

## SECTION VIII

### SONG AND VOCALIZATION

#### THE AMOUNT OF INFORMATION OF VARIOUS TYPES OF MOTIF-SONGS WITHIN THE PASSERINES

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Analyses of the motif-songs of many different passerine birds, European, North American and Australian, are gradually revealing a characteristic pattern or style. The further one advances from stereotyped, almost certainly inherent compositions, through bound compositions to free ones, the more clearly does one gain an impression of an open system of communication with varying degrees of productivity, a basic repertoire over and above which the bird can compose a new song.

In the same way, the degree of information increases from birds producing simple calls and short stereotyped songs through songs with a bound composition, when the phrases are repeated with little or no variation, to songs with a free composition. It is now possible to make a model of the relation between the degree of information in the songs of various groups of passerine birds as compared with variability and redundancy.

With an increasing degree of variability or originality without any possibility of predicting the order of elements in a message (a signal like a bird song) we are approaching a maximum of information. The perception of a signal will then depend on the style of the signal and will consequently form a contrast to the maximum information. As an example of the relation of the redundancy to the information in the message, the calls and different types of songbirds' motif-songs have been inserted in the model showing an increasing degree of complexity.

#### A COMPARISON OF OSCINE AND NON-PASSERINE VOCAL PHYSIOLOGIES

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During prolonged loud vocalizations (distress calls) by oscines, pressure in the air sac rises to forty times that of respiration, but tracheal pressure remains near that of respiration or drops to nearly atmospheric. Tidal volume increases by no more than 35 per cent. These and other data suggest that the oscine syrinx can impose a severe resistance to flow. In contrast, tracheal pressure during prolonged loud calls of chickens usually remains well above atmospheric and often parallels pressure in the air sacs. Thus, oscines and non-passerines may be using different techniques to produce and modulate sound. The difference appears to be associated with external labium, a structure not present in most non-passerines and one that could impose the syringeal resistance observed in oscines.

Ability to prolong calls or passages of song may confer as much selective advantage as increased acoustic complexity. Suitable adaptations may be either physiological, e.g. better control of flow, or behavioural, e.g. minibreaths. Such adaptations are not mutually exclusive; their use may vary at the whim of the individual. Various other models will be presented and discussed in the light of studies of pressure, flow and electromyographical events.

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### THE BEGGING AND DESERTION NOTE OF THE HERRING GULL'S CHICKS AS FORERUNNER OF THE ADULT'S WARNING CALL

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The repertoires of unfeathered chicks and adults of Herring Gulls *Larus argentatus* have two different call notes in the chicks and about ten in the adults, from which the chief or call note is divided into several variations and different functions. The so-called yodelling or long-call is a composition of chief notes.

At first, the 'vocables' of adult Gulls seemed to have no connexion with the chicks' calls. From long experience, I noticed a vocal similarity between the chick's intensive begging call, 'tschällele', and the call of the adults, which I characterize as staccato-call. Regarding the vocal forms, circumstances, motivations and social functions in both, I come to the conclusion that there is considerable similarity in the form. Though the chick's begging call may be considered as the forerunner of the adult's staccato, the social functions of the call have changed, so that they now are homologous but not completely analogous.

The ontogenetic development of call notes towards calls of the adults is also found in other non-passerine birds, whose repertoire of calls is otherwise completely innate.

### THE GEOGRAPHY OF DEVELOPMENT OF SONG

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Ability to sing is a variable skill which, as I try to show in my book 'Born to Sing,' can be measured roughly. It varies sharply among species and families, less sharply from region to region or climate to climate. The major zoogeographical regions have rather similar numbers of species with highly developed song. Such species are territorial and visually inconspicuous; nearly all (except the 'virtually oscine' lyrebirds) have oscine syrinxes.

Arid regions are somewhat unfavourable to song because visibility is good. Similarly, the strong light of the tropics (least so in montane cloud-forests) favours visual display. Tropical conditions also favour gregariousness. But these factors reduce the percentages, more than the absolute numbers, of visually elusive, territorial tropical species. Nearly half the complex, musical, imitative or otherwise well-developed songs are by tropical forms.

Some regions which, in numbers or percentages of good singers are subnormal (Arabia, Madagascar, Amazonia, New Guinea, Chile) or supernormal (Mexico, Europe, Sikkim) are cited, with possible reasons for their exceptional status. North America and Queensland seem normal and Australia as a whole (mostly arid but with a moist eastern coast) slightly subnormal.

### MORPHO-FUNCTIONAL SYSTEM AS ADAPTIVE PHENOMENON

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Our conclusions are drawn from the multi-disciplinary study (morphology, physiology, bio-acoustics, ethology) of the adaptive processes optimizing the locational function of the auditory system of birds. These processes are based on the interaction between the

specific acoustic environment, morpho-physiological adaptations of the auditory system and adaptational behaviour.

The auditory system is tuned to the parameters of the important biological signal at the expense of the characteristic of the structures fixed in phylogenesis. Owing to the tuning adaptations the auditory system is always ready to secure an advantage for the biological signal. When the probability of the signal increases the expectation, adaptations are engaged that intensify the tuning of the auditory system to the biologically important signal. Interdeterminate deformations and noise factors of the signal brought about by the varying ecological conditions require that the auditory system should possess the ability to display suitable subtuning change in its characteristics and operating conditions. This is attained at the expense of the subtuning adaptations that are engaged after the detections and primary identification of the signal.

Each section of the auditory system has its own structure and functional specificity and makes use of its own mode of signal transfer, its code and its transmitting substrate. Certain special adaptations optimize the work of every section and provide for the junctions between the sections and the cumulative work of the sections.

The adaptational behaviour determines the character of the adaptive process, its dynamics, participation of individual adaptations and their display. The first phase (expectation) presumes a high probability of the suggested signal, the second phase is detection and preliminary identification as well as a rough localization and the third phase is the final identification and location.

#### **CULTURAL TRANSMISSION OF PATTERNS OF SONG AND ORIGIN OF DIALECTS IN THE SADDLEBACK *PHILESTURNUS CARUNCULATUS***

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The almost flightless Saddleback *Philesturnus carunculatus* has been successfully re-established on four islands, one of which is Cuvier Island. The pair-bond is permanent, is maintained throughout the year, is reaffirmed at dawn and breaks down each evening; these events are brought about by vocal rituals. Territories are maintained throughout the year by a system of mutual avoidance based on very loud songs; there is a stratification of age in which unbonded birds up to a year old are vertically restricted to the lower three metres of the forest where they move freely, while the pair-bonded territorial adults spend most of their time above this level.

Sonographic study of their songs has established that small areas of different dialects developed as the colonization of Cuvier Island proceeded, each dialect centred on one of the original successful males, most of which had been colour-banded. Each dialect was sharply delineated and birds in each area had a highly ritualized song that was extraordinarily different from the others, but similar within the area. After several years some overlap occurred in the dialects and investigation on the island from which the birds were captured for release revealed six of the seven dialectal patterns still persisting there six years after the transfer, but highly significant individual variations occurred within those dialects.

Three males of known parentage have set up territories, all in areas of dialect with patterns of song markedly different from those of their natal areas. A long-established male that shifted from one dialect to another changed its pattern of song to match that of its new location.

Sonographic evidence is provided for an hypothesis to account for the derivation of the patterns of song based on ritualization during ontogeny. The evolution of the system is thought to result from the conflicting pressures of successful countersinging, which places a premium on accurately learning the neighbour's song, and individual

recognition, which has obvious advantages in economy of effort required to maintain a permanent sequestrative social system. The use of dialects has been related to the ecological circumstances and social organization of the species.

### ON THE TYPES OF ANIMALS' VOICES IN A PERUVIAN TROPICAL RAINFOREST

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In a study area of two square kilometres of tropical rainforest crossed by a small river a representative collection of animals' voices was made by tape recorder. About sixty species of mammals, 355 of birds, sixty of frogs and seventy of Orthoptera and Cicadidae have been found in that area. Many animals, specially the birds, have more than one call; the number of different calls (including songs) is probably more than one thousand. The taped calls are analysed and a list of the principal elements of calls in the study area was made. Types of calls and songs in respect to their composition of these elements are studied in detail (examples are shown). Many authors suppose that different species of animals with the same or a very similar voice (with sexual or territorial significance) cannot live together in the same community. For this reason it would be expected that each of the hundreds of calls in the study area would be strikingly different from all others. This diversity was confirmed to occur, although there are some interesting examples of similarity.

### AN ANALYSIS OF BIRD SONG BY USE OF THE A-WHEEL SYSTEM

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Records of the song of the North American Wood Peewee (*Myiochanes virens* Linnaeus) have been analysed by previous workers by means of Markov chain models. In this paper such records are analysed by a new method: a given finite sequence of symbols is taken as the input sequence to a self-organizing system called the 'A-wheel system'. A set of *A* wheels can be interpreted by representation in automata theory as 'acceptor' and from this acceptor one can obtain a sequential machine that can simulate the singing of a given song by an individual bird. The sequential machine has, as an output tape, the sequence of symbols representing a given record of song by the bird. The input tape of the machine consists of a sequence of blank and non-blank symbols. The machine is said to operate autonomously when its input symbols are blanks. When the input symbol is not a blank, the machine prints that symbol. Hence the input sequence indicates a sequence of non-autonomous events in the simulation.

### THE AUDITORY MEMORY AND ITS EFFECT ON THE BEHAVIOUR OF PARROTS

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Young Grey Parrots *Psittacus erithacus* were confronted with specially selected auditory patterns vocalized by human beings as social partners. The selected patterns were: single whistles; single harmonics; sequences of whistles; sequences of harmonics (human words); combinations of sequences of whistles and harmonics. Some units of sets of the first two of these were given in correlation to distinct situations relevant to the

birds. Some units of sets of the remainder were taught to the birds, with and without additional commands ('speak slowly', 'speak very slowly').

After the birds had learned the vocal programme, we investigated which of the learned patterns were used in correlation with special situations, how the birds responded to variations and new combinations of the patterns produced by the communicating partner and how the birds themselves reproduced the patterns when vocalizing them without any relation to a partner ('vocal play'). The birds used the vocal patterns not only in the same way as given and learned. They produced new combinations and special variations of the patterns. The findings elucidate the effect of memory and its subsystems on the vocal behaviour of the Grey Parrot. (The results could be compared to observations made on other species of parrots).

### UNDIRECTED SONG IN POEPHILA GRASSFINCHES ESTRILDIDAE

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Most species of grassfinch studied to date sing their song-phrase in two different circumstances: courtship song is directed by the male at the female a few centimetres away seconds before she invites copulation; undirected song is inhibited by the sight of the female and produces no response. Courtship song has a sexual function and undirected song has a social function in some species but in most it is either unknown or functionless. In *Poephila* undirected song is most frequent during nest-building and laying; the male entices the female into the nest: then he leaves and sings just outside. The circumstance suggests that the song, which is unique for each male, acts as link between the visually separated mates and bonds the female to the nest. This loosening of the pair-bond in two stages is necessary because the bond is extremely tight and life-long. Once the eggs are laid the undirected song ceases because the female is now completely bonded to the eggs and nest and can tolerate vocal as well as visual separation from the male. The performance of undirected song in a group also aids in cohesion of flocks in one species of *Poephila*.