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Synthetic bird calls and their application to scaring methods

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This paper suggests means of synthesizing efficient signals for bird scaring and examines five ways in which synthetic signals may be more efficient: the coding/decoding process, transmission through the environment, interspecificity, habituation and broadcasting techniques. Examples are taken from our own studies comparing natural and synthetic distress calls.

The study of bird vocalizations has mostly concerned songs, especially from the viewpoint of species-specific coding (see Becker 1982 for a review). These studies have shown that the manipulation of parameters does not modify the information content but leads to a diminution of the effect of the signal. Other authors (Richard & Thompson 1978, Brémond 1980, Aubin & Brémond 1983) have demonstrated that there are modifications in songs that could have the opposite effect, i.e. birds react more strongly to a modified signal than they would have done to the natural one. This last point is of particular interest when we consider the practical applications for scaring birds by means of sounds.

This paper discusses some of the points which have to be taken into account in synthesizing acoustic signals whose efficacy is greater than that of natural signals, in particular: (a) how to obtain a maximum effectiveness in the coding of information; (b) how to improve the efficiency of transmitting information to a receiver; (c) how to elicit multispecific responses; (d) how to prevent habituation; and (e) how to broadcast the signal (scaring techniques).

To support this review, I have used results obtained in the study of distress calls, signals often employed in acoustic scaring techniques to repel birds.

Coding of information

To elicit an appropriate response, a signal must be understood by the receiver: the processes of coding/decoding must be unequivocal. Consequently, it is necessary to isolate in the signal the key features implicated in the information. In order to discover what these key features are, acoustic experimentation is needed. Only the use of synthetic signals as lures allows the experimenter to manipulate separately and with accuracy the parameters of a sound. Different sounds are presented to birds in the wild and their reactions to the experimental signals determine which are the relevant parameters for the recognition of a given signal. When the variation of a parameter leads to a clear decrease in intensity of response relative to the response to a natural signal, the parameter is judged to be of importance in recognition. Conversely, when the variation does not greatly alter the response intensity, the parameter is judged not to be crucial for recognition. This method enables us to

understand the coding/decoding processes used by many bird species, particularly for territorial songs (Emlen 1972, Goldman 1974, Rice 1978, and see Becker 1982 for a review). Once the key features have been identified in the signal, it is possible to manipulate them, in order to build a signal eliciting very strong responses.

Earlier studies (Robisson 1986, Aubin 1986, 1987, 1989, Aubin & Brémond 1989, Brémond & Aubin in press) have examined the mechanisms of coding/decoding in the distress calls of some species such as Starlings *Sturnus vulgaris*, Black-headed and Herring Gulls *Larus ridibundus* and *L. argentatus* and Lapwings *Vanellus vanellus*. Their distress calls, in spite of their complex structure, follow a very simple law of coding/decoding. A simple slope (slow frequency modulation) applied to a carrier frequency that corresponds to the acoustic shape of a distress call was sufficient to confer a distress meaning to the signal. Amplitude modulation and fine details of structure of the frequency modulation were not necessary for the decoding. This was true for all species studied and could certainly be extended to distress calls of other species.

In carrying out these studies on distress calls, numerous synthetic signals were constructed. Some of them emphasized the relevant parameters of the decoding. These parameters were simpler than natural ones and parameters not necessary for the decoding were removed (Fig. 1). These signals were more effective than a real distress call in eliciting a response. The super-normal effect of 'caricatures' that are simpler than natural signals was pointed out by Brémond (1980) for some bird songs. Similar effects occur in visual signalling (Inglis 1980). The accentuation of the characteristics of the relevant parameters seems to reinforce the information content of a signal, while the non-relevant parameters seem to act as 'disturbing' elements (noise intra-signal).

Transmission of information

To elicit a response, a signal must be transmitted without great alteration. Many distortions occur during propagation through the environment, such as frequency-dependent attenuation, boundary interference, reverberation and irregular amplitude fluctuations (Wiley & Richards 1978, 1982). These processes degrade the structure of acoustic signals and consequently the information contained by important parameters can be lost. This is particularly obvious with signals that birds use for long-range communication. Parameters such as amplitude modulation or fast frequency modulation are altered by propagation (Morton 1975, Marten & Marler 1977, Richards & Wiley 1980, Bérengier & Habault 1983, Cosens & Falls 1984). A knowledge of these transmission effects is necessary in order to determine the acoustic structures which must be used to build signals that are efficient over distance.

Distress calls are long-range communication signals. In order to study the laws of propagation of distress calls, we conducted sound propagation tests in open grass fields. Distress calls were broadcast at 1·50 m above the ground and recordings were made at 0·40 m and 150 m from the loudspeaker, 0·20 m above the ground. Calls were then analysed through different numeric techniques. As predicted by sound propagation theory, distress calls were modified with attenuations essentially at both ends of the spectrum (Fig. 2): below 1·5 kHz (ground effect) and above 3 kHz (due to scattering and atmospheric absorption). In addition, all the details of the amplitude and frequency modulations were greatly altered. Structures that were only slightly modified were the harmonic distribution, the slow frequency modulations and the

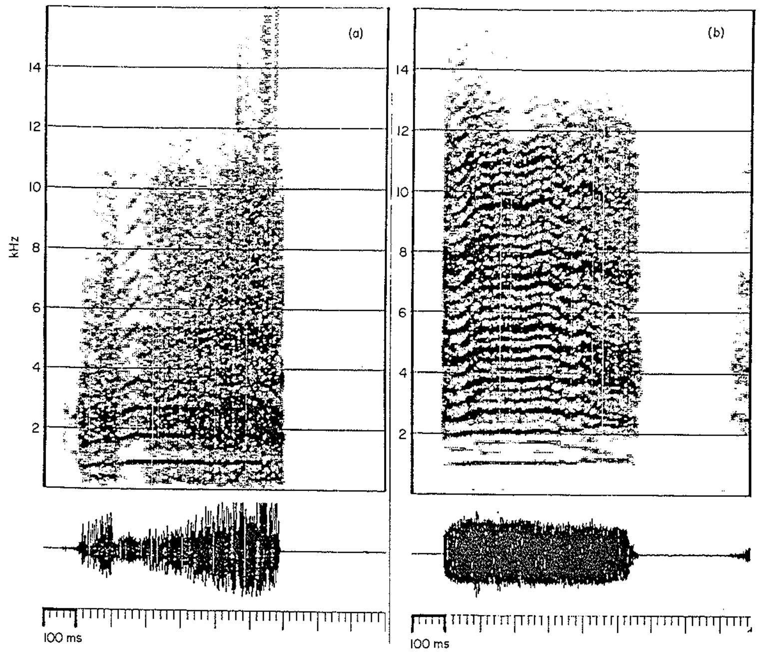

Figure 1. Digital sonagrams and oscillograms of Black-headed Gulls' distress calls: (a) natural signal; (b) synthetic signal without amplitude modulations and with frequency modulations simplified compared to the natural call. This synthetic call is more effective than the natural one in eliciting a response.

length of the signal. These parameters are precisely those used by the bird for the coding/decoding of its calls. The decoding of distress calls appears to be adapted to the constraints of long-range transmission. Nevertheless, there was no perfect agreement between the parameters not degraded by the environment and the parameters used for the decoding. Birds tended to react more strictly to signals containing only higher harmonics than they did with those containing only the lower ones (Morgan & Howse 1974).

Thus, to increase the efficiency of the signal it seems necessary to minimize the attenuation of higher harmonics. This agrees with information theory (Shannon & Weaver 1949): to increase the quantity of information transmitted, one possibility is to expand the width of the spectrum. This can be done with synthetic signals. The enhancement of the acoustic level of higher harmonics (Fig. 3), in order to prevent the degrading effect of the transmission channel, leads to an increase in the signal's efficiency (unpublished data).

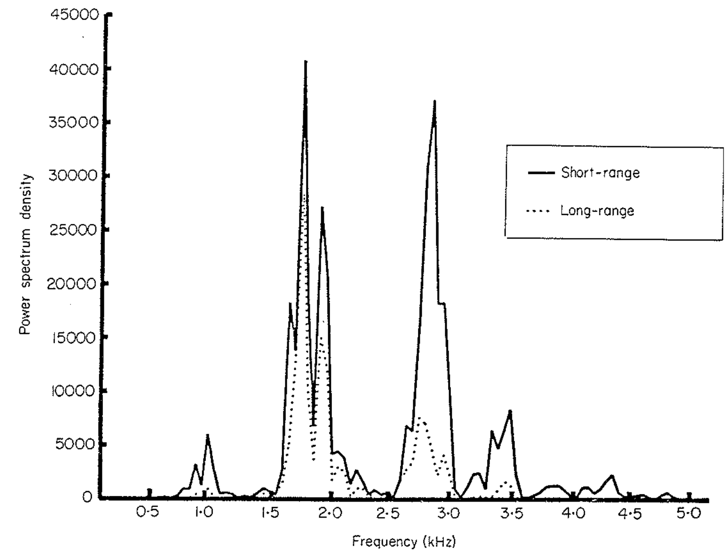

Figure 2. Spectrum analysis of a Black-headed Gull distress call re-recorded at 0·40 m (short-range transmission) and at 150 m (long-range transmission). The effects of transmission are noticeable below 1·5 kHz and above 3 kHz.

Interspecificity

To elicit multispecific responses, a signal emitted by one species must be understood by others. There are numerous accounts in the literature describing interspecific responses among birds elicited by acoustic signals, such as alarm, distress, flight and aggressive calls (Marler 1957, Busnel & Giban 1960, 1965, Bridgman 1980). Interspecific responses are also evoked by some territorial songs (Catchpole 1978, Rice 1978). This interspecificity of reactions has been associated with the structural convergences between signals of different species (Marler 1957, Busnel & Giban 1960, 1968, Cody 1969). More recent studies suggested that interspecificity might also be related to similarities in the process of recognition of the different species (Stefanski & Falls 1972, Murray 1976, 1981): interspecific responses arise through a failure to discriminate between signals of other species. Additionally, for some categories of signals, learning may also play a role (Catchpole 1978, Catchpole & Leisler 1986). Birds learn to recognize and respond to the signals of species that are regularly encountered.

In the case of alarm calls and particularly of distress calls, it seems most unlikely that learning contributes to interspecific recognition. Distress call are rarely given in nature so that opportunities for learning are extremely limited. Furthermore, the learning of such signals seems to be limited to a perinatal auditory exposure (Miller & Blaich 1984). Thus, the interspecificity observed with distress calls can be explained by only two factors: convergence of structure and similarities in the process of recognition. Aubin & Brémond (1989) have shown that distress calls follow a very

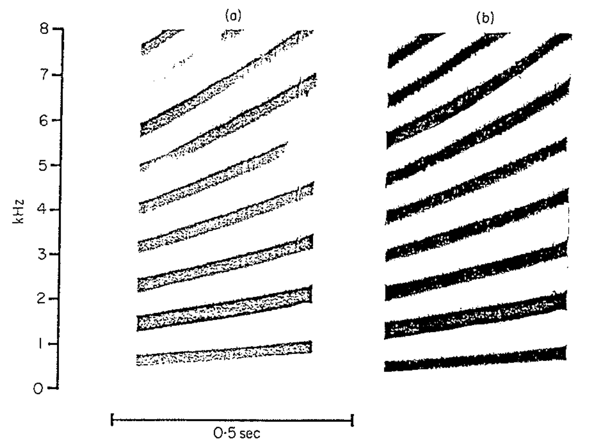

Figure 3. Simplified synthetic distress calls of a Starling: (a) the different level ratios between harmonics are those of a natural call; (b) the levels of the higher harmonics are reinforced. The second signal elicits stronger responses than the first one.

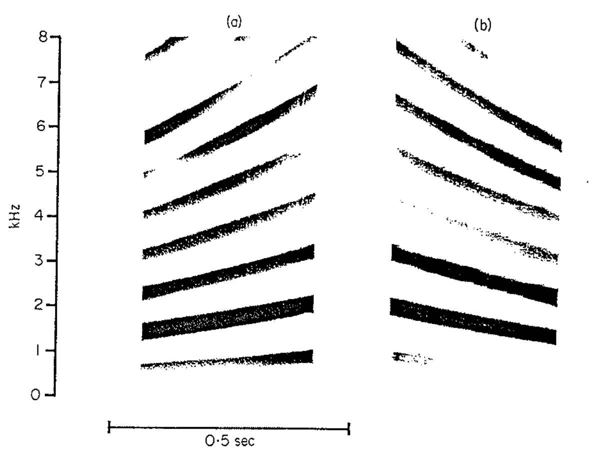

Figure 4. Synthetic distress signals of a Starling: (a) with slowly increasing frequency modulation; (b) with slowly decreasing frequency modulation. Unlike the first signal, the second one is ignored by the bird (from Aubin 1989).

simple common law of coding/decoding, and that the basic rules of this common law are the same for different species. Consequently, to build a signal that elicits interspecific responses, it is necessary to include all common acoustic parameters judged to be of importance in recognition by each species. These common key

features correspond closely to those described above for the coding of information: a fundamental frequency and harmonically related frequencies that increase or decrease. It is important to note that the signal must not contain parameters termed by Brémond (1976) as 'rejection markers'. These are elements which, when added to or withdrawn from the eliciting signal, bring about a rejection of that signal by the receiver. For example, a signal with a slow decreasing frequency modulation applied to the carrier is not accepted as a distress call by Starlings (Fig. 4b). This rejection marker is specific to Starlings as similar signals are readily accepted by other species such as Herring Gulls (Aubin & Brémond 1989), Black-headed Gulls (Brémond & Aubin in press) and Lapwings (Robisson 1986). In the same way, the lack of harmonics between 3 and 4 kHz leads to a rejection of the signal by Lapwings but not by the other species (Robisson 1987).

To build an efficient interspecific signal, it is therefore necessary to include all the relevant parameters that are involved in the process of identification and which are common to the species concerned, and to exclude all the specific rejection markers. We thereby effectively obtain a signal eliciting multispecific responses. Such a signal (Fig. 4a) has been tested with success against Starlings, Rooks *Corvus frugilegus*, Magpies *Pica pica*, Lapwings, Black-headed and Herring Gulls. The interspecific value is greater than with a natural call, as, for example, Starlings react only weakly to the natural distress calls of other species (Busnel & Giban 1960).

Habituation

Repeated presentation of the same stimulus to an individual leads to a decline in response. Habituation was first described in detail for bird songs by Hartshorne (1956) who postulated the existence of a 'monotony threshold', where the duration and rate of emission of songs on the one hand, and variety of songs on the other, were adjusted to prevent monotonous acoustic behaviours and consequent habituation. The functional significance of habituation has been often discussed. Some authors (Verner & Mulligan 1971, Petrinovich & Peek 1973, McGregor 1986) consider habituation to be a basic mechanism involved in the maintenance of lowered levels of aggression between conspecifics. However, this remains somewhat speculative and experimental evidence is lacking. Furthermore, this theory applies only to territorial songs.

In the case of alarm and distress calls, the almost complete loss of response to an enemy appears to have little adaptive value. Nevertheless, this type of behavioural adaptation is very often observed with these calls in the acoustic control of bird flocks on airfields or crops (Busnel & Giban 1960, 1965, Blokpoel 1976, Bridgman 1980). Unfortunately, in this context, habituation has not been studied from a quantitative point of view, nor in terms of learning processes. In many cases assessment of the habituation was based solely on subjective estimates and was seldom scrutinized by trained experimenters. In addition, in natural conditions habituation is also subordinated to the birds' motivation. For example, to repel Night Herons *Nycticorax nycticorax* from fish ponds with their distress calls, Spanier (1980) considered that bio-acoustic methods could be relied upon for an extended period only if the birds have convenient alternative resources to those from which they are being repelled. Brough (1968, 1969) also stated that feeding birds were more difficult to repel when food was scarce than when plentiful. In addition, Langowski *et al.* (1969) indicated that adult Starlings habituate faster than juveniles. Such an influence of environmental and physiological factors increases the difficulty of establishing a reliable test.

Habituation also emerges as a problem with synthetic calls. Indeed, a synthetic signal is just as likely to be learnt by the bird as a natural one. In a previous study (Aubin 1982) I demonstrated that Skylarks *Alauda arvensis* habituate very quickly to a monotonous synthetic signal which initially elicited very strong responses. In another study with Chaffinches *Fringilla coelebs*, Zucchi & Bergman (1975) showed that birds' responses decreased when they were exposed for a long time to a series of alarm signals. Nevertheless, every change in the original stimulus resulted in an enhancement of the responses. Using a combination of calls allowed more recovery time between presentations of the same calls and greater likelihood that the bird continued to perceive them as at the initial response. The response strength in the tests, however, never reached the original level. Thus, it seems that the habituation process can be slowed down, not by the synthetic signal itself, but indirectly by the broadcasting method. In actual bio-acoustic scaring techniques, the broadcasting of distress calls is always limited to repeated rigid playback sessions recorded on continuous loop tape. By using a computer to broadcast synthetic calls, it is possible to enhance the efficiency of the method at two levels in regard to habituation: by introducing variety into the signal and into the rhythm of emission and by reducing the quantity of sounds delivered to birds. These last points will be discussed in more detail below.

It is important to note that habituation is a natural biological phenomenon. It can never be totally suppressed, but only slowed down. Several fundamental principles may be used in order to prevent a rapid habituation (Slater 1980): (a) stimuli should be varied as much as possible; (b) stimuli should be presented as infrequently as possible; and (c) occasional reinforcements should occur.

Broadcasting methods

To disperse birds effectively by means of acoustic signals, it is necessary to use good apparatus that can achieve both loud volume and high quality reproduction. For distress calls, a volume of about 80 dB is recommended in the area needing protection (Briot *et al.* 1988). Brémond *et al.* (1968) demonstrated with gulls and corvids that high fidelity equipment produces better results than low fidelity. The use of a loudspeaker having a wide frequency response is important. Until recently, broadcasting equipment consisted of analog instrumentation, e.g. tape recorders (Brough 1965, Kuhring 1965, Sugg 1965, 1968, 1969, Pearson *et al.* 1967, Bridgman 1980). Nowadays the development of digital techniques has allowed the production of sophisticated synthetic sounds (Shiovitz & Lemon 1980, Dabelsteen & Pedersen 1985, Brémond & Aubin in press). Digital methods using a programmable synthesizer do not have the physical and biological drawbacks of analog equipment with regard to bird scaring.

At a physical level, signals obtained by digital methods have a very good signal/noise ratio, better than those obtained by playing recorded natural signals. A synthetic sound does not deteriorate with time, as is the case with sounds recorded on tape, and with digital equipment there are fewer mechanical components that may fail. These factors contribute to a much greater reliability of the total system.

At a biological level, the improvements provided by these new techniques are very important. First, it is possible to produce synthetic signals that are efficient with regard to coding/decoding processes, transmission through the environment and interspecificity. Secondly, and this is the most important point, it seems possible with these techniques to delay the development of habituation. Indeed, with a synthesizer driven by a microprocessor, it is easy to program variety during broadcasting, both between successive signals and in the rhythm of emission. The use of a computer provides nearly unlimited possibilities for modifications of sounds

or rhythm of emission. Thirdly, a microprocessor can also receive information from the environment. For example, the computer can detect the presence of birds by means of Doppler radar or infrared and then decide whether to broadcast or not. The punishment effect (the distress signal) only occurs when the bird comes into the area being protected. The number of emissions is thus limited and this scaring method conditions birds to avoid particular areas.

In our laboratory, we have built and patented a device which includes a synthesizer driven by a microprocessor (Brémond & Aubin 1989). A commercial version of this device has been used with reasonable success at airports (Briot & Eudot 1989) and linkage with Doppler radars to detect birds has been studied (Dupuis 1987).

Conclusions

The information content of an acoustic signal can be greatly altered by numerous factors. First, defective coding of information or distortions of relevant parameters during propagation through the environment elicit inappropriate responses. Secondly, the presence of a specific marker reduces the interspecific value of a signal. Thirdly, excessive presentation of the same signal to the same individuals leads to a decline in response. These phenomena can greatly reduce the effectiveness of acoustic signals in bird scaring. With synthetic signals, these problems can largely be solved. Once the background knowledge of a given signal has been acquired, it is easy to manipulate the relevant parameters to build a signal eliciting stronger responses. Some parameters can be reinforced or added, others weakened or removed. The result is a signal with a clear, unambiguous message, that will resist degradations during transmission. In the case of signals eliciting interspecific responses, such as distress calls, it is possible to obtain very good results with synthetic signals by keeping all the parameters common to the different species and by removing specific markers. Thus, with synthetic calls, it is possible to create a 'super-normal' stimulus, a signal which is more effective than the natural call in eliciting a response.

With habituation, the solution seems to lie with the broadcasting method rather than the synthetic call itself. A synthesizer driven by a microprocessor allows us to attack habituation at two levels: by varying the signals and their rhythms of emission and by limiting the number of signals emitted. The precision in the construction of synthetic signals and the flexibility of the broadcasting method provide an invaluable enhancement to the classic bird scaring techniques. The use of synthetic calls broadcast by an 'intelligent' device is also quite new.

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References

Aubin, T. 1982. Habituation au chant territorial chez l'alouette des champs. Rôle de la diversité et de la monotonie. Biol. Behav. 7: 353–362.

Aubin, T. 1986. Le phénomène deux voix et le codage de l'information dans les signaux acoustiques d'oiseaux. Etude appliquée aux cris de détresse de l'étourneau *Sturnus vulgaris*. Comptes Rendus. Acad. Sci. 302: 553–556.

Aubin, T. 1987. Respective parts of the carrier and of the frequency modulation in the semantics of distress calls. An experimental study on *Sturnus vulgaris* by means of digital synthesis methods. Behaviour 100: 123–133.

AUBIN, T. 1989. The role of frequency modulation in the process of distress call recognition by the starling *Sturnus vulgaris*. Behaviour 108: 57–72.

AUBIN, T. & BREMOND, J.C. 1983. The process of species-specific song recognition in the skylark *Alauda arvensis*. An experimental study by means of synthesis. Z. Tierpsychol. 61: 141–152.

AUBIN, T. & BREMOND, J.C. 1989. Parameters used for recognition of distress calls in two species: *Larus argentatus* and *Sturnus vulgaris*. Bioacoustics 2: 22–33.

BECKER, P.H. 1982. The coding of species-specific characteristics in bird sounds. *In* Kroodsma, D.E. & Miller, E.H. (eds) Acoustic Communication in Birds, Vol. 1: 213–252. New York: Academic Press.

BERENGIER, M. & HABAULT, D. 1983. Propagation au dessus d'un sol. Rev. Acoustique 65: 86–89.

BLOKPOEL, E. 1976. Bird hazards to aircraft. Montréal: Irwin & Co. Ltd.

BREMOND, J.C. 1976. Specific recognition in the song of Bonelli's warbler *Phylloscopus bonelli*. Behaviour 58: 99–116.

BREMOND, J.C. 1980. Prospects for making acoustic super-stimuli. *In* Wright, E.N., Inglis, I.R. & Feare, C.J. (eds) Bird Problems in Agriculture: 115–120. Croydon: British Crop Protection Council Press.

BREMOND, J.C. & AUBIN, T. 1989. Choice and description of a method of sound synthesis adapted to the study of bird calls. Biol. Behav. 14: 229–237.

BREMOND, J.C. & AUBIN, T. in press. Responses to distress calls in black-headed gulls (*Larus ridibundus*): the role of non-degradable features. Anim. Behav.

BREMOND, J.C., GRAMET, P., BROUGH, T. & WRIGHT, E.N. 1968. A comparison of some broadcasting equipment and recorded distress calls for scaring birds. J. Appl. Ecol. 5: 521–529.

BRIDGMAN, C.J. 1980. Bio-acoustic bird scaring in Britain. Proc. Pan-Afr. Orn. Congr. IV: 383–387.

BRIOT, J.L. & EUDOT, A. 1989. Etude statistique des collisions oiseaux-aéronefs survenues en France durant les années 1986–1987. Paris: Aéroports de Paris Press.

BRIOT, J.L., CLOUD, C. & EUDOT, A. 1988. Projet d'implantation de bruiteurs sur la piste de Paris-Orly. Paris: Aéroports de Paris Press.

BROUGH, T. 1965. Field trials with the acoustical scaring apparatus in Britain. *In* Busnel R.G. & Giban, J. (eds) Colloque sur le problème des oiseaux sur les aérodromes: 279–286. Paris: Institut National de la Recherche Agronomique Press.

BROUGH, T. 1968. Recent developments in bird scaring on airfields. *In* Murton, R.K. & Wright, E.N. (eds) The Problems of Birds as Pests: 29–38. London: Academic Press.

BROUGH, T. 1969. The dispersal of starlings from woodland roosts and the use of bio-acoustics. J. Appl. Ecol. 6: 403–410.

BUSNEL, R.G. & GIBAN G. 1960. Colloque sur le protection acoustique des cultures et autres moyens d'effarouchement des oiseaux. Paris: Institut National de la Recherche Agronomique Press.

BUSNEL, R.G. & GIBAN G. 1965. Colloque sur la problème des oiseaux sur les aérodromes. Paris: Institut National de la Recherche Agronomique Press.

BUSNEL, R.G. & GIBAN G. 1968. Prospective considerations concerning bio-acoustics in relation to bird-scaring techniques. *In* Murton, R.K. & Wright, E.N. (eds) The Problems of Birds as Pests: 17–27. London: Academic Press.

CATCHPOLE, C.K. 1978. Interspecific territoriality and competition in *Acrocephalus* warblers as revealed by playback experiments in areas of sympatry and allopatry. Anim. Behav. 26: 1072–1080.

CATCHPOLE, C. & LEISLER, B. 1986. Interspecific territoriality in reed warblers: a local effect revealed by playback experiments. Anim. Behav. 34: 299–300.

CODY, M.L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor 71: 222–239.

COSENS, S.E. & FALLS, J.B. 1984. A comparison of sound propagation and song frequency in temperate marsh and grassland habitats. Behav. Ecol. Sociobiol. 15: 161–170.

DABELSTEEN, T. & PEDERSEN, S.B. 1985. A method for computerized modification of certain natural animal sounds for communication study purposes. Biol. Cybern. 52: 399–404.

DUPUIS, P. 1987. Effarouchement d'oiseaux en agriculture et en aquaculture avec détection microonde. C.R.I.T.T. Lannion: Electronic & Communication Press.

EMLEN, S.T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 41: 130–171.

GOLDMAN, P. 1974. Song recognition by field sparrows. Auk 90: 106–113.

HARTSHORNE, C. 1956. The monotony-threshold in singing birds. Auk 73: 176–192.

INGLIS, I.R. 1980. Visual bird scarers: an ethological approach. *In* Wright, E.N., Inglis, I.R. & Feare, C.J. (eds) Bird Problems in Agriculture: 115–120. Croydon: British Crop Protection Council Press.

KUHRING, M.S. 1965. Equipment used in Canada for dispersing birds. *In* Busnel, R.G. & Giban, J. (eds) Colloque sur le problème des oiseaux sur les aérodromes: 279–286. Paris: Institut National de la Recherche Agronomique Press.

LANGOWSKI, D.J., WIGHT, H.N. & JACOBSON, J.N. 1969. Responses of instrumentally conditioned starlings to aversive acoustic stimuli. J. Wildl. Mgmt. 33: 669–677.

MARLER, P. 1957. Specific distinctiveness in the communication signals of birds. Behaviour 11: 13–39.

MARTEN, K. & MARLER, P. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav. Ecol. Sociobiol. 2: 271–290.

MCGREGOR, P.K. 1986. Song types in the corn bunting *Emberiza calendra*: matching and discrimination. J. Orn. 127: 37–42.

MILLER, D.B. & BLAICH, C.F. 1984. Alarm call responsivity of mallard ducklings: The inadequacy of learning and genetic explanations of instinctive behavior. Learn. Motiv. 15: 417–427.

MORGAN, P.A. & HOWSE, P.A. 1974. Conditioning jackdaws *Corvus monedula* to normal and modified distress calls. Anim. Behav. 22: 688–694.

MORTON, E. 1975. Ecological sources of selection on avian sounds. Am. Nat. 109: 17–34.

MURRAY, B.G. 1976. A critique of interspecific territoriality and character convergence. Condor 78: 518–525.

MURRAY, B.G. 1981. The origins of adaptive interspecific territorialism. Biol. Rev. 50: 1–22.

PEARSON, E.W., SKON, P.R. & CORNER, G.W. 1967. Dispersal of urban roosts with records of starling distress calls. J. Wildl. Mgmt. 3: 502–506.

PETRINOVICH, L. & PEEKE, H.V.S. 1973. Habituation to territorial song in the white-crowned sparrow *Zonotrichia leucophrys*. Behav. Biol. 8: 743–748.

RICE, J.C. 1978. Behavioural interactions of interspecifically territorial vireos. I: Song discrimination and natural interactions. Anim. Behav. 26: 527–549.

RICHARD, D.B. & THOMPSON, N.S. 1978. Critical properties of the assembly call of the American crow. Behaviour 64: 184–203.

RICHARDS, D.G. & WILEY, R.H. 1980. Reverberation and amplitude fluctuations in the propagation of sounds in a forest: implications for animal communications. Am. Nat. 115: 381–399.

ROBISSON, P. 1986. Etude expérimentale des caractéristiques physiques du cri de détresse du vanneau huppé (*Vanellus vanellus*): mise en évidence des paramètres réactogènes au moyen de la synthèse digitale. PhD thesis: Paris XIII.

ROBISSON, P. 1987. L'adaptation des règles de décodage des signaux acoustiques des oiseaux au canal de transmission. Etude appliquée aux cris de détresse du vanneau huppé *Vanellus vanellus*. Comptes Rendus. Acad. Sci. 304: 275–278.

SHANNON, C.E. & WEAVER, W. 1949. The Mathematical Theory of Communication. Urbana: University of Illinois Press.

SHIOVITZ, K.A. & LEMON, R.E. 1980. Species identification of song by indigo buntings as determined by responses to computer generated sounds. Behaviour 74: 167–199.

SLATER, P.J.B. 1980. Bird behaviour and scaring by sounds. *In* Wright, E.N., Inglis, I.R. & Feare, C.J. (eds) Bird Problems in Agriculture: 115–120. Croydon: British Crop Protection Council Press.

SPANIER, E. 1980. The use of distress calls to repel night herons *Nycticorax nycticorax* from fish ponds. J. Appl. Ecol. 17: 287–294.

STEFANSKI, R.A. & FALLS, J.B. 1972. A study of distress calls of song, swamp, and white-throated sparrows (Aves: Fringillidae). II Interspecific responses and properties used in recognition. Can. J. Zool. 50: 1513–1526.

SUGG, R.W. 1965. The development of acoustical bird scaring equipment used in Britain. *In* Busnel, R.G. & Giban, J. (eds) Colloque sur le problème des oiseaux sur les aérodromes: 279–286. Paris: Institut National de la Recherche Agronomique Press.

VERNER, J. & MILLIGAN, M. 1971. Responses of male white-crowned sparrows to playback of recorded song. Condor 73: 56–64.

WILEY, R.H. & RICHARDS, K.D.G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3: 69–94.

WILEY, R.H. & RICHARDS, D.G. 1982. Adaptation for acoustic communication in birds: sound transmission and signal detection. *In* Kroodsma, D.E. & Miller, E.H. (eds) Acoustic Communication in Birds, Vol. 1: 131–181. New York: Academic Press.

ZUCCHI, H. & BERGMAN, H.H. 1975. Long-term habituation to species-specific alarm calls in a song-bird *Fringilla coelebs*. Experientia 31: 817–818.