthropogenic effects and address a conservation problem (Conservation Bioacoustics studies)

Table 2. Example of the applications of bioacoustics to conservation science.

Conservation application	Disadvantages	Advantages	References
Early detection of human driven environmental stress, isolation processes, habitat deterioration and poor population viability	Only applicable to the acoustically active members of a population	Non intrusive, less time consuming and cheaper than other direct or indirect monitoring methods	See Table 1
Inference of population viability	Only applicable to species with sexual signaling sensitive to demographic oscillations	Non intrusive, less time consuming and cheaper than other direct or indirect monitoring methods	Ahitiainen et al. 2004 Laiolo et al. 2008
Inference of survival rates through acoustic individual identification (acoustic marking)	Only applicable to species with individual-specific acoustic signals, and to the acoustically active members of a population	Non intrusive, less time consuming with respect to physical marking	Gilbert et al. 2002 Laiolo et al. 2007b Vögeli et al. 2008 Terry et al. 2005 Bretagnolle and McGregor 2006
Inference of ongoing pre-dispersal among populations by tracking acoustic differences among populations	Only applicable to pre-dispersal learners that maintain stable repertoires, and to the acoustically active members of a population	Non intrusive, less time consuming with respect to long term population monitoring	Adkisson 1981 Holland et al. 1996 Cunningham et al. 1987 Kroodsma 1989 McGuire 1996 Warren 2003 Osiejuk and Ratynska 2003 Soha et al. 2004 Förschler and Kalko 2008 Laiolo and Tella 2008 Sewall 2009
Encourage the recolonization of suitable patches through the manipulation of acoustic cues (broadcasting vocalizations)	Only applicable to species forming conspecific aggregations, either colonial or territorial	Less time and energy consuming than reintroducing individuals from captivity or relocated from other occupied sites	Ahlering and Faarborg 2006 Ward and Schlossberg 2004 Fletcher 2007, 2008 Hahn and Silverman 2007
Estimate of animal density / diversity through automated recording procedures	Only applicable to the acoustically active members of a populations and species	Useful to monitor visually cryptic but vocal taxa	Dawson & Efford 2009