Vocal Communication of the Brown Hawk Owl
<u>Ninox scutulata</u> in Japan

A thesis submitted for the degree of PhD in Zoology

by

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To the praise and glory of God

ABSTRACT

Vocalizations of the largely nocturnal Japanese Brown Hawk Owl Ninox scutulata japonica were studied, with paricular reference to the function of vocal communication. The adult owls were found to have thirteen types of vocalization and three non-vocal sounds with the possible addition of one other vocal sound. Nestlings had four vocal and one non-vocal sound. The development of the vocal repertoire was also studied from captive juveniles. Most of the vocal repertoire was recorded and sonagraphically analysed, and their behavioural contexts were investigated to give an idea of their various functions.

The main function of primary calls was in interactions with conspecific birds from a distance. The daily calling of territorial males was not time-related and appeared to be greatly influenced by the intraspecific environment. Seasonal production was concentrated during breeding activity, showing four peaks which are discussed in terms of territorial, sexual and family interactions. The unusual vocal activity of a replacing male was studied and gave valuable additional information.

Primary calls were also considered to convey different types of information through variation in their physical structure. From the examination of calls in natural conditions and in aggressive responses to playback, variations of frequency and rate were related to location in the territory, the breeding cycle and the caller's motivational state.

There were consistent individual variations in temporal and frequency features of the calls. Playback of neighbour and stranger's calls and that of the mate and other females' calls at various locations in the territory elicited differential responses, suggesting individual recognition by voice.

A general description of the species, including their classification, distribution, migration and inter-racial differences, is also given.

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CORRIGENDA

	Mistake	Correction
p.2, 1.3	paricular	particular
p.21, 1.28	streetlamps	street lamps
p.106, 1.30	Firsly	Firstly
p.150, 1.35	Hutchinson	Hutchison
p.151, 1.21	view	viewer
Fig. 2-5C	The Y-axis is wrongly labelled. Deduct each value by 0.5 kHz.	

1. INTRODUCTION

1.1. The Aims of the Study

The background to this work lies in the many recent studies of vocal communication in a variety of avian species. These studies were made possible by remarkable advances in reliable sound-recording, analysis and playback systems. The majority of research has been on the song of passerine birds, as shown by the recent extensive review edited by Kroodsma and Miller (1982). Most research has been carried out on songs of the oscines rather than their calls. As a general rule, songs are long and complex in structure and produced by males in the breeding season, whereas calls are shorter and simpler and are produced by both sexes throughout the year. The long-standing question of whether songs are territorial or for courtship has been discussed by workers who have used a combination of field observations and playback experiments (Morse 1970; Lein 1972, 1978; Peek 1972; Catchpole 1973, 1977; Krebs 1976). Non-oscine birds do not possess songs, and their vocal repertoire consists only of calls. However, one call is generally recognized as a primary call, which is characteristic to the species. It will be suggested in this study that the primary call may play an equivalent role to oscine songs.

The relevance between physical structure and the information encoded in the signal has been another important aspect of study of vocal communication (Marler 1957, 1967; Morton 1977, 1982). The modality of physical structure characterized as conformity and variability encodes different kinds of information. Firstly, stable features of physical structure encode the information for identity at different hierarchies such as species, sex, individual and so on. Information about identity has been investigated in oscine songs (e.g. species: Bremond 1968, 1976; Emlen 1972; Shiovitz 1975, local population and kin: Marler & Tamura 1964; Thielcke 1969; Baker et al 1984, neighbours: Weedon & Falls 1959; Emlen 1971; Brooks & Falls 1975ab; Falls & Brooks 1975, mates: Beletsky 1983a; Ritchison 1983a). Non-oscine calls have also been investigated (e.g. species: Van der Weyden 1975; Hjorth 1976; Massey 1976, neighbours: Falls & McNicholl

1979, mates and sex: Hutchison et al. 1968; White & White 1970; Jouventin 1972; Brooke 1978; James 1984, parent-young: Tschanz 1968; Beer 1970; Evans 1970; Stevenson et al. 1970). Secondly, variable features carry information concerning the probability, intensity, relative stability and direction of behaviour (Smith 1977a). Graded signals have been suggested to carry motivational information in primates (Marler 1965; Green 1975) and in birds (Huxley & Wilkinson 1977). Without mentioning the highly variable and complex song structure in oscine songs, variability has been one of the important characteristics during the evolution of vocal communication. It is hoped that knowledge of the physical structure and encoded information content compiled in this thesis will contribute something to the study of vocal communitation in birds.

In general, crepuscular and nocturnal owls are believed to rely more upon acoustic than visual communication. To date observations on vocalizations have been reported in a wide variety of owls. Complete vocal repertoires have been constructed for some species of owls both in captivity (Scherzinger 1974, 1980) and in the wild (Martin 1973a; Forsman et al. 1984), but more studies on wild owls are needed. Individual differences in the primary calls have been noted by several authors. However, difficulty in visual observation during the night has prevented researchers from working further on the subject. Attempts at playback experiments brought only inconclusive results in the Tawny Owl Strix aluco (Hirons 1976). The Japanese Brown Hawk Owl Ninox scutulata japonica, a mainly nocturnal species (see Plates I and II), is relatively easy to observe at night. The aim of this study is to reveal as much as possible about its behaviour in the wild state and particularly its vocal communication. It is hoped that this work would provide evidence of the ability of the owl to communicate by the use of vocal sounds. The following points will be considered in detail:-

1. The vocal repertoire of adult birds, and their physical structure, contexts and functions (Chapter 2).

2. The nocturnal and seasonal production of male primary calls, the

PLATE I

An adult Japanese Brown Hawk Owl

PLATE II

A juvenile Japanese Brown Hawk Owl

effect of various environmental conditions (Chapter 3).

3. The role of male primary calls in aggression and territorial behaviour (Chapter 4).

4. The role of primary calls in individual recognition (Chapter 5).

1.2. The Brown Hawk Owl

Ninox scutulata was first described by Raffles in 1822. The common name 'Brown Hawk Owl' was used in checklists (Vaurie 1965; the Ornithological Society of Japan 1974ab; Gruson 1976; Howard & Moore 1980) and has been extensively referred to by successive authors since 1862 (Jerdon). Later, it also became known as the 'Hawk Owl' in some of the literature published between 1927 (Robinson) and 1969 (Sálim), and recently as the 'Oriental Hawk Owl' (Delacour & Mayr 1946; Grossman & Hamlet 1964; Voous 1964; Sparks & Soper 1970; Harrison 1973; Everett 1977; Clark *et al*. 1978). In the present work, the first common name, 'Brown Hawk Owl', is used, as it is the original common name and more closely describes its appearance than the other names.

The Brown Hawk Owl is a medium-sized brown bird, normally 254-320 mm in length. It has a hawk-like appearance, and the facial disc and ear tufts, which are common characteristics of other owls, are absent. The sexes are generally considered to be alike in size and appearance. However, males tend to be bigger than females (Ripley 1953; Mishima 1956; Ripley & Rabor 1958; Dement'ev 1966).

It is widely distributed through Asia (Peters 1940; Vaurie 1965; Howard & Moore 1980). This vast range is considered to be inhabited by eleven races (see Fig. 1-1A). In Japan, *N. s. japonica* is one of the six breeding strigidine species. It is a common summer visitor throughout the country. Japanese people, who are very conscious of the seasons, associated the arrival of the owls with fresh plant growth in spring and call them by the Japanese name of 'Aoba-zuku'. 'Aoba' (青葉) means fresh green leaves and 'zuku' (木菟) an owl.

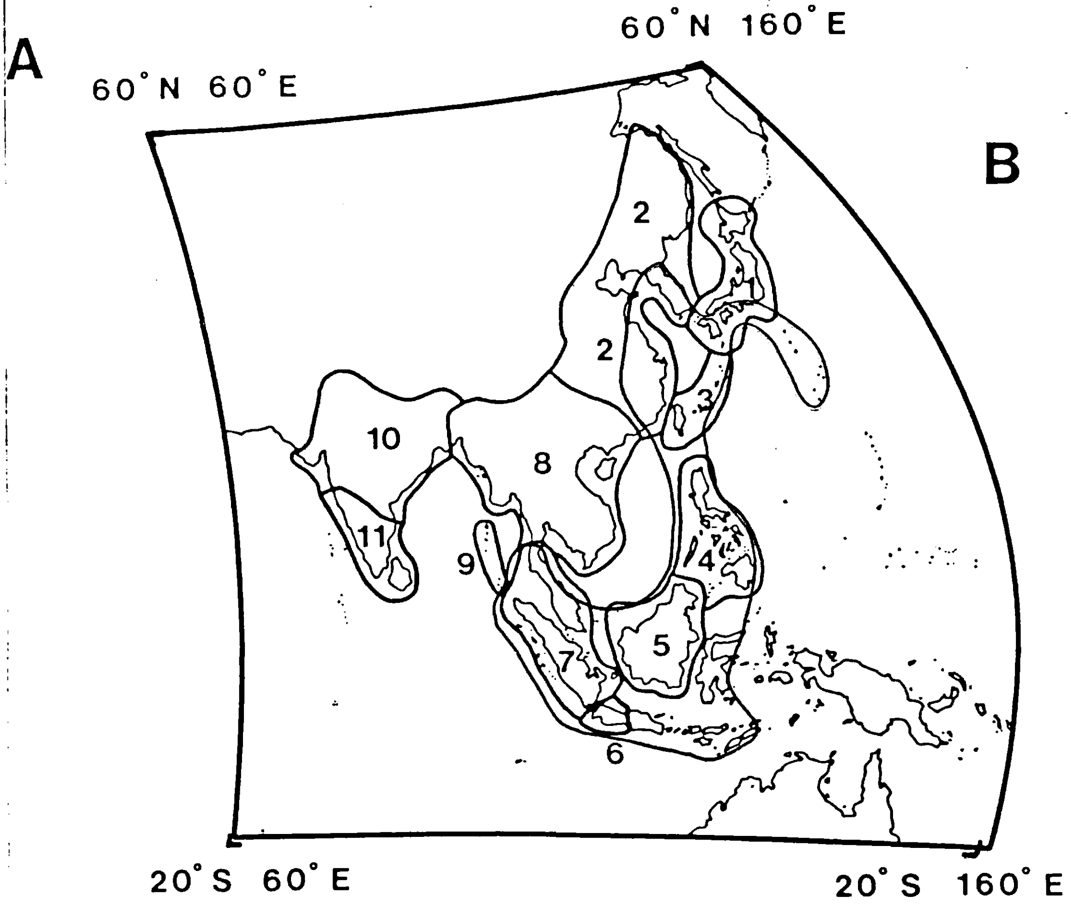


Fig 1-1. Distribution of the Brown Hawk Owl. **A**, eleven races of Ninox scutulata: (1) japonica, (2) ussuriensis (or macropterata), (3) totogo, (4) randi, (5) bornensis, (6) javanensis, (7) scutulata (or malaccensis), (8) burmanica, (9) obscura, (10) lugubris, (11) hirsuta. Nominate scutulata has been misguidedly applied to N. s. japonica, Malayan and Sumatran migrants from the north (e.g. Peters 1940; Vaurie 1965; Howard & Moore 1980). The type described by Raffles (1822) is darker and smaller than the migrants. From tangible evidence, Dickinson (1975) concluded that nominate scutulata correctly refers to Malayan and Sumatran residents, N. s. malaccensis (Baker 1927; Mees 1970). There are disagreements in the boundary between the two northern races of japonica and ussuriensis, at east China from Kiangsu to Fukien and also at central and south Korea (Peters 1940; Kiyosu 1965; Vaurie 1965; Dement'ev 1966; the Ornithological Society of Japan 1974ab; Zheng 1976; Etchécopar & Hüe 1978; Howard & Moore 1980). **B**, winter ranges of N. s. japonica and N. s. ussuriensis are shown as a combined area.

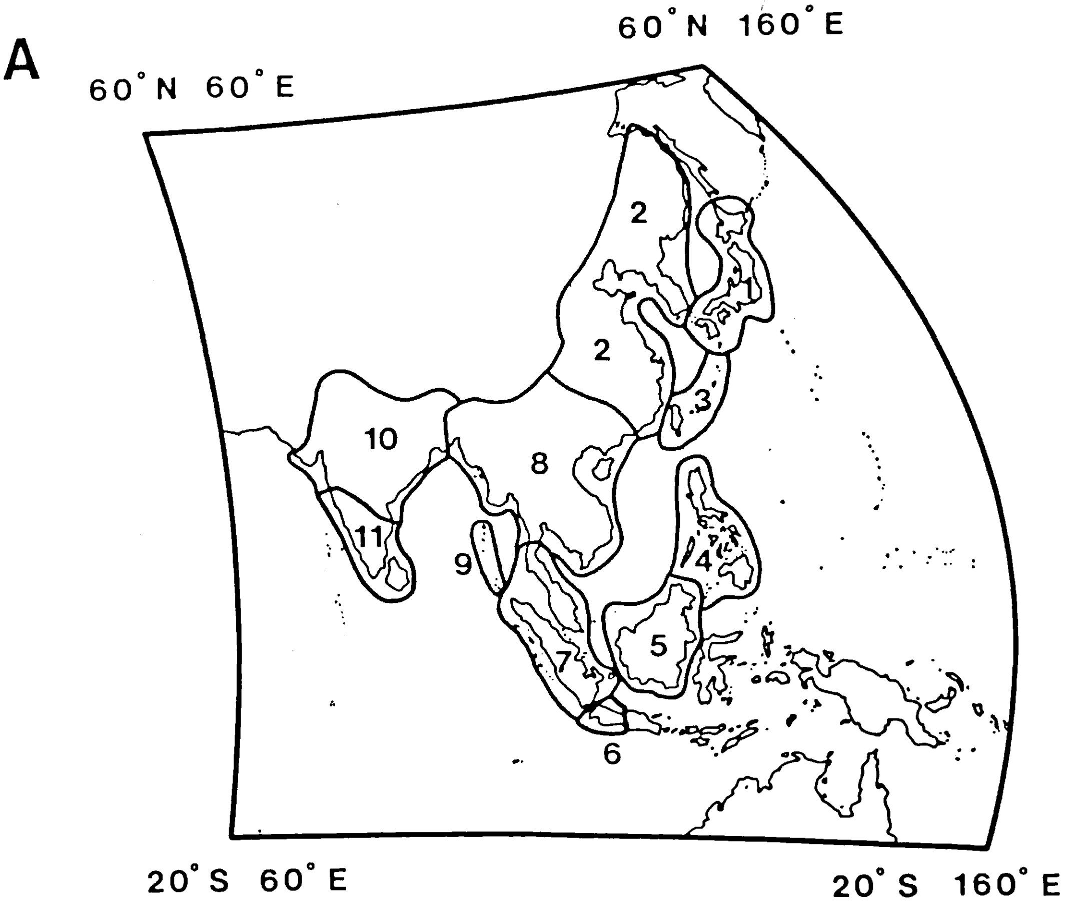


Fig 1-1. **Distribution of the Brown Hawk Owl.** **A**, eleven races of Ninox scutulata: (1) japonica, (2) ussuriensis (or macropterata), (3) totogo, (4) randi, (5) bornensis, (6) javanensis, (7) scutulata (or malaccensis), (8) burmanica, (9) obscura, (10) lugubris, (11) hirsuta. Nominate scutulata has been misguidedly applied to N. s. japonica, Malayan and Sumatran migrants from the north (e.g. Peters 1940; Vaurie 1965; Howard & Moore 1980). The type described by Raffles (1822) is darker and smaller than the migrants. From tangible evidence, Dickinson (1975) concluded that nominate scutulata correctly refers to Malayan and Sumatran residents, N. s. malaccensis (Baker 1927; Mees 1970). There are disagreements in the boundary between the two northern races of japonica and ussuriensis, at east China from Kiangsu to Fukien and also at central and south Korea (Peters 1940; Kiyosu 1965; Vaurie 1965; Dement'ev 1966; the Ornithological Society of Japan 1974ab; Zheng 1976; Etchécopar & Hüe 1978; Howard & Moore 1980). **B**, winter ranges of N. s. japonica and N. s. ussuriensis are shown as a combined area.

In the Shizuoka prefecture, people even simply say 'Aoba' (Kiyosu 1965). It breeds in the main islands, Izu Islands (all islands except Shikine-jima and Aoga-shima), and possibly other coastal islands such as Sado, Oki, Tsushima and Iki (Seebohm 1892; Kuroda 1922a; Takatsukasa & Ikeda 1936; Peters 1940; Kiyosu 1965; Vaurie 1965; Higuchi 1973; the Ornithological Society of Japan 1974ab; Howard & Moore 1980). Their winter ranges are shown in Fig. 1-1B as a combined area with those of another migratory race N. s. ussuriensis.

Japanese Brown Hawk Owls have been reported from many different types of country from lowlands to hills and mountains up to 1000 m above sea level. In general, they are found in forests and woodlands consisting of broad-leaved deciduous and broad-leaved evergreen trees mixed with needle-leaved trees, and often on the edge of forests. They are also associated with human habitation, such as the woodlands of Shinto shrines and Buddhism temples, and well-wooded parks and gardens (Yamashina 1961; Kiyosu 1965; Kobayashi 1976; the Wild Bird Society of Japan, Shizuoka Chapter 1982).

Brown Hawk Owls are known to be mainly insectivorous. They also hunt frogs, lizards, small snakes, small birds, mice, small bats, and crabs (Armstrong 1876; Robinson 1927; La Touche 1931-1934; McCann 1933; Ishizawa 1934; Hoogerwerf 1949; Ikeda & Ishizawa 1949; Kiyosu 1965; Dement'ev 1966; Smythies 1968; Sálim & Ripley 1969; Abe et al. 1979; Taniguchi 1983). Hunting grounds consist of a perch with a good view and an open space approximately 10-20 m from the perch. The birds are often seen hunting from tree stumps and bare branches on forest edges, isolated trees in open fields, and also on river banks. In the urban environment they utilize television aerials and electric wires in the vicinity of streetlamps which attract moths and beetles.

Brown Hawk Owls are monogamous and maintain the pair-bond for years unless one of the pair dies (Masuda 1974). They are regarded as single-brooded. Due to their migratory habit, Japanese birds have a shorter breeding season (May-July) than the southern sedentary races (Kiyosu 1965; Sálim 1979). The owls arrive in Japan from early April to early May and stay in the breeding area until late September - early October. The owls return to the same breeding sites every year. On arriving at breeding sites, males start to produce primary calls and engage in interactions with other conspecific birds in the surrounding area, by countersinging, confrontation and fighting. By mid-May territory boundaries are established. The terriroty has two zones. The central zone is an area within about 100 m of the nest, where basic needs for individual maintenance and breeding activity are fulfilled. The outer zone surrounds the central zone and extends outwards to approximately 200 m from the nest. Males regularly visit to patrol this latter zone, and territorial encounters and countersinging take place frequently.

1.3. Study Areas

1.3.1. Zushi

Field work was carried out mainly at Zushi during 1974-1981. Zushi is situated in the neck of the Miura Peninsula, 35°18'N, 139° 35'E (see Fig. 1-2A). It has developed as one of the satellite cities of the Tokyo megalopolis and Keihin industrial area. The study area was a narrow piece of land along the River Tagoe, facing Sagami Bay to the west (see Fig. 1-2B). To the south of the study area, low hills up to 50-100 m above sea level with complicated systems of narrow valleys, extended both east and west. While the south-eastern hilltops had been stripped and flattened for the development of residential areas, hillside forests provided a rich natural environment. The forests were mainly composed of deciduous broad-leaved trees such as *Prunus jamasakura*, *Quercus serrata*, *Stachyurus praecox*, *Zanthoxylum ailanthoides*, *Arundinaria chino*, and evergreen broad-leaved trees such as *Castanopsis cuspidata* var. *sieboldii*, *Quercus salicina*, *Q. acuta*, *Ilex integra*, *Machilus thunbergii*, *Camellia japonica*, *Aucuba japonica*. Such forests were often mixed with coniferous plantation consisting of *Cryptomeria japonica*, *Chamaecyparis obtusa*, *Neolitsea sericea*, *Cinnamomum japonicum*, *Liriope platyphylla* (Miyawaki *et al*. 1971). To the north of the study area, a narrow plain spread to another row of low hills which were up to 50 m high. This plain was almost completely

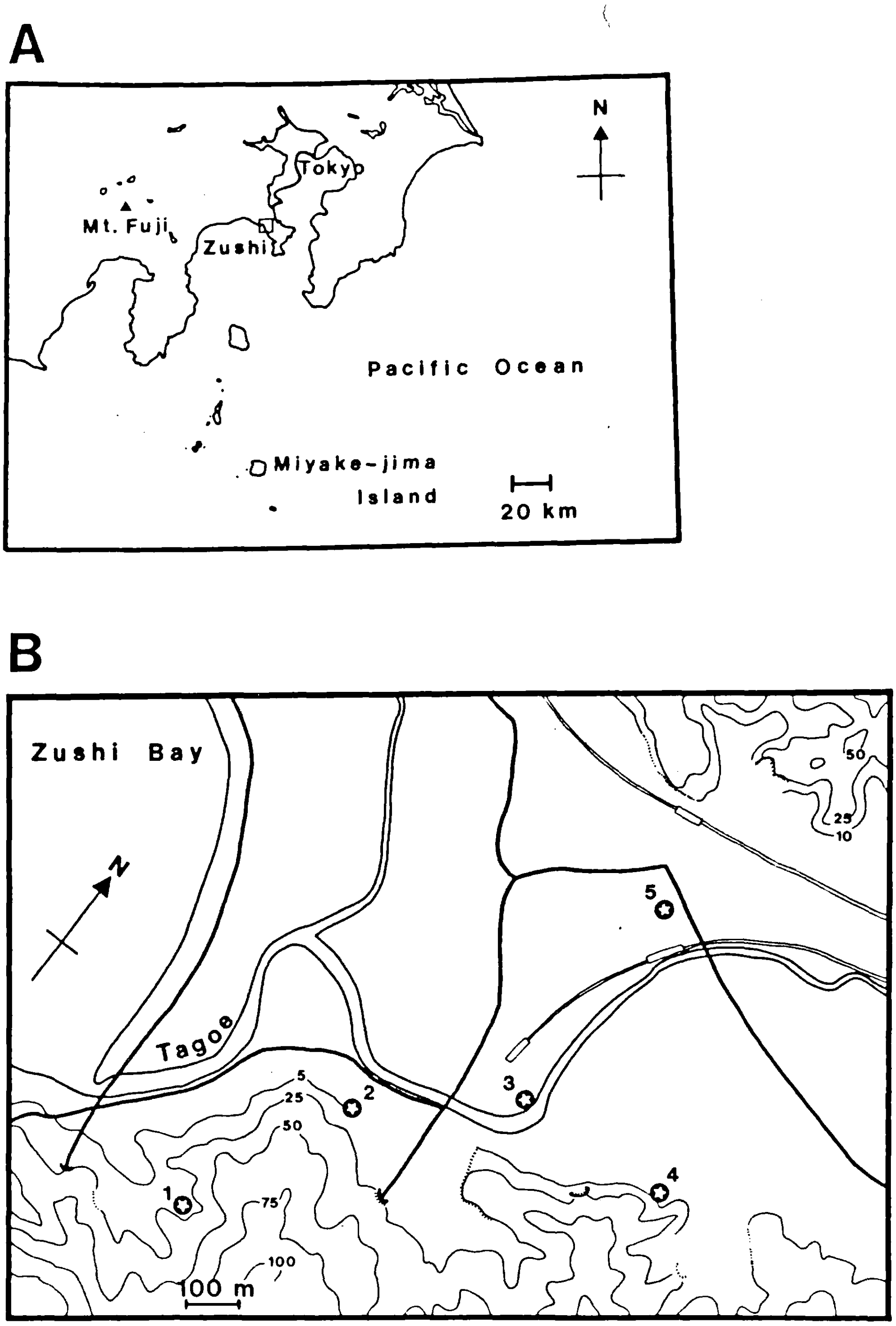


Fig. 1-2. Study Areas. A, location of Zushi and Miyake-jima Island in Japan. B, study area in Zushi. Nest sites studied in 1981 (stars): (1) Fuboku, (2) Rokudai, (3) Sotaiji, (4) Kongoji, (5) Kamegaoka. Main roads (bold line), railways (double lines) and stations (rectangle) are also shown.

residential, and towards the seashore and hills there were quieter quarters with gardens. The owls were found in housing areas with gardens and cultivated fields surrounded by hillside forests (see Plate III). They also used residential areas away from forests, provided that suitable nesting trees and easy access to wooded quarters were available. Territory size was between 0.15 and 0.20 km^2, and the nests were found in *Zelkova serrata* and *Castanea sativa* at a height of 6-18 m from the ground (see Plate IV).

1.3.2. Miyake-jima Island

Miyake-jima Island was visited for short periods in April and June during 1980-1981. The island is one of the Izu Seven Islands and is situated at approximately 150 km south of Zushi in the Pacific Ocean (see Fig. 1-2A). The coast was studded with villages, which depended upon fishery, agriculture and tourism. The study area was a strip of land on a gentle slope 40-100 m above sea level on the northern foot of volcanic Mt. Oyama. The area extended east and west along the road and consisted of well-developed evergreen broad-leaved forests (e.g. *Castanopsis cuspidata*, *Machilus thunbergii*, *Camellia japonica*, *Neolitsea sericea*), deciduous broad-leaved forests (e.g. *Alnus sieboldiana*, *Mallotus japonicus*, *Styrax japonica*, *Ligustrum ovalifolium* var. *pacificum*, *Morus australis*, *Celtis sinensis*, *Hydrangea involucrata*, *H. macrophylla*, *Stachyrus praecox*, *Weigela coraeensis*), needle-leaved plantations (e.g. *Cryptomeria japonica*), housing areas and patches of cultivated field. The eastern half of the study area was more populated by man than the western half.

The population density of Brown Hawk Owls at Miyake-jima Island was higher than at Zushi with a territory size of 0.05-0.06 km^2. However, it was less easy to observe the owls because of the thick vegetation and low illumination. As a consequence, observation spots were limited to well-illuminated open places, such as parks, car-parks, graveyards and roadsides.

PLATE III

Nesting environment of the Japanese Brown Hawk Owl

PLATE IV

A nest of the Japanese Brown Hawk Owl

2. THE VOCAL REPERTOIRE

2.1. Introduction

The Japanese Brown Hawk Owl has been named locally as 'Pon-pon dori', 'Hou-hou dori', 'Ho-ho dori' (Kiyosu 1965), 'Teku-po' and 'Yoshi-ko' (Momiyama & Nomura 1919) after the acoustic characteristics of the main vocalization 'k.hoo-k.hoo'. However, no other vocalizations of the owl have been described apart from brief accounts (Hayashi 1902; Kuroda 1914; Kawaguchi & Ikemura 1920; Kawaguchi 1937; Ito et al. 1979). The present chapter describes the vocal repertoire of the adult and its development. The physical features are studied by sonagraphic analysis of recorded vocalizations in the field and captivity. The behavioural contexts are investigated and interpreted into messages, meanings and functions following Smith (1965, 1966, 1977ab). Information can be defined as that which permits choices to be made. Messages are a kind of information encoded in a signal and shared among animals while communicating. They are deduced from the caller's behaviour and non-behavioural nature. Meanings are specific to the recipient of signal, and are interpreted from the recipient's response to the signal. Functions are the short-term and long-term consequences of the signal which increase the fitness of individuals and bearers of particular genes. Functions can be different between the caller and recipient, and also among classes of recipients.

2.2. Methods

2.2.1. Birds

During 1976-1979, the study of the vocal repertoire of Japanese Brown Hawk Owls was carried out on breeding pairs and their broods which occupied a nest site in Zushi. During 1980-1981, observations were extended to the birds at other nest sites in Zushi, where five neighbouring nest sites were regularly visited. Vocalizations were recorded from a total of twenty-six adult birds (sixteen males and ten females) and three broods. Excursions to Miyake-jima Island supplemented the study. In addition to wild birds, a male juvenile taken from the Zushi population was studied for a year after fledging in 1980-1981. It was kept in a room 4 m x 3 m x 3 m, where the bird had an opportunity to see and hear wild non-parent birds. Recordings of two other captive juveniles were also available in 1978.

2.2.2. Identification of individuals and sexes

As owls are strongly territorial, individuals could be recognized by their presence at particular nest sites. Individuals and sexes could also be identified from their behavioural context, their primary calls, and in some cases by their breast plumage patterns. In 1980, catching and marking owls was attempted to assist the identification of individuals. In order to capture adults, Duonset Balchatris traps with baits (Berger & Hamerstrom 1962) and mistnets coupled with playback of recorded primary calls were tried, but proved unsuccessful. Juveniles were easily caught with a long-handled net during daytime. They were ringed with a registered number ring and reflective colour rings (see Plate II). To attach the latter, a strip of plain aluminium sheet of 7 mm width was put on the tarsus. Then a strip of self-adhesive reflective colour tape was tightly wound around over the ring. During night-time, the colour was strongly reflected in light from an electric torch. During daytime, it was as effective as conventional colour rings, and durable for more than a year.

2.2.3. Observation of owls

Observing the owls at night was not difficult in Zushi. They were familiar with humans and allowed observers to approach close. Various sorts of illumination in residential quarters, such as street lamps and gate-lamps, largely supplemented the moonlight to provide sufficient light to watch the owls. Residential areas were open enough to follow them visually. Television aerials and electric wires provided well-exposed perches. The owls were mainly observed with 10 x 50 Topcon and 7 x 30 Nikon binoculars at a distance of up to 100 m. In 1980, a NEC Noctovision NVD2001 (an infra-red telescope 4.2 x 75) with an infra-red torch IRW2001 and a battery NVC2001 was used to observe the birds near the nest. A hide was used near the nest particularly in the rainy season. Otherwise observers either made use of natural hides or simply kept stationary.

2.2.4. Recording sounds

Vocalizations for sonagraphic analysis (see 2.2.5.) were recorded during 1980-1981, using a Nagra 4.2 tape recorder coupled with a Grampian DP4 dynamic microphone. A windshield was used for most of the time. Sony UHL BL tapes were operated at a tape speed of 19 cm per second. The frequency response of the system was 30-15000 Hz, which was sufficient for the owls' vocalizations. A Grampian 609 mm aluminium spun parabolic reflector of 178 mm focal length was used to record high-frequency calls of nestlings and young fledglings. Adult calls were recorded without the reflector, since it cancels reflected sound waves partially by direct sound waves in the frequency range between 500 and 1000 Hz, where adult calls tended to have fundamental frequency (Patchett 1973; Fisher 1977). The recordist either waited where the owls perched or approached without disturbing them. The distance from calling birds was 5-15 m.

2.2.5. Analysis of recorded sounds

The Nagra 4.2 tape recorder was coupled with the following two types of analysers:-

1. A Uniscan spectrum analyser Model 4500 facilitated visual scanning of recordings. Frequency ranges used were 1 kHz, 5 kHz and 10 kHz, and the time windows 0.125 s, 0.0625 s and 0.0125 s respectively.

2. A Kay Sonagraph 6061B was used to obtain sonagrams. The

frequency range of 80-8000 Hz was set on the analyser. Sonagrams were prepared in the range of 80-8000 Hz or 40-4000 Hz by manipulating the playback speed of recorded sounds. Two types of trace were made: wide-band traces for accurate prints of temporal and harmonic structure and narrow-band traces for detailed prints of frequency structure.

2.2.6. Physical structure of vocalizations

An element of vocalization refers to a piece of continuously produced sound. It may be composed of parts which are visually recognizable as separate blocks. For each type of vocalization, up to twenty elements per bird were sampled. The following physical dimensions were measured for elements or parts:-

duration (ms)
duration of interval between elements (ms)
maximum fundamental frequency (Hz)
minimum fundamental frequency (Hz)

For each physical dimension, a mean, its standard error, standard deviation and coefficient of variation (CV) were obtained. CV is a convenient statistic to consider the degree of variation of a sample in a ratio to the mean (%):-

$$CV = 100 \times \frac{\text{standard deviation}}{\text{mean}}$$

CV at less than 10% was considered to have a small degree of variation (Simpson et al. 1960). CV was mainly used for comparison of variations in temporal structure, while standard deviation was applied to compare those in frequency structure.

In addition, harmonic structure was classified into the following six categories which indicate relative strengths of harmonic:-

0 - absent
1 - vague
2 - weakly present

3 - clearly present
4 - strongly present
5 - stronger than the fundamental frequency

Frequency modulations were examined for graded vocalizations. Categories were devised in terms of relative locations of inflection points, as shown in Table 2-1.

Sexual differences in vocalizations were tested by applying to respective physical dimensions one-way analysis of variance (ANOVA) with a priori test. Mutually graded vocalizations in the adult vocal repertoire were compared for respective physical dimensions by one-way ANOVA. A priori test was applied to find the relationships of different types (Sokal & Rohlf 1973).

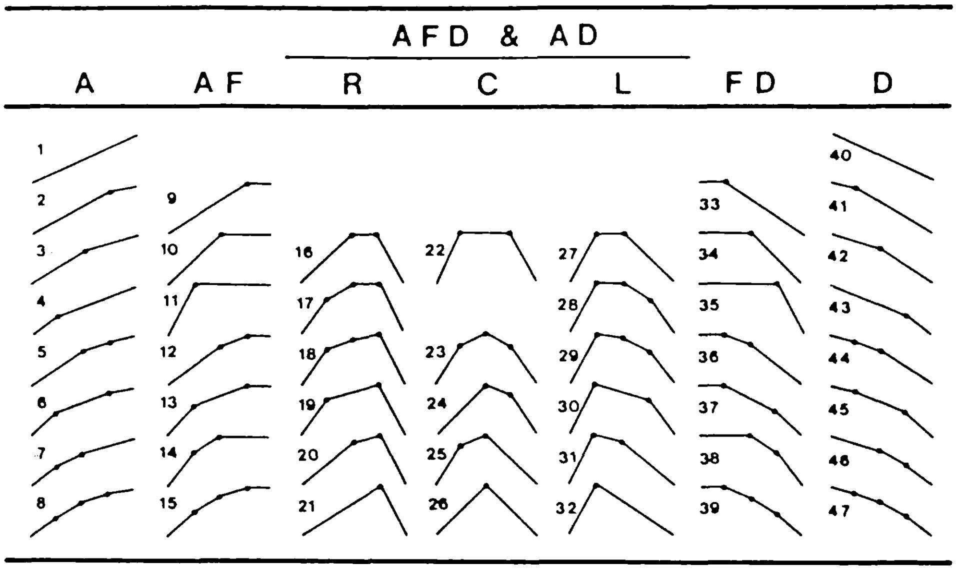
2.2.7. Contexts of vocalizations

Contexts of adult vocalizations observed on 2130 occasions during 1976-1978 were analysed in the following way. Each vocal occasion contained a vocal display, which was either a singly produced call element or audibly identical elements emitted in a bout. The context of the vocal display was examined for the following three phases:-

1. preceding phase up to thirty seconds immediately before the vocal display;
2. simultaneous phase with the vocal display;
3. following phase up to thirty seconds immediately after the vocal display.

For each phase, behaviour of both caller and non-callers (see Appendix B, p. 227), their identities, and information on location and orientation with regard to the nest, mate, offspring, parents or other conspecific birds were noted. The number of occurrences of different behaviours was obtained for the sexes and the three phases. No vocal display occurs at random, and a particular caller of a particular sex should perform appropriately. However, the caller may not necessarily

Table 2-1. Categories of frequency modulation of graded vocalizations.



Other types : F, ———; DA & DFA, upside-down forms of AFD & AD.

Note: A, ascending frequency; F, flat frequency; D, descending frequency; R, inflected towards the right; C, inflected near the centre; L, inflected towards the left.

go through the appropriate actions as circumstances change. Thus, an attempt was made to sort out the most probable behaviour patterns by the binominal test (Siegel 1956; Poole 1974). When behaviour u, B(u), and vocalization v, V(v) are associated, the observed frequency O(B(u), V(v)) was compared with the expected frequency E(B(u), V(v)). The expected frequency was obtained from the following formula:-

$$E(B(u), V(v)) = \frac{O(B(u)) \times O(V(v))}{N}$$

where O(B(u)) = total number of occurrences of B(u)

O(V(v)) = total number of occurrences of V(v)

N = total number of vocal occasions

A probability level of less than 0.05 was regarded as significantly different from chance. When the observed frequency was less than four, the test was not applied. The result was further checked and supplemented by observations during 1979-1981.

2.2.8. Interpretation of messages, meanings and functions of vocalizations

Messages were analysed from the physical feature of vocalizations, behavioural contexts and non-behavioural nature of callers, neglecting the responses of other birds. However, assumptions were sometimes made from the behaviour of recipients as a clue. Here the list of possible messages is given:-

1. Behavioural messages (behavioural selections)
    - attempt to have or avoid interactions
    - attack
    - escape
    - copulation
    - association
    - indecisiveness
    - locomotion
    - incompatible set of behavioural alternatives

- site
- food
- care
- seeking
- attentiveness
- receptiveness

2. Behavioural messages (behavioural supplement)
   - probability
   - intensity
   - relative stability
   - direction

3. Non-behavioural messages
   - species
   - subspecies
   - local population
   - individual
   - age
   - sex
   - breeding condition
   - pairing condition
   - family group
   - location

Definitions of respective messages were based upon those by Smith (1977a). Meanings were interpreted from the response of recipients, and functions were inferred from meanings to the recipients.

2.3. The Vocal Repertoire

Adult Japanese Brown Hawk Owls have thirteen types of vocalization. Eleven out of them were common between the sexes, and one was specific to each sex. They also made two types of non-vocal sounds by the wings. From observations on juvenile birds, a vocal sound 'byahbyah' and a non-vocal noise 'pack' produced by snapping the beak were also thought to be used by adults.

2.3.1. K.hoo (the primary call)

'K.hoo' was the most characteristic vocalization and was produced by both male and female (see Fig. 2-1).

Physical structure

Male primary calls were constructed of the four hierarchical structures: parts, elements, units (see Fig. 2-2) and bouts.

1. Elements and parts

An individual element 'k.hoo' was composed of two parts: part A, 'k', and part B, 'hoo'. 'K' was a low, short sound of a hoarse quality, and 'hoo' was noted for its full, clear sound of a pure tone. 'K.hoo' sounded different between individuals and showed gradation into a different but mutually related call, 'hoh' (see 2.3.2.).

Part A occupied the first 18-33% of element, lasting less than 100 ms and being variable in the duration within an individual (N = 9; see Appendix A-1, p. 208). The individual mean maximum frequency was between 319 and 503 Hz, and the individual mean minimum frequency was between 248 and 476 Hz (see Appendix A-2, p. 209). It was produced at a low amplitude, and tended to diminish quickly as it propagated through the air. Some calls did not have part A.

As for part B, the individual mean duration was between 198 and 245 ms (see Appendix A-1). The duration was less variable within an individual than that of part A (*t*-test for CV values after Bailey (1959): d = 8.999, df = 11.5, $p < 0.001$). The individual mean maximum frequency was between 633 and 772 Hz, and the individual mean minimum frequency was between 458 and 638 Hz (see Appendix A-2). Part B was loud enough to reach up to 300 m from the caller on calm days.

Over the frequency range of 40-4000 Hz, part A exhibited occasional weak harmonics at the second and third, whereas part B showed harmonics from the second to the fifth (see Appendix A-3, p. 210). The third and fifth harmonics tended to be emphasized, and this contributed to the sound quality. A third harmonic added

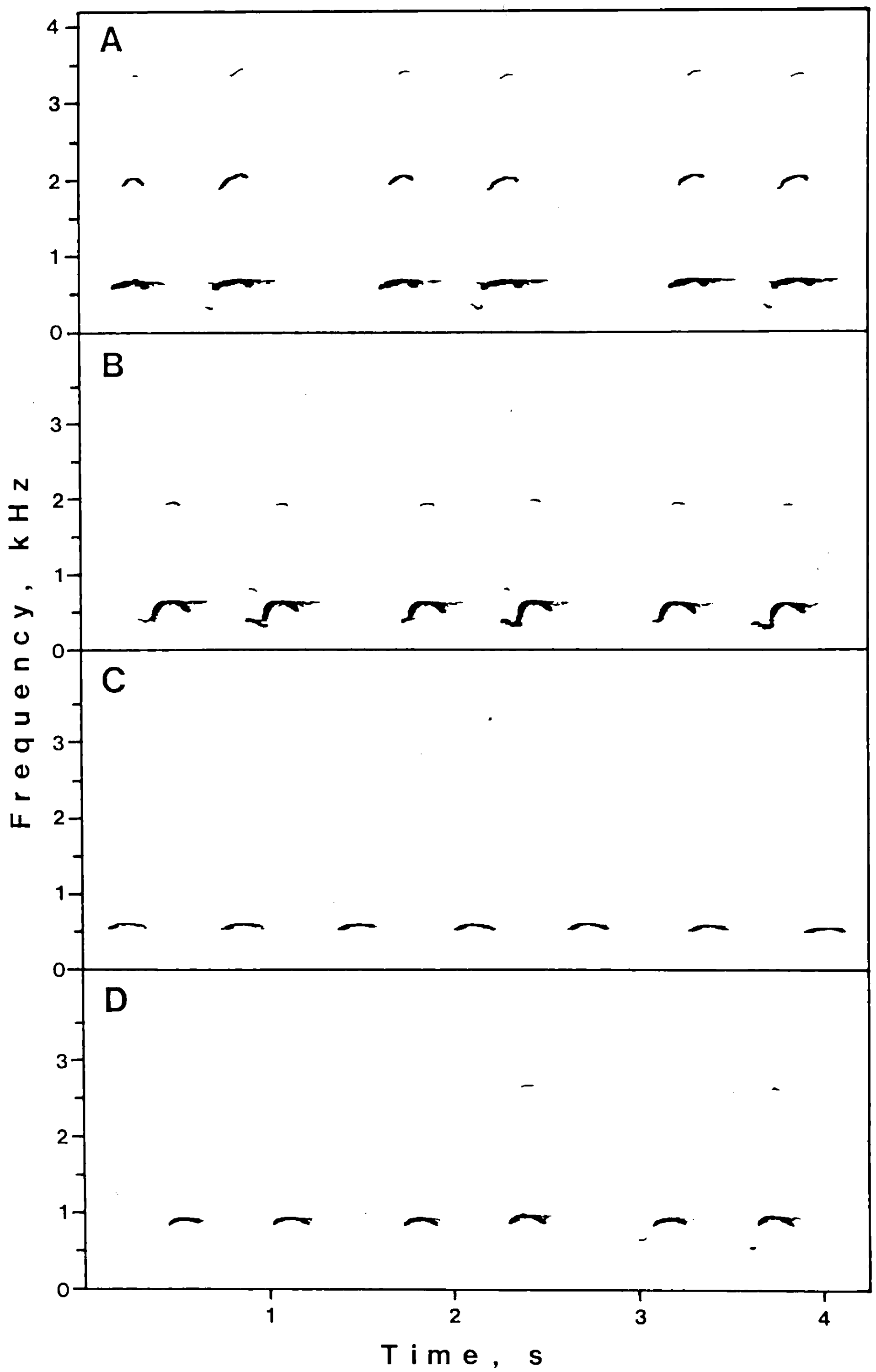


Fig. 2-1. **Sonagrams of Adult Calls.** 1. primary calls 'k.hoo': sonagrams are prepared at narrow-band setting in the range of 40-4000 Hz. Male calls: **A**, **B** and **C**. Female calls: **D**. Unit structure is missing from C.

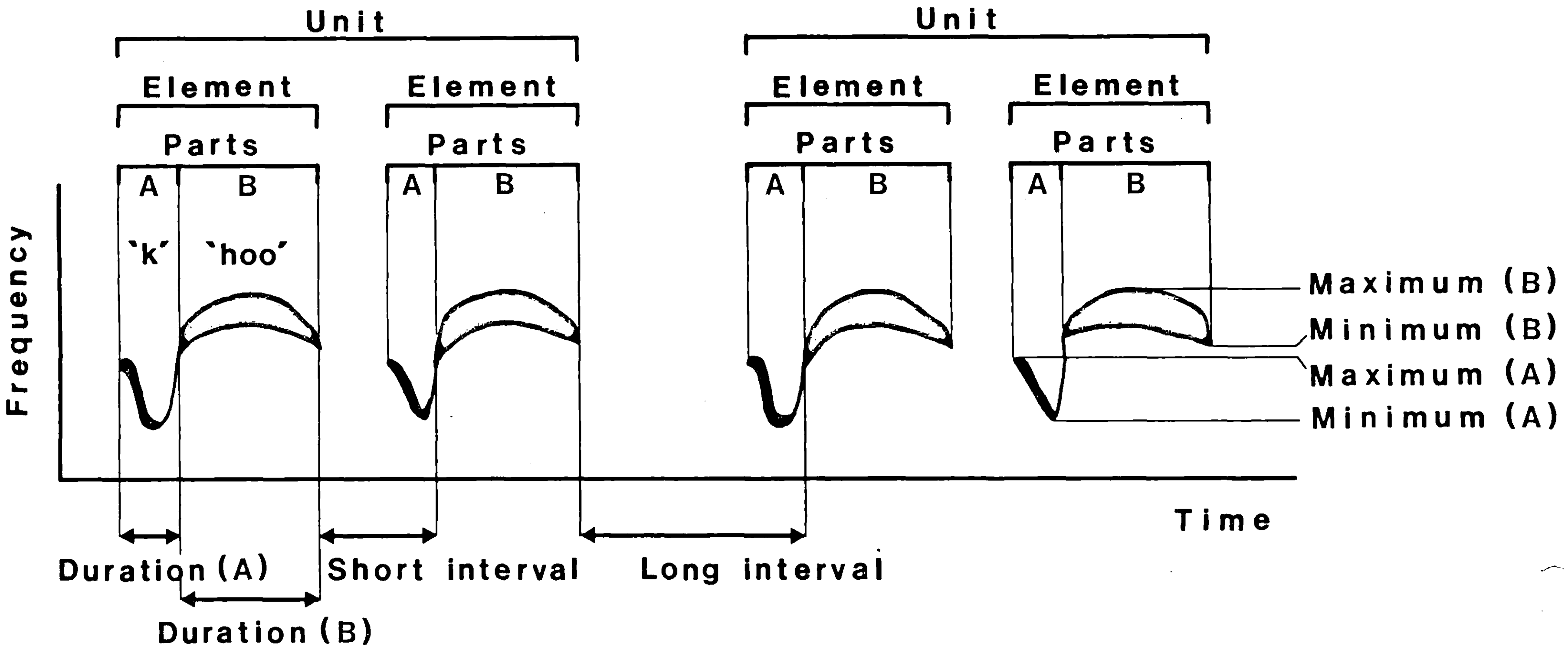


Fig. 2-2. The physical structure of 'k·hoo'.

brilliance and a hollow, throaty and nasal quality, and a fifth a somewhat horn-like quality (Jeans 1937). Types of frequency modulation of part A were most commonly A, F, and DA. The major type of frequency modulation of part B was AFD & AD, the inflection of which was located from the centre to the right half of part (see Appendix A-4, p. 211).

2. Units and bouts

Two elements tended to form a unit as described 'k.hoo-k.hoo' (see Fig. 2-2). The individual mean of a short interval between the elements ranged from 303 to 423 ms. Units were generally repeated more than twice in succession to form a bout as described 'k.hoo-k.hoo, k.hoo-k.hoo.... k.hoo-k.hoo'. Units were separated by long intervals, the individual mean of which ranged from 565 to 850 ms (see Appendix A-1). The temporal structure of the unit was stable, since short intervals had lower variation within an individual than long intervals ($d = 4.117$, $df = 7.4$, $p < 0.001$). However, some individuals did not have the unit structure at all (e.g. Fig. 2-1C). The number of elements in a bout exhibited a skew distribution toward lower numbers ($sk > 0$, see Appendix A-5, p. 212). Males produced most typically 6-8 elements and uncommonly over 20 elements in a bout (N = 4). Frequency fluctuation in a bout provided the intonation. Gradually ascending frequency in a bout yielded a rising intonation, accompanying gradual increase in amplitude.

Female primary calls possessed the same hierarchical structures described for male calls. The individual means of various physical features of female calls (N = 6, see Appendices A-1 and A-2) were as follows:-

part A's	duration	...	69 - 71 ms
	maximum frequency	...	520 - 564 Hz
	minimum frequency	...	439 - 458 Hz
part B's	duration	...	177 - 235 ms
	maximum frequency	...	663 - 837 Hz
	minimum frequency	...	552 - 673 Hz
duration of short interval		...	353 - 448 ms
duration of long interval		...	532 - 1000 ms

While there was no sexual difference in the duration of part A, the duration of part B was significantly shorter in female calls than male calls. Female calls tended to have longer durations for both of the intervals and also to be higher in pitch than male calls (see Table 2-2 for statistics). Patterns of harmonics were not clear in female calls (see Appendix A-3), and females presented more A and AF types of frequency modulation than males (binominal test: $z = 2.862$, $p < 0.01$; see Appendix A-4).

Behavioural contexts

For the details of behaviour before, during and after 'k.hoo', see Appendix B-1 (p. 229).

1. Spontaneous calling

'K.hoo' was most frequently produced spontaneously by solitary territorial males. They occasionally called on the wing but mainly at conspicuous perches in the territory. They changed perches as they called from the outer zone of territory. Males also called near the nest site. Persistent calling was observed from males visiting the nest hollow early in the pre-incubation stage.

2. Interactions with conspecific individuals

When neighbouring pairs or strangers invaded the territory, the resident male immediately orientated itself, approached them, and called 'k.hoo' vigorously and powerfully. Unless invaders retreated, intense vocal interactions developed and sometimes the vocalization switched to 'guf' (see 2.3.3.). Territorial males were likely to attack and chase intruders away from the territory. When a neighbouring male called 'k.hoo' from its territory, resident males orientated and emitted 'k.hoo' in the direction of the calling neighbour. Vocal interactions were delivered in a manner of antiphony or countersinging, and also as a general chorus when several birds were involved. Their mates often approached the dispute site, orientated themselves towards the opponents and also emitted 'k.hoo'.

Table 2-2. Sexual differences in the primary call 'k.hoo' (one-way ANOVA with a priori test)

Physical feature	F_S	df	p
Part A			
- duration	1.074	[1, 98]	$p > 0.05$
- maximum frequency	410.367	[1, 63]	$p < 0.01$
- minimum frequency	92.786	[1, 98]	$p < 0.01$
Part B			
- duration	25.785	[1, 165]	$p < 0.01$
- maximum frequency	63.340	[1, 164]	$p < 0.01$
- minimum frequency	302.504	[1, 165]	$p < 0.01$
Short interval	66.569	[1, 80]	$p < 0.01$
Long interval	5.177	[1, 48]	$p < 0.05$

Note: F_S, sample statistics of F-distribution; df, degrees of freedom; p, probability associated with the occurrence under the null hypothesis of a value as extreme as or more extreme than the observed value.

3. Interactions between mates

Brief exchanges or prolonged antiphonal calling were recorded from a pair perched close together. The male initiated 'k.hoo' near the nest hole. His mate gradually approached the hole, calling 'k.hoo' also. When a female called from a perch or from inside the nest, her mate tended to attend or feed her during the pre-incubation and incubation stages.

4. Interactions between parents and offspring

During the nestling stage, parents often produced 'k.hoo' while being perched near or approaching the nest. The call was immediately followed by nestlings' 'leee' or 'gililili' (see 2.4.). The female parent uttered 'k.hoo' when flying back and forth between fledglings and the site to which she attempted to take her young.

Males tended to produce a bout of 'k.hoo' starting with 'hoh' (see 2.3.2.) when they interacted with their mates and also when they were by the nest in which their mates were sitting. Bouts of 'k.hoo' concluded by 'hoh' were produced after hunting and before visiting the nest with food and followed by nestlings' 'leee' and 'gililili'.

Messages

1. Identity and mating status

'K.hoo' probably carries information concerning species' identity, but an absence of clear dialects suggests that it is unlikely to contain additional information about the identity of local populations. Audible differences among individuals and those between the sexes suggest that it may carry information concerning the individual identity and sex of the caller (see Chapter 5). Unpaired males tended to produce 'k.hoo' more frequently than paired ones (see 3.5.1.), suggesting further information about mating status.

2. Interactional behaviour and supplementary information

'K.hoo' may contain a message about attempting to interact or avoiding interactions. It may also encode a message of seeking behaviour, attempting to gain the opportunity to perform an interaction without specifying the type. These may be from the following set of incompatible alternatives: attack, escape and association. Their conspicuous behaviour during spontaneous calling at an exposed perch seems to facilitate the chance of interactions. However, since callers often performed none of the alternatives, hesitating between selections, 'k.hoo' could also encode a message of indecisive behaviour. The caller may be able to send an additional message about attentiveness to other conspecific birds' primary calls and movement by beaming 'k.hoo' in a particular direction.

Variation in amplitude, frequency and temporal structure seems the most probable method to encode messages about the probability, intensity and relative stability of likely interactions. For example, when birds were involved in a vigorous territorial dispute, they tended to utter calls loudly, persistently and frequently. When members of a pair communicated with each other, their calls were soft, less persistent and less frequent.

3. Sites and distance

'K.hoo' appears to contain a message about the location of the caller, since repetition of short, loud calls with an abrupt start and finish render it easily locatable from a distance (Marler 1957). It may also encode a message about the location of the nest, territory boundary, and the site to which female parents attempt to guide their young. Further, it may carry a message about the distance of the caller, since part A, which attenuates more quickly than part B, can be used as an indicator of travelling distance.

Meanings

The meanings of 'k.hoo' may be summarized as instructions on how to interact with the caller in a beneficial way. To conspecific birds, except for the mate and offspring, male primary calls may be a territorial 'keep out' signal. Since female calls occur only in the presence of the simultaneously calling male during a territorial dispute, they may mean that the female assists her mate in advertising the territory. To unmated females, an unmated male's primary calls may mean that a possible mate is available. To mated birds, the mate's primary calls may mean assurance and reaffirmation. To juveniles, their parents' primary calls may also mean reassurance.

Functions

Functions of primary calls may be that both callers and recipients can choose their location and distance, so that they may pursue the following types of interactions:-

1. Male primary calls
    - territorial advertisement
    - the first line of territorial defence
    - sexual advertisement, attraction and stimulation
    - pair association and coordination
    - nest advertisement and invitation
    - family association and cohesion

2. Female primary calls
    - pair association and coordination
    - sexual stimulation
    - family association and cohesion
    - territorial defence by associating with the male

2.3.2. Hoh

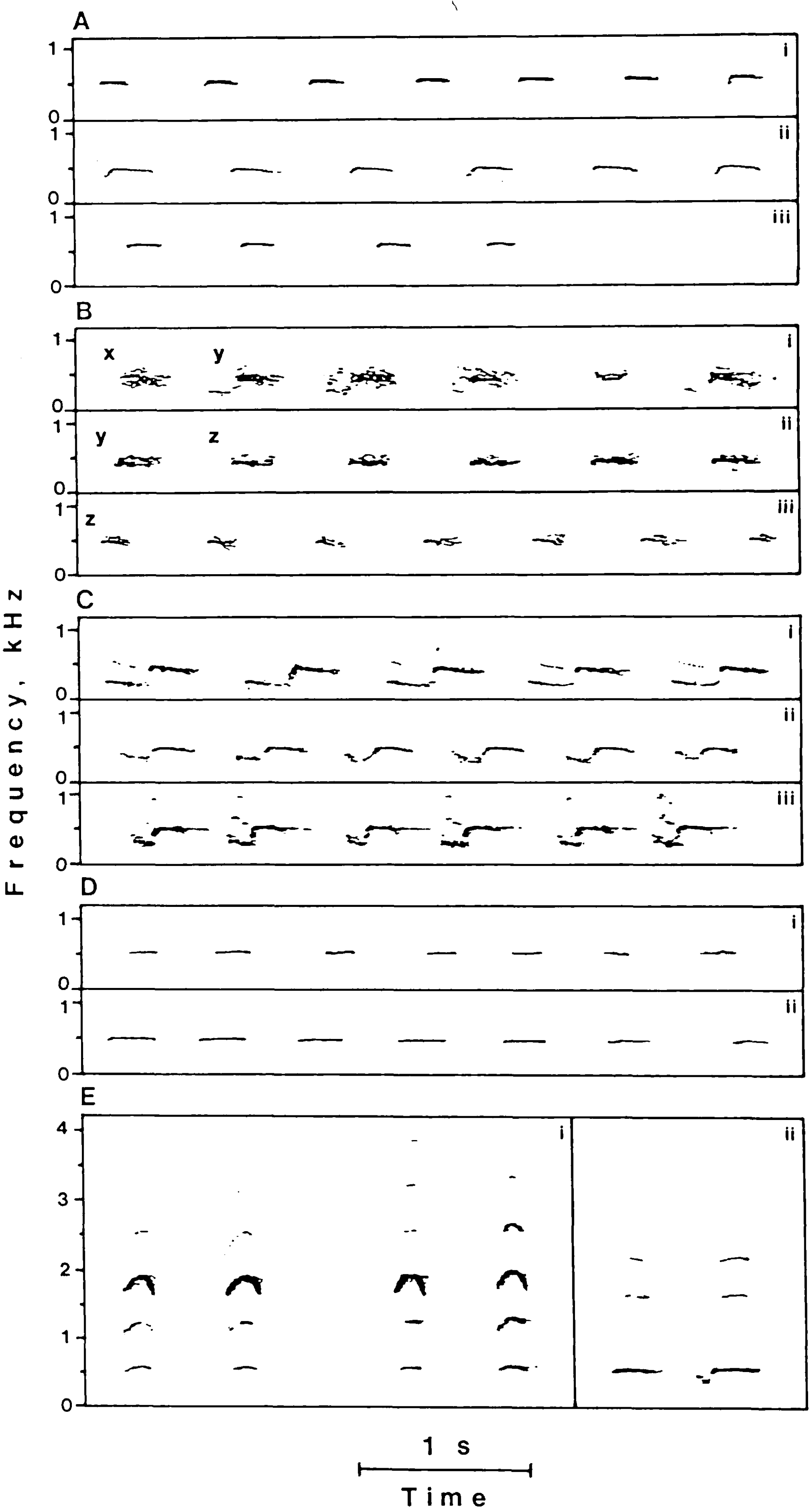
Physical structure

'Hoh' was a low, gentle sound with a hollow quality and did not reach over 100 m. It was produced by both male and female birds (see Fig. 2-3A).

The male 'hoh' was constructed from two parts, A and B. Part A was too faint a noise. The duration was variable with the individual mean between 27 and 157 ms (N = 7, see Appendix A-6, p. 213). The individual mean maximum frequency was from 307 to 420 Hz and the individual mean minimum frequency was from 283 to 335 Hz (see Appendix A-7, p. 214).

Part B also had a variable duration with the individual mean

Fig. 2-3. **Sonagrams of adult calls.** 2. graded calls: 'hoh', 'guf', 'oo.coo', 'poo' and 'hyu'. Sonagrams are prepared at narrow-band setting in the range of 40-4000 Hz. The whole range is shown only when harmonics are noticeable. **A**, 'Hoh' produced by males (i and ii) and female (iii). **B**, 'Guf' produced by female (i) and males (ii and iii). For x, y and z, see the text (p. 47). **C**, 'Oo.coo' produced by males (i and iii) and female (ii). **D**, 'Poo' produced by females (i and ii). **E**, 'Hyu' produced by female (i) and male (ii).


A
B
C
D
E
i
ii
iii
x
y
z
0
1
2
3
4
Frequency, kHz
1 s
Time

between 87 and 252 ms (see Appendix A-6). The individual mean maximum frequency was from 467 to 634 Hz, and the individual mean minimum frequency was from 388 to 530 Hz (see Appendix A-7). Harmonics were seldom observed. The major types of frequency modulations were AF and AFD & AD, the inflections of which were located from the centre to left half of part (see Appendix A-8, p. 215).

The element was repeated in bouts. Short bouts contained two or three elements, while long bouts lasted up to fifteen minutes or longer without noticeable breaks. The interval between elements showed individual means between 403 and 540 ms (see Appendix A-6). It was sometimes constant enough to characterize calling as monotonous murmuring. Other times it was variable enough to give an accelerating or decelerating effect.

Sexual differences in the sound quality was negligible to human ears. The individual mean interval of female 'hoh' was from 409 to 560 ms ($N = 5$, see Appendix A-6) and did not exhibit a significant difference from that of male 'hoh' ($F_s = 0.492$, df = [1, 88], $p > 0.05$). However, the duration of part B of female calls, having a range of individual means over 130-211 ms (see Appendix A-6), was significantly shorter than that of male calls ($F_s = 11.657$, df = [1, 103], $p < 0.001$). The minimum frequency of part B of female calls, having a range of individual means over 451-544 Hz (see Appendix A-7), was significantly higher than that of male calls ($F_s = 25.174$, df = [1, 103], $p < 0.001$). The maximum frequency of part B of female calls, having a range of individual means over 519-584 Hz, did not show a significant difference from that of male calls ($F_s = 3.276$, df = [1, 103], $p > 0.05$). However, female calls lacked frequencies below 500 Hz (see Appendix A-7).

Behavioural contexts

'Hoh' was mainly produced in interactions with the mate and breeding behaviour (see Appendix B-2, p. 231).

1. Close range contact between mates

When a bird perched close to the mate, either or both of them uttered a short bout. It also emitted a short bout before flying away from the mate. Males tended to utter a short bout when attending incubating females.

2. Courtship feeding

Males emitted a short bout as they approached with food and presented it to their mates. Females tended to interact with 'krrr' (see 2.3.7.) before receiving food. The vocal interaction was sometimes prolonged. Males also produced 'hoh' on feeding incubating females in the nest.

3. Pre-copulatory duetting

Males started to call 'hoh' continuously, as they perched next to their mates. Females also uttered 'hoh' but less continuously. Duetting continued while mounting. Calls of both birds changed to 'oo.coo' (see 2.3.4.) as copulation was about to happen.

4. Nest calling

Early in the pre-incubation stage, males called 'k.hoo' in a prospective nest tree and repeatedly visited a possible nest hole (see p. 40). On entering the hole, males' calls shifted to 'hoh' in long bouts. As soon as their mates entered the hole, males ceased to call. Afterwards the pair was often heard duetting 'hoh' inside the nest.

Message-meaning analysis

'Hoh' may not contain messages about the identity of the caller, since vocalizations tended to take place when recognition had been established. However, it may contain a message about close interactions, attempting to associate to different degrees: staying together, courtship feeding, duetting and mounting. The level of association is not always clear until an opportunity is found, suggesting that 'hoh' may encode a message about indecisiveness. The number of elements in a bout may carry a message about the probability, intensity, and relative stability of likely association. To the mate, 'hoh' may mean assurance and reaffirmation in the pair-bond and breeding coordination. It may function to maintain interactions between a pair in close proximity. It may also suppress agonistic and evasive tendencies arising at a short distance from other individuals. It may also coordinate the breeding behaviour.

2.3.3. Guf

Physical structure

'Guf' was a low-pitched, powerful grunt. It was unlikely to travel farther than 30 m. Males emitted it more readily than females (see Fig. 2-3B).

It seemed that 'guf' also had two parts: part A, 'o', and part B, 'guf'. However, part A was neither regular nor loud enough to hear. In male calls, part B showed a widely variable duration between and within individuals, having the individual mean over 173-248 ms (N = 3, see Appendix A-9, p. 216). It occupied a low frequency range, showing the individual mean maximum frequency from 448 to 503 Hz and the individual mean minimum frequency from 392 to 416 Hz (see Appendix A-10, p. 216). It exhibited formation of frequency structures: a cloud over a wide range of frequency (x), double or triple fundamental frequencies in the cloud (y), and one dominant fundamental frequency partially with a cloud (z). As the structure advanced from (x) to (z), raucousness reduced. Most common types of frequency modulation of the main fundamental frequency were AFD & AD, the inflections of which were located from the centre to left half (see Appendix A-11, p. 217). Rarely harmonics were weakly seen at the second and third. The element was repeated at a fairly stable interval, having the individual mean from 412 to 453 ms (see Appendix A-9). Female calls sounded lighter than male calls, which was possibly due to a higher maximum frequency of 568 ± 9 Hz.

Behavioural contexts

When an intense territorial confrontation developed, territorial males switched their vocalizations from 'k.hoo' to 'guf' (see Chapter 4). They were perched close and seldom moved their positions. They faced their opponent firmly, showing the white patches below the carpals. They continuously called 'guf' and were likely to attack the opponent at any moment. Otherwise, they switched back to 'k.hoo', and became silent or withdrew.

Message-meaning analysis

'Guf' may encode a message about incompatible behavioural alternatives, attack and escape. The caller seemed to be in conflict between selections, suggesting a message about indecisive behaviour. The number of elements, rate of repetition and sound frequency may carry a message about the probability, intensity and relative stability of likely behaviour. To conspecific opponents, 'guf' may mean that the caller is aggressive enough to attack. The function may be to control the interaction when the caller's territorial and social state is really threatened. It seems to act as a final threat and the last deterrent before overt aggression.

2.3.4. Oo.coo

Physical structure

'Oo.coo' was a dulcet, cooing sound. It was not loud and did not reach beyond 30-40 m. Both male and female birds produced it (see Fig. 2-3C).

An element of 'oo.coo' showed two parts, A and B. Part A, 'oo', was a low-pitched, sustained sound, covering one-third to half of the element. The individual mean duration of male calls was from 118 to 276 ms (N = 7), showing a high variation within an individual (see Appendix A-12, p. 218). The individual mean maximum frequency was from 238 to 428 Hz and the individual mean minimum frequency was from 181 to 332 Hz (see Appendix A-13, p. 219). Harmonics were often present at the second. Most common types of frequency modulation were D and F (see Appendix A-14, p. 220).

Part B, 'coo', was a higher-pitched, clear, emphatic sound. The duration had a range of individual means over 179-287 ms and was variable within an individual (see Appendix A-12). The individual mean maximum frequency was from 398 to 529 Hz, and the individual mean minimum frequency was from 324 to 480 Hz (see Appendix A-13). Harmonics were observed at the second and third. The types of frequency modulation were mostly AFD & AD, the inflections of which were located from the centre to left half of part (see Appendix A-14).

The element tended to repeat itself a few or more times. The interval between elements was variable between individuals, showing the individual mean between 328 and 532 ms (see Appendix A-12). Sexual differences were not apparent in both temporal and frequency features (see Appendices A-12, A-13 and A-14). However, females called part B in a slightly higher maximum frequency ($F_s = 26.620$, df = [1, 175], $p < 0.001$) and minimum frequency ($F_s = 63.407$, df = [1, 177], $p < 0.001$) than males.

Behavioural contexts

1. Pre-copulatory calling

While mounting, mates changed their vocalizations from 'hoh' (see 2.3.2.) to 'oo.coo'. Males called it until copulation, when they replaced it with 'cheee' (see 2.3.8.). Females sometimes kept calling until after copulation.

2. Intense contact of male to female

Males tended to call 'oo.coo' when they were close to females. Mated males produced it, as they were perched side by side with their mates, and also when they visited them in the nest.

Message-meaning analysis

'Oo.coo' seems to carry a message of sexual interactions. It may also encode a message of seeking behaviour, attempting to gain the opportunity to associate sexually with the opposite sex. However, it may carry a message about indecisiveness, since the level of association is not clear until the opportunity is found. Acceleration in the rate of production towards the moment of coition suggests a message about the probability and relative stability of sexual behaviour. 'Oo.coo' may mean that the caller is sexually receptive. The functions may be to coordinate the sexual behaviour between mates.

2.3.5. Poo

Physical structure

'Poo' was a faint, short-range peep produced by females (see Fig. 2-3D). The duration was about 200 ms with a high degree of variation within an individual. The frequency range was low and narrow around just above 500 Hz. Harmonics were not detected, and the types of frequency modulation were mostly A, F and AF. The element was repeated in bouts and the interval was variable within an individual (see Appendices A-15, A-16 and A-17, p. 221).

Behavioural contexts

Females called 'poo' while attending eggs in the second half of incubation stage. There was no association with their mates' behaviour and other events outside the nest. It is speculated that it is related to communication between the female parent and embryos.

2.3.6. Hyu

Physical structure

'Hyu' was a nasal and slightly shrill sound. Kawaguchi (1937) described it as 'hyoo', 'kyew' or 'hyew'. It reached up to 50 m. Both male and female birds produced it (see Fig. 2-3E).

Male calls tended to sound softer than female calls. The individual mean duration was ranged between 108 and 204 ms (N = 6) and showed a large variation within an individual (see Appendix A-18, p. 222). The individual mean maximum frequency was from 525 to 661 Hz and the individual mean minimum frequency was from 464 to 584 Hz (see Appendix A-19, p. 223). Harmonics were generally observed from the second to the fourth (see Appendix A-20, p. 224). Emphasized harmonics at the third and fourth contributed to the tonal quality: the third for nasality and the fourth for shrillness (Jeans 1937). Types of frequency modulations were mostly AF and AFD & AD, the inflections of which were located from the centre to right half of element (see Appendix A-21, p. 224). The element tended to be repeated in pairs. However, the unit structure was loose due to the large variation of both short and long intervals within an individual. The individual mean short interval was from 327 to 423 ms, and the individual mean long interval was from 560 to 818 ms (see Appendix A-18).

Female calls sounded sharp and could be described as 'kyu'. They were significantly similar to male calls in all the temporal features (see Appendix A-18). However, they were higher pitched than male calls. The individual mean maximum frequency was from 633 to 700 Hz ($F_S = 27.196$, df = [1, 87], $p < 0.001$). The individual mean minimum frequency was from 548 to 588 Hz ($F_S = 70.290$, df = [1, 85], $p < 0.001$).

Behavioural contexts

From the study during 1976-1978 (see Appendix B-3a, p. 233), 'hyu' was significantly associated with parental behaviour in attending nestlings and fledglings. Kawaguchi (1937) has defined the use of 'hyu' from parents to their young. However, in later observations during 1979-1981 (see Appendix B-3b, p. 234), 'hyu' was repeatedly produced by birds with food in the beak, perching alone out of sight of the recipient. The caller was approached by an individual or sometimes made an approach to an individual. Then the food was transferred either from males to their mates or from parents to offspring.

Message-meaning analysis

'Hyu' may encode a message of seeking behaviour, attempting to gain the opportunity to feed. The rate of production may carry a message about the intensity of seeking behaviour. The repetition of short, clear elements with an abrupt start and finish seems to provide the call with a message about the location of the caller (Marler 1957). Sexual and individual differences in the physical structures may suggest a message about the identity of the caller. 'Hyu' may mean that food is available from the caller. It may function to inform the time and place of feeding, and prevent recipients from wasting energy by soliciting for food in vain and also from missing the offer by depending solely upon visual information.

2.3.7. Krrr

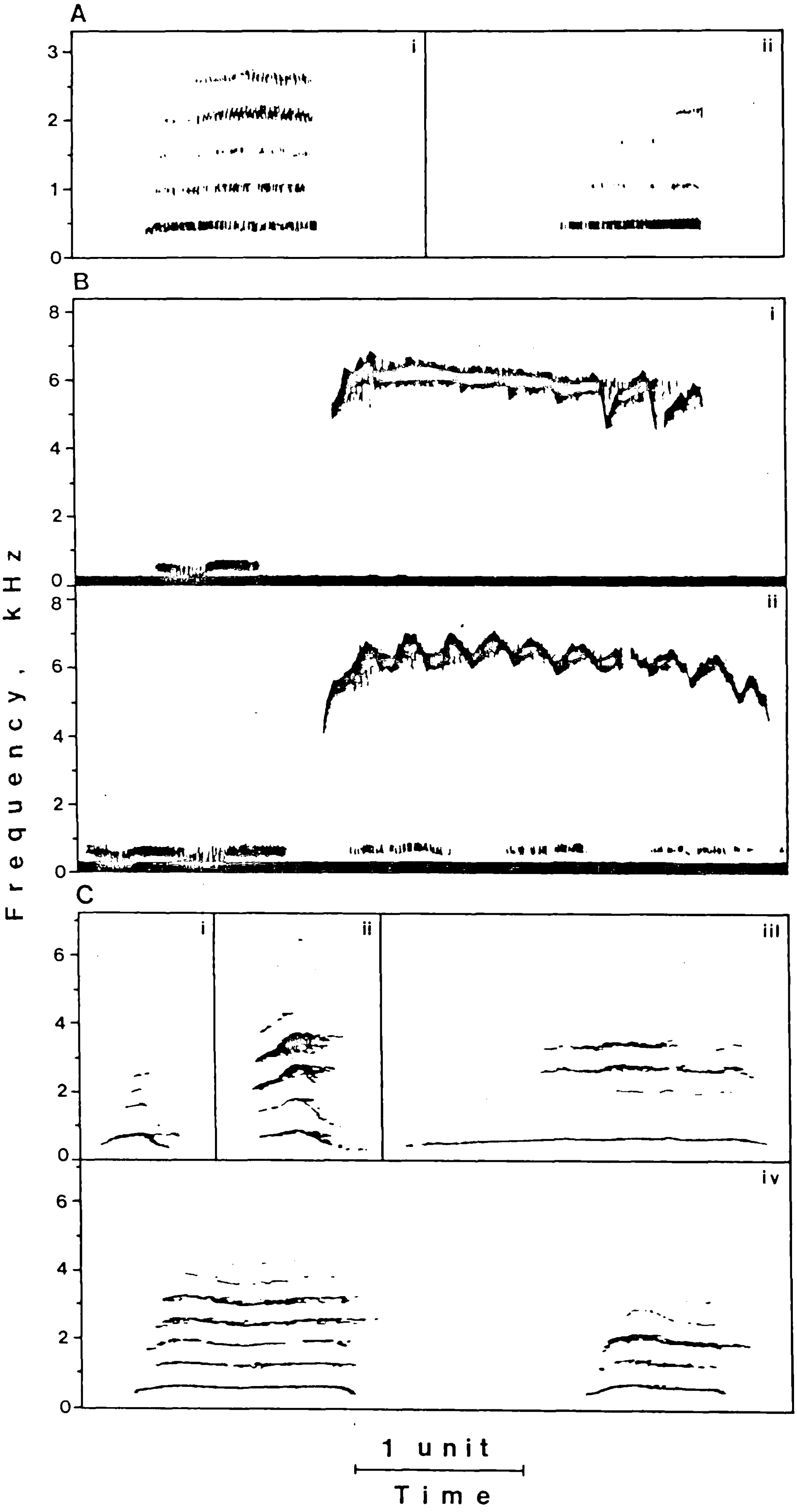
Physical structure

'Krrr' was a quiet, rolling, protracted noise, resembling cats' purring (see Fig. 2-4A). It was described by Hayashi (1902) as a whispering note, 'jewreree', and by Kawaguchi and Ikemura (1920) as a low-pitched call, 'froo' or 'froo-o'. It did not range over 20-30 m from the caller. Females called it more often than males. Calls were similar between the sexes. For female calls (see Appendix A-22, p. 225), the individual mean duration was well over 900 ms up to at least 1500 ms, having a large variation within an individual. The frequency sometimes fluctuated but was generally stable over the range of 400-600 Hz. Harmonics were found in some individuals at the second, third, fourth and sixth. Amplitude tended to increase towards the end of element. 'Krrr' was produced singly or repeatedly.

Behavioural contexts

Later observations during 1980-1981 strongly suggested that females emitted 'krrr' most frequently when they were likely to be fed by their mates during the pre-incubation and incubation stages (see Appendix B-4, p. 235). Males were near their mates, hunting for prey, preparing food, or carrying food and calling 'hyu' (see 2.4.6.). As 'krrr' was emitted by females, males approached the caller or were approached by the caller, and food was quickly given to the female. Parent birds called 'krrr' when they fed nestlings and fledglings. Birds also uttered 'krrr' when they were separated from their mates by a short distance - between 1 and 20 m - and the distance between them was often shortened after the vocalization. 'Krrr' was significantly associated with preening, which led to mutual preening of the pair.

Fig. 2-4. **Sonagrams of adult calls.** 3. 'krrr', 'cheee', 'mew' and 'meeew'. Sonagrams in **A** are prepared at wide-band setting in the range of 40-4000 Hz. The unit time indicated at the bottom of figure is one second. Sonagrams shown in **B** and **C** are prepared at narrow-band setting in the range of 80-8000 Hz. The unit time is 0.5 second. **A,** 'Krrr' produced by female (i) and male (ii). **B,** 'Cheee' was produced by males during copulation. It was preceded by bouts of 'oo.coo', the last calls of which can be seen in the sonagrams. In the second case, the mate also called 'oo.coo' in a duet with the male and kept calling during and after 'cheee'. **C,** 'Mew' (i and ii) and 'meeew' (iii and iv). (ii) and (iii) were called by the same bird.


A
i
ii
B
i
ii
C
i
ii
iii
iv
Frequency, kHz
0
1
2
3
4
6
8
1 unit
Time

Message-meaning analysis

'Krrr' may contain a message that the caller seeks for and is receptive to an interaction at a short distance. The message about the probability, intensity, and relative stability in seeking a close range interaction can be encoded possibly by repetition and amplitude modulation. Meanings of 'krrr' seem to change with situations. To a male hunting or holding prey, his mate's 'krrr' may mean that the caller is asking for prey. To an individual which is not engaged in hunting, 'krrr' may mean that the caller wants contact. When the caller is seen preening itself, the meaning may be that the caller is soliciting for preening. To the offspring, it may mean that parents are going to bring food to them shortly. The function of 'krrr' may be to control the behaviour of other birds at a close range.

2.3.8. Cheee

Physical structure

'Cheee' was a long, piercing squeal. It was heard from a distance of up to approximately 100 m, and was produced only by males (see Fig. 2-4B). The physical features for three birds were as follows:-

duration	...	1149 ± 51 ms
maximum frequency	...	7240 ± 339 Hz
minimum frequency	...	4590 ± 290 Hz

Behavioural contexts

'Cheee' was produced as males copulated. After copulation, males left females immediately and females stayed at the site of copulation.

Message-meaning analysis

'Cheee' may contain a message about the caller's sexual and specific identity and also a message about the location of the caller.

Another possible message may be locomotory behaviour that the caller is about to leave the female. To females, 'cheee' may mean that the male's flight after copulation does not constitute danger. A possible function may be mate assurance after copulation.

2.3.9. Mew and Meeew

Physical structure

As Japanese Brown Hawk Owls are locally known as 'Neko-dori (Cat-birds)' or 'Miyah-tsuku (Miaow-owls)' (Kiyosu 1965), both male and female birds had cat-like vocalizations. They varied between soft 'mew' and caterwauling 'meeew' (see Fig. 2-4C).

'Mew' of an individual showed a mean duration of 220 ms with a CV of 26.1%. The maximum frequency was 994 ± 6 Hz and the minimum frequency was 700 ± 27 Hz (N = 8). The frequency ascended slowly and descended quickly, and its range widened towards the end. The third and fourth harmonics were emphasized. 'Mew' could be as quiet as to reach only the vicinity of the caller or as powerful as to be heard from up to 100 m away.

'Meeew' was a longer and lower-pitched call than 'mew'. The individual mean duration (CV, n) was as follows:-

Owl 1 ... 599 ms (15.7%, 8)
Owl 2 ... 960 ms (21.8%, 3)
Owl 3 ... 1300 ms (38.8%, 3)

The individual means of maximum and minimum frequency with one standard error (n) were as follows:-

Owl 1 ... 678 ± 15 Hz, 415 ± 24 Hz (8)
Owl 2 ... 730 ± 15 Hz, 580 ± 40 Hz (3)
Owl 3 ... 697 ± 49 Hz, 493 ± 52 Hz (3)

The frequency was almost flat or gradually ascended, and its range widened towards the end. Harmonics were found at the third, fourth and fifth. 'Meeew' was always loud enough to travel over 100 m.

Behavioural contexts

'Mew' was heard from parents, whose young fledglings were perched near the ground or were wandering on the ground, being in potential danger from ground-living animals including humans (see Appendix B-5, p. 237). Parents orientated towards the enemy and called. As the distance between young birds and enemy shortened, parent birds increased the calling rate and loudness but seldom flew. Young birds became stationary. There was no clear response from the enemy.

'Meeew' was often heard from parent birds watching the nest, when larger bird species, such as the Ural Owl Strix uralensis, the Black Kite Milvus migrans and the Night Heron Nycticorax nycticorax came near. In some cases, parent birds called it when humans approached their nest trees. Unlike 'mew', it accompanied dashing flights toward the enemy, which kept out. To human ears, it sounded weird enough for the listener to withdraw. 'Meeew' was also used against conspecific birds. Firstly, it was emitted by territorial males in the middle of territorial dispute, when the opponents were chased off. Secondly, the widowed female called it whenever the replacing male disturbed her to attend her offspring.

Message-meaning analysis

The caller of both 'mew' and 'meeew' is believed to be in conflict between the two motivations of fear and aggression. The message may be that the caller is interactional but indecisive between the two incompatible alternatives, attack and escape. Two forms and their variations seem to provide behavioural supplemental messages. They may also encode a message about the location of the caller. To young birds, 'mew' may mean that it is dangerous to move. To enemies, it may mean that their movement is monitored. To both other species and conspecific rivals, 'meeew' may mean that the caller is intensely antagonistic to their presence. It can be suggested that 'mew' functions as an alarm to warn kin in possible danger, and that 'meeew' functions as a more intense threat to the receiver.

2.3.10. Hooh

Physical structure

'Hooh' was a hollow call stressed at the onset, and emitted singly (see Fig. 2-5A). Both sexes called. The physical features were as follows:-

duration	...	230 - 290 ms
maximum frequency	...	800 - 880 Hz
minimum frequency	...	620 - 700 Hz
harmonics	...	none

Behavioural contexts

'Hooh' was produced most frequently before parents flew to their young fledglings to feed. Although uncommon, it was also produced when nestlings were fed. It was heard only during the late nestling and early fledgling stages (see Appendix B-6, p. 239).

Message-meaning analysis

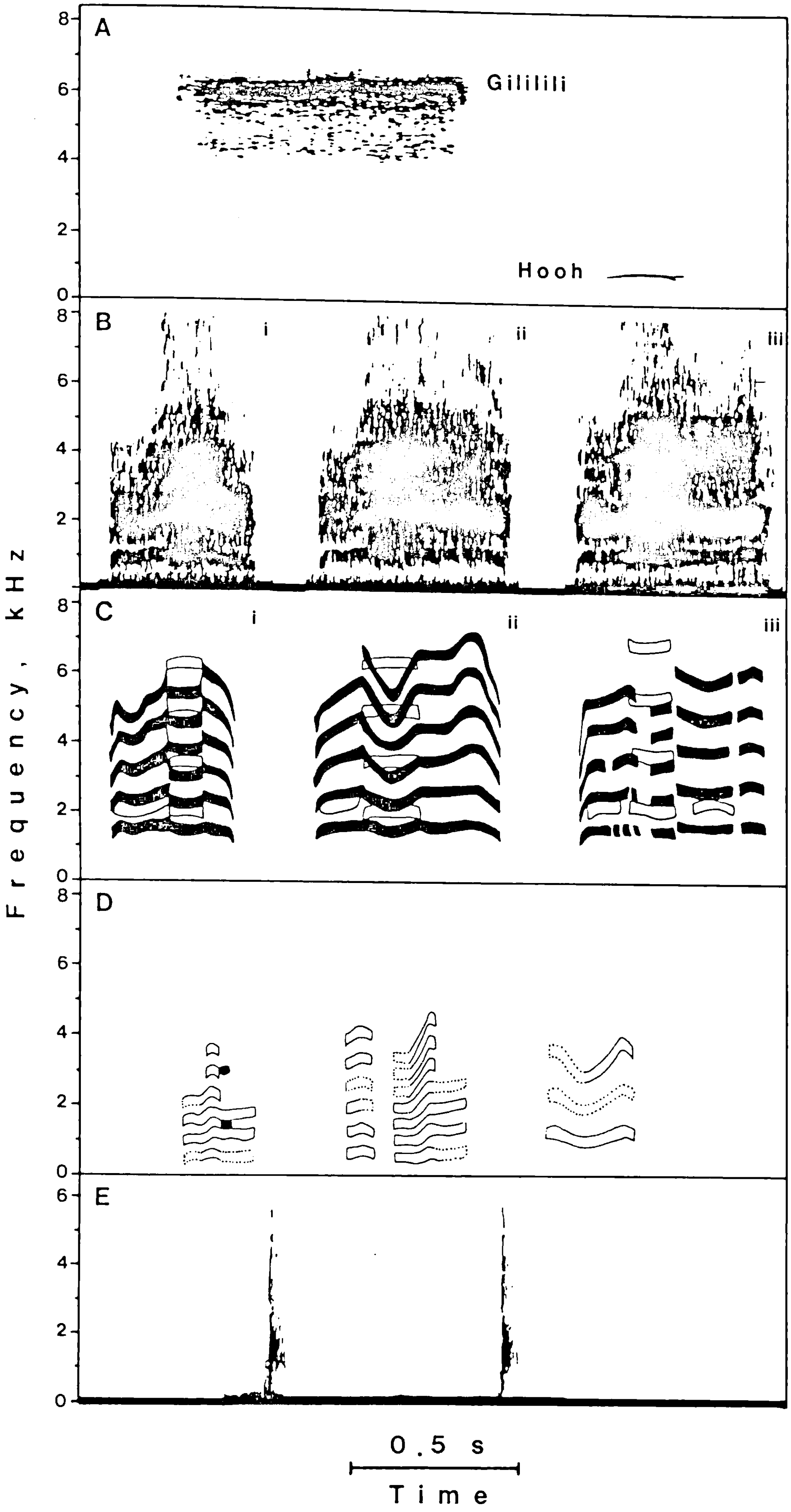
Messages, meanings and functions are not known. However, 'hooh' is considered not to contain messages about feeding and food.

2.3.11. Quay

Physical structure

'Quay' was a harsh, rusty sound and could be heard from up to 50 m away. No calling bird was identified as female. 'Quay' was composed of two simultaneously produced elements, which were not related in the temporal mode and modulated frequency (see Fig. 2-5 B and C). The fundamental frequency occupied from 600 to 1500 Hz in one element, and from 800 to 1800 Hz in the other. Harmonics were observed up to the eighth and those from the second to the fifth were more emphasized. The individual mean duration ranged between 286 and 490 ms and the variation was high within individuals (CV: 20.5 - 26.0%).

Fig. 2-5. <u>**Sonagrams of adult calls**</u>. 4. 'hooh', 'quay', 'buf' and 'pack': sonagrams are prepared in the range of 80–8000 Hz. **A,** 'Hooh' was produced after a nestling's 'gilililí' (narrow-band setting). **B,** three calls of 'quay' prepared at wide-band setting. **C,** 'Quay': analysis of main frequencies and their harmonics from the sonagrams shown in **B.** **D,** 'Buf': analysis of main frequencies and their harmonics from sonagrams of three calls (not shown). The first call accompanied an unrelated short sound (black). Dotted line indicates weakly presented parts. **E,** two consecutive sounds of 'pack' prepared at wide-band setting. They were recorded from a young male.


A
Gililili
Hooh
B
i
ii
iii
C
i
ii
iii
D
E
8
6
4
2
0
Frequency, kHz
0.5 s
Time

Behavioural contexts

'Quay' was only rarely heard from solitary birds near the nest site. On an occasion, a male called 'k.hoo' (see 2.3.1.), and his mate joined in calling. Suddenly the male started to utter 'quay' several times and switched to 'guf' (see 2.3.3.).

2.3.12. Buf

Physical structure

'Buf' was heard on only a few occasions from a bird of unidentified sex. It was a harsh, short sound, and was rather quiet reaching not farther than 30 m. The diagrams of sonagrams from one individual are shown in Fig. 2-5D. The duration was 270 ± 38 ms with a CV of 24.2% and the range of fundamental frequency was from 500 to 700 Hz. The second harmonics were more emphasized than the fundamental.

Behavioural contexts

On one occasion, a bird produced 'buf' between 'meeew' calls (see 2.3.9.). On the other occasion, a bird was perched near the nest tree.

2.3.13. Wing Noises

Although birds did not usually make flight noises with their wings, males made sharp clapping sounds when they flew toward their rival to fight. Parents produced light rustling as they approached the nest to feed nestlings. The message, meaning and function of these noises are unknown; however, the former may contain a message of attack.

2.3.14. Byahbyah

'Byahbyah' was a strikingly bizarre yowl. No recording was made, but it lasted for a few seconds. It was heard from birds which were in distress. Being caught in the hands of man, they cried, struggling to escape. It sounded frightening enough for the observer to release them.

Message-meaning analysis

'Byahbyah' may contain a message that the caller attempts to avoid interactions. In spite of lack of knowledge concerning the response of recipients, it is assumed that it signifies crisis. To enemies, it may mean that the prey can be dangerous and that it is better to avoid interactions. It may function to inform of danger to conspecific birds, namely the mate and family, and also to increase the caller's chance of escape from the enemy.

2.3.15. Pack

Physical structure

'Pack' was a short, sharp noise produced by closing the beak quickly and strongly. It occupied a wide frequency range between 0.4 and 5.5 kHz at the start and then between 0.9 and 2.0 kHz for about 50 ms (see Fig. 2-5E).

Behavioural contexts

'Pack' was made when callers were either approached by the observer or exposed to a strange object such as a long-handled net. It lifted the wings backwards with the head held low, raised plumages of the head, breast and underpart, and withdrew.

Messages and functions

The message of 'pack' may be interactional behaviour and indecisiveness between incompatible behavioural alternatives, attack and escape. It may function as a threat at a short distance.

In Table 2-3, a summary of messages proposed for the adult vocal repertoire of Japanese Brown Hawk Owls is given.

2.4. Development

Nestlings generally hatched from the end of June to the beginning of July. They emerged from the nest 24-27 days after hatching in late July. Fledglings dispersed into the surrounding area by early September. Nestlings have four vocal and one non-vocal sound. Fledglings have eight vocal and one non-vocal sound. Five types of vocalization were added during the first year of development. In the present section, juvenile vocal repertoire is briefly surveyed and a summary of proposed messages is given in Table 2-4.

Young birds emitted 'leee' and 'gilililі' (see Fig. 2-6 A, B and C) from an early stage of development until 13 weeks old. 'Chilililі' (see Fig. 2-6 D) appeared late in the nestling stage. 'Chewlee' was emitted between 7 and 15 weeks (see Fig. 2-6 E and F). All of them were produced in the context of feeding, presence of parents, siblings' utterance, and play. It may function to guide parents to feed or contact young birds while controlling their agonistic tendency. 'Kyrrkyrr' (recorded but not analysed sonagraphically) was uttered when nestlings were alone or handled. 'Byahbyah' (see 2.3.14.) was produced at the latest after 6 weeks. 'Puh' (see Fig. 2-7 A) and 'soo' (see Fig. 2-7 C) appeared between 8 and 14 weeks and 'py.o' (see Fig. 2-7 B) between 9 and 26 weeks. These three calls were mainly heard when the captive male was playing with materials. It also uttered 'puh' while grooming, and 'py.o' whenever it was approached while handling prey. 'Scheee' (see Fig. 2-7 D) was heard from the birds over 8 weeks old, and identified as 'cheee' of the adult repertoire (see 2.3.8.) at 12 weeks. It appeared during the play which was the prototype of the copulatory behaviour. 'Pooh' (see Fig. 2-8 A) was first noticed at 7 weeks and developed to 'mew' and 'meeew' of the adult repertoire (see 2.3.9.) by the 25th week. The captive bird called it, when it saw any flying objects outside the window, e.g. birds and aeroplanes. 'Beh' (see Fig. 2-8 B) was heard between 9 and 26 weeks, but its context was unknown.

Table 2-3. A summary of proposed messages encoded in the adult vocal repertoire of the Japanese Brown Hawk Owl

Message	K.hoo	Hoh	Guf	Oo.coo	Hyu	Krrr	Cheee	Mew & Meeew	Wing clapping
Behavioural selection									
- interaction	X					X		X	
- attack			X						X
- escape			X						
- copulation or sexual behaviour				X					
- association		X							
- indecisiveness	X	X	X	X				X	
- locomotion							X		
- incompatible set of behaviour alternatives	X		X						
- site	X								
- food					X				
- seeking	X			X	X	X			
- receptiveness						X			
- attentiveness	X								
Behavioural supplement									
- probability	X	X	X	X		X		X	
- intensity	X	X	X		X	X		X	
- relative stability	X	X	X	X		X		X	
- direction	X								
Non-behavioural									
- species	X						X		
- individual	X				X				
- sex	X				X		X		
- mating status	X								
- distance	X								
- location	X				X			X	

Table 2-4. A summary of proposed messages encoded in the juvenile vocal repertoire of the Japanese Brown Hawk Owl

Message	Leee etc	Kyrrkyrr	Byahbyah	Py.o	Puh & Soo	Scheee	Pooh	O.guf	K.hoo	Pur	Pack
Behavioural selection											
- interaction		X	X				X		X		X
- attack								X			
- escape				X				X			
- association										X	
- indecisiveness							X	X	X	X	X
- incompatible set of behaviour alternatives								X	X		X
- site									X		
- care	X										
- seeking	X	X							X		
- receptiveness	X	X									
- attentiveness									X		
- exertion and/or play				X	X	X					
Behavioural supplement											
- probability			X					X	X	X	
- intensity	X	X	X					X	X	X	
- relative stability	X	X	X					X	X	X	
- direction									X		
Non-behavioural											
- species	X								X		
- individual									X		
- sex									X		
- age	X	X							X		
- location	X								X		

Note: 'Leee etc' includes 'leee', 'gilililі', 'chilililі' and 'chewlee'.

Fig. 2-6. **Sonagrams of juvenile calls**. 1. 'leee', 'gililili', 'chilililili' and 'chewlee': sonagrams are prepared at wide-band setting in the range of 80-8000 Hz. **A,** 'Leee' produced by a seventeen-day-old bird. **B,** 'Gililili' produced by a thirty-day-old bird. **C,** combination of 'leee' and 'gililili' produced by thirty-day-old bird. **D,** two calls of 'chilililili' produced by thirty-day-old bird. **E** and **F,** 'Chewlee' produced by a three-month-old bird.

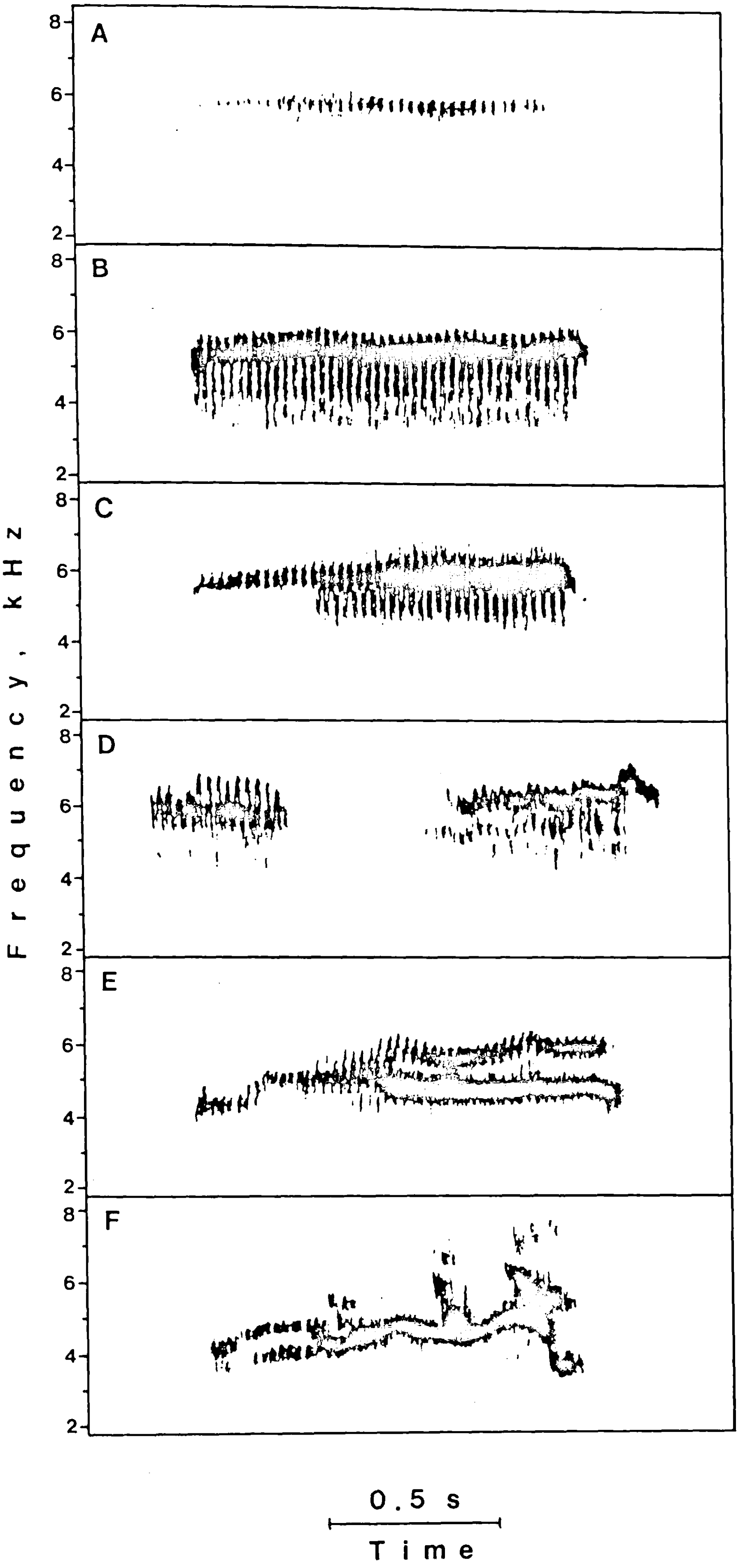
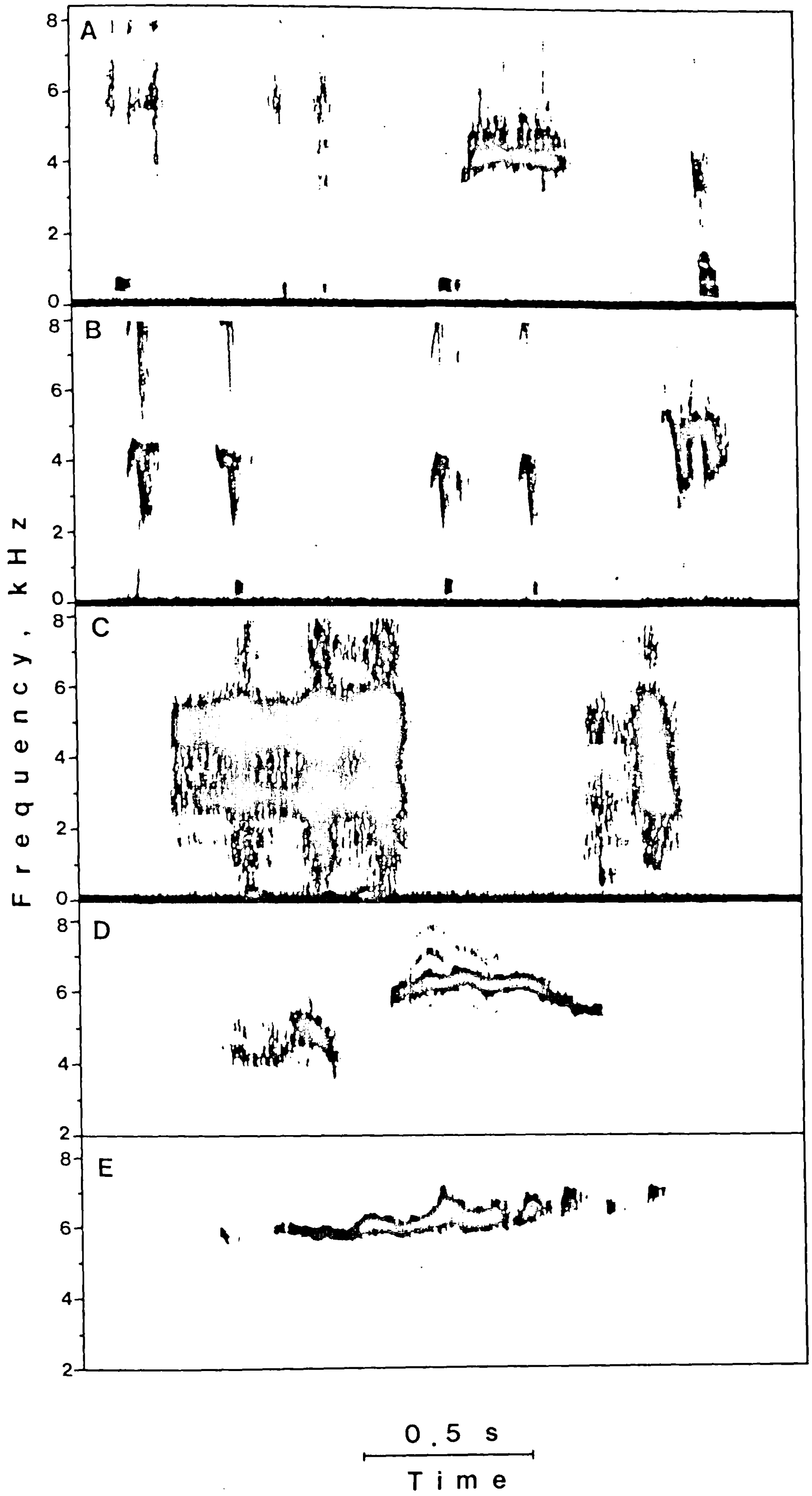

A
B
C
D
E
F
8
6
4
2
Frequency, kHz
0.5 s
Time

Fig. 2-7. **Sonagrams of juvenile calls**. 2. 'puh', 'py.o', 'soo' and 'scheee': sonagrams are prepared at wide-band setting in the range of 80-8000 Hz. **A**, 'Puh'. The first three calls were produced as a young male handled paper which caused the noise in higher frequencies. The fourth call was immediately followed by 'chilililі'. The last call followed a short 'py.o'. **B**, 'Py.o'. In the last call, 'py.o' was repeated twice in succession. **C**, two bouts of 'soo'. **D**, 'Scheee' produced by a three-month-old male immediately following its 'chililili'. **E**, 'Scheee' produced by a two-and-a-half-month-old male.


A
B
C
D
E
8
6
4
2
0
Frequency, kHz
0.5 s
Time

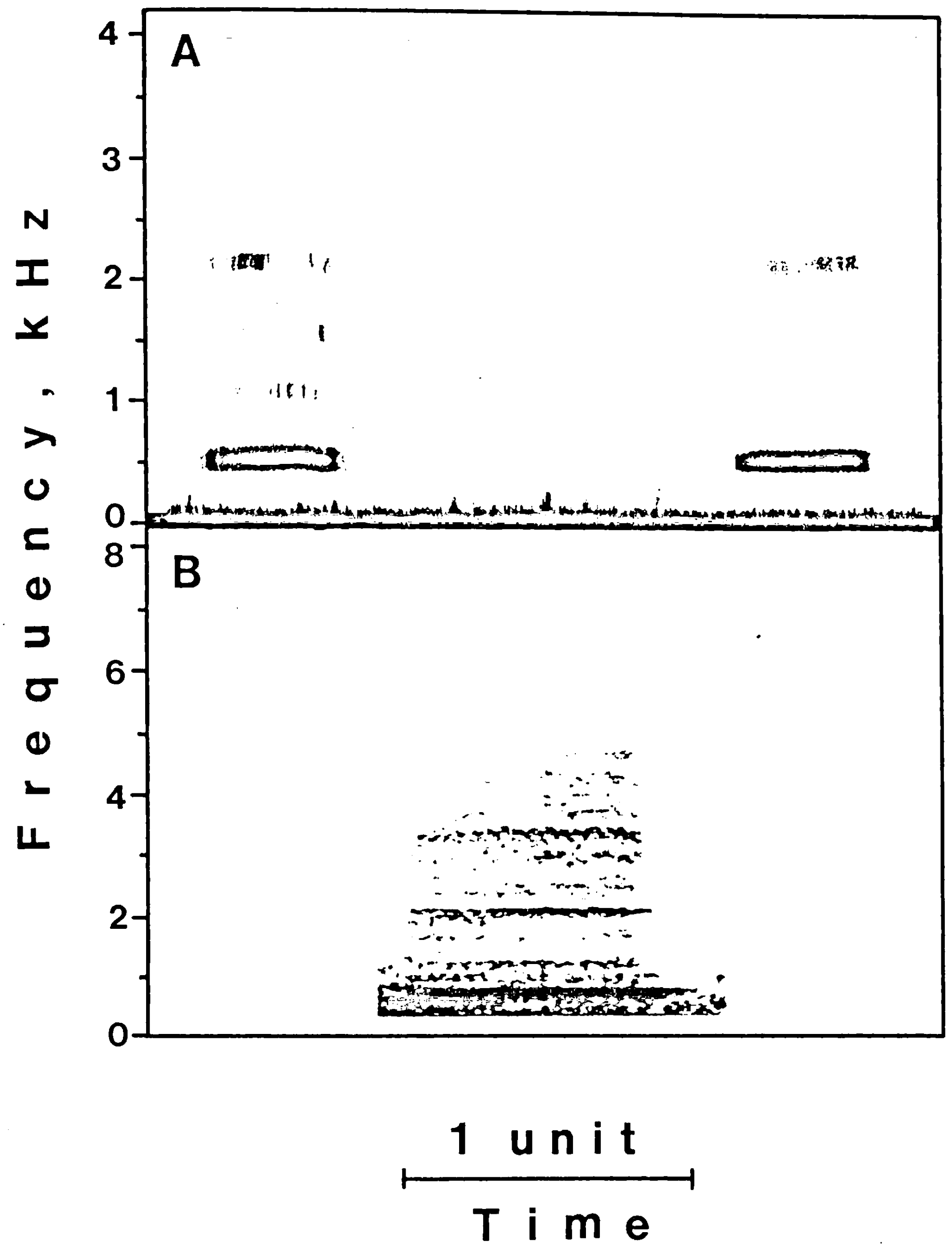


Fig. 2-8. Sonagrams of juvenile calls. 3. 'pooh' and 'beh'. **A**, Two calls of 'pooh' prepared at wide-band setting in the range of 40-4000 Hz. The unit time was one second. **B**, 'Beh' prepared at narrow-band setting in the range of 80-8000 Hz. The unit time was 0.5 seconds.

'O.guf' (see Fig. 2-9 A and B) was heard after 7 weeks. The captive juvenile uttered it when it heard people approaching, when unfamiliar objects were presented, and before the pseudo-copulatory behaviour. Some birds produced immature versions of primary calls as early as 8 days after fledging, when the male parent called away from them (see Fig. 2-9 C and D). In the captive male, the prototype of the primary call emerged as 'o.guf', produced in the unit structure between 10 and 14 weeks, and again after 27 weeks. The full primary call was heard after 32 weeks. It was produced spontaneously or induced by playback of recorded primary calls. Uki (1973) reported that a high-pitched 'woo' in the unit structure was produced in the third year, and that the full primary call appeared in the fourth year. Nakanishi (1936) also observed the first full primary call in the fourth year. 'Pur' (see Fig. 2-9 E and F) was added to the repertoire at 28 weeks and related to 'hoh' (see 2.3.2.) and 'hyu' (see 2.3.6.) of the adult repertoire. It was heard while the young male was preparing and presenting food to the observer.

2.5. Relationships between vocalizations

In the adult vocal repertoire, the following six types of vocalization - 'k.hoo', 'hoh', 'guf', 'oo.coo', 'poo' and 'hyu' - are related in their sound characteristics. The structure (part, element, unit, bout), types of frequency modulation and harmonic patterns are compared in Table 2-5. The common feature for all the types is repetition of elements in a bout. The first four types are more homogeneous than the rest, by sharing the two-part structure of element and being produced interchangeably in a bout. Unit structure and frequency modulation clearly distinguish 'k.hoo' from the other three calls. Harmonic patterns seem to contribute to differences in tonal quality among the four. 'Hyu' shares the unit structure and major types of frequency modulation with 'k.hoo' but lacks part A.

In Fig. 2-10, these vocalizations are compared in various physical dimensions. Individual means are plotted, and outermost points are connected to show distributions of the respective vocalizations. It can be seen that each vocalization occupies a

Fig. 2-9. Sonagrams of juvenile calls. 4. 'o.guf', 'k.hoo' and 'pur': sonagrams are prepared in the range of 40-4000 Hz. **A**, 'O.guf' produced by a three-month-old bird (narrow-band setting). **B**, 'O.guf' produced by a six-and-a-half-month-old bird (narrow-band setting). **C** and **D**, 'K.hoo' produced by one-month-old birds (narrow-band setting). **E**, 'Pur' produced by a six-and-a-half-month-old bird (wide-band setting). **F**, 'Pur' produced by an eleven-month-old bird (wide-band setting). Towards the end of bout, 'pur' graded to 'k.hoo'.

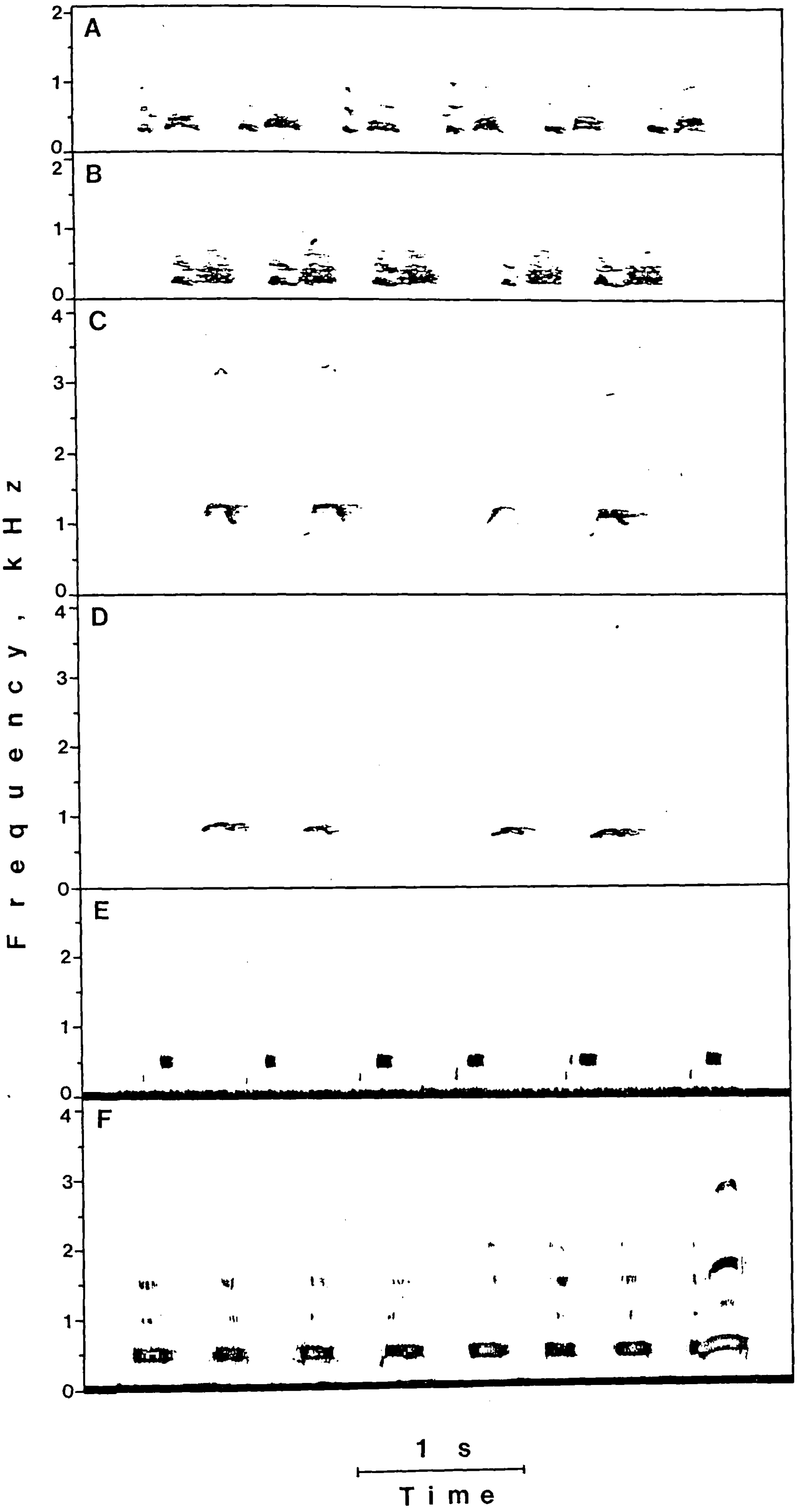

A
B
C
D
E
F
Frequency, kHz
0
1
2
3
4
1 s
Time

Table 2-5. Comparison of physical structure between graded vocalizations

Feature	K.hoo	Hoh	Guf	Oo.coo	Poo	Hyu
Part A	x	(x)	(x)	x	–	–
Part B	x	x	x	x	x	x
Unit	x	–	–	–	–	x
Bout	x	x	x	x	x	x
Frequency modulation						
– Part A	A, F, DA	None	None	D, F, AD & AFD	–	–
– Part B	AF, AFD & AD (C, R)	AF, AFD & AD (L, C)	AFD & AD (L, C)	AFD & AD (L, C)	AF, A, F	AF, AFD & AD (C, R)
Harmonics						
– Part A	(2, 3)	None	None	2(3)	–	–
– Part B	(2)3(4)5(6)	3	Irregular	(2, 3)	None	(2)3, 4(5–10)

Note: x = present, (x) = the presence could not be denied.
The harmonics which were not emphasized are in brackets.

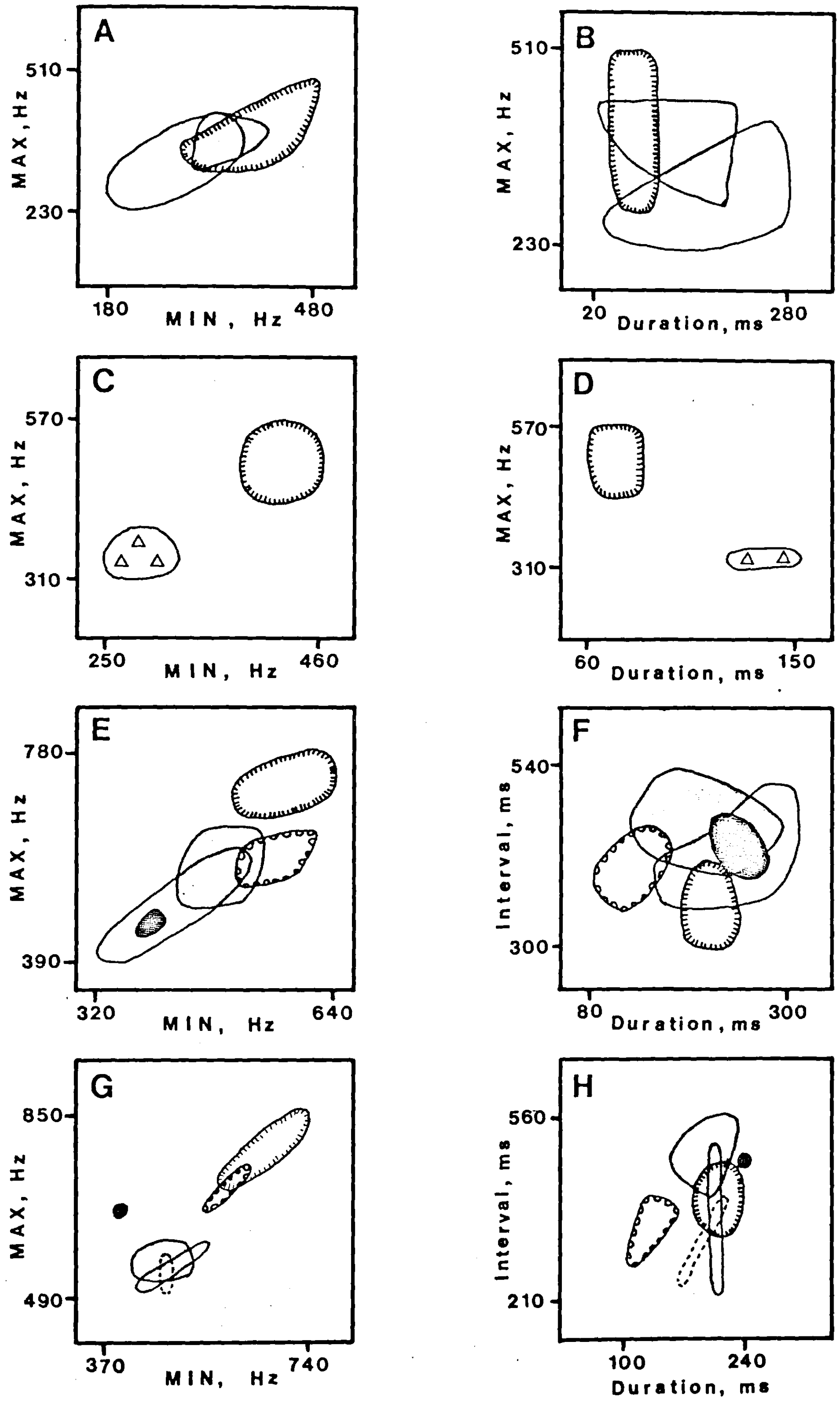


Fig. 2-10. Distribution of graded vocalizations in temporal and frequency dimensions. Part A: male (**A, B**), female (**C, D**). Part B or element where no part structure found: male (**E, F**), female (**G, H**). Graded vocalizations: 'k.hoo' (toothed), 'hoh' (shadowed), 'guf' (dark), 'oo.coo' (plain), 'hyu' (semi-circled), 'poo' (broken), combined distribution of 'hoh', 'guf' and 'oo.coo' (triangles).

narrow physical area at a specific location. The pattern of overlapping and distance between different types may suggest that limited acoustic space is fully exploited by these vocalizations. As for part A, male vocalizations of 'k.hoo', 'hoh' and 'oo.coo' are contained in the following ranges:-

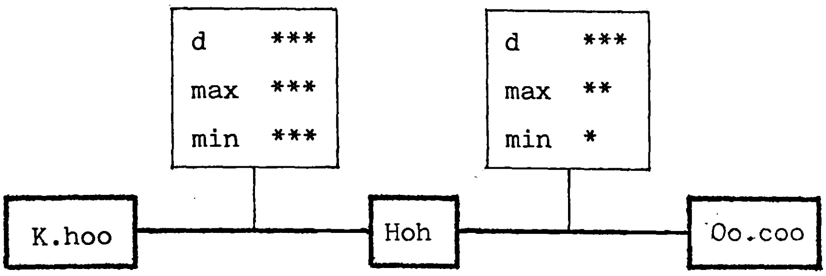
mean duration ... 20 - 280 ms
mean maximum frequency ... 230 - 510 Hz
mean minimum frequency ... 180 - 480 Hz

This shows a linear arrangement from 'k.hoo' to 'oo.coo' via 'hoh' in the dimensions of maximum and minimum frequencies (Fig. 2-10 A) and a gradual expansion of the range of duration from 'k.hoo' to 'oo.coo' via 'hoh' (B). In females, physical distributions are separated between 'k.hoo' and the other three of 'hoh', 'guf' and 'oo.coo' (C and D). The relationships in the latter are not apparent. As for part B or the element where no part structure is found, male vocalizations of 'k.hoo', 'hoh', 'guf', 'oo.coo' and 'hyu' are found in the following ranges:-

mean duration ... 80 - 300 ms
mean duration of interval (short) ... 300 - 540 ms
mean maximum frequency ... 390 - 780 Hz
mean minimum frequency ... 320 - 640 Hz

From the distributions in frequency dimensions (E), it can be seen that the vocalizations are arranged in a linear fashion from 'k.hoo' to 'guf' or 'oo.coo' via 'hoh'. 'Hyu' is shifted towards lower maximum frequency range, while sharing minimum frequency with 'k.hoo'. In the distributions of temporal dimensions (F), the interval range appears to increase from 'k.hoo' to 'hoh' through 'oo.coo' and 'guf'. Again, 'hyu' shifts from the other four by the duration. In females, relationships of 'k.hoo', 'hyu' and 'hoh' (G and H) almost coincide with those of males. It is suspected that 'oo.coo' and 'poo' are closely related. In Fig. 2-11, relationships among the vocalizations based upon male calls are shown. Statistical probabilities for differences are given for the respective physical features.

1. Part A



2. Part B or element where part structure is not found

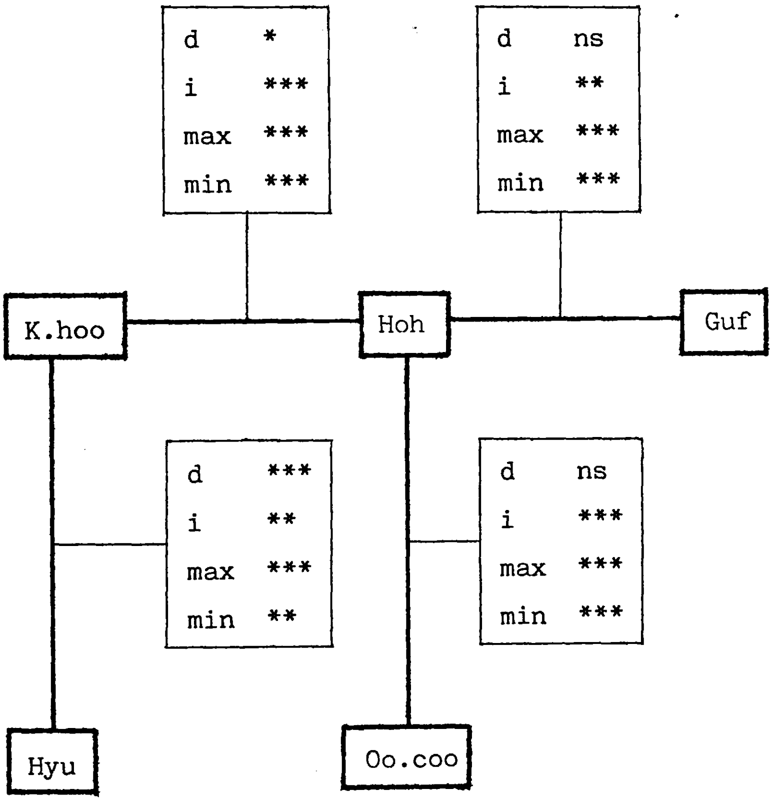


Fig. 2-11. Relationships among the graded vocalizations of males. Physical features: d, duration; i, duration of interval; max, maximum frequency; min, minimum frequency. Statistical probabilities for differences between the vocalizations (one-way ANOVA with *a priori* test): ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, $p \geq 0.05$.

2.6. Comparisons

2.6.1. Vocal repertoire of *Ninox*

There were some interracial differences in the primary call of *Ninox scutulata* (see Appendix H, p. 280). The pair of *N. s. ussuriensis* were observed to perform a duet using 'k.hoo'. One of them had higher-pitched calls than the other (Panov 1973). Vocalizations similar to 'meeew' were reported from *N. s. lugubris* (Jerdon 1862), *N. s. hirsuta* (Wait 1921) and *N. s. burmanica* (Smythies 1953).

Vocalizations of three other *Ninox* species have been described phonetically. The Powerful Owl *N. strenua* has at least six types of adult vocalization. These are the primary call 'who-whoo', loud 'woo' used when the bird was mobbed by Ravens, a deep, low, sheep-like contact note used between mates, a shriek, a scream given in response to the former, and another scream given in response to an intruder. Juveniles have a shrill whistle (Ramsay 1919; Fleay 1940; Favaloro (& Fleay) 1946; Harrison 1973). The Barking Owl *N. connivens* possesses at least five types of adult vocalization. These are the primary call 'wook-wook', a loud growl used by males when the nest was disturbed, a shriek accompanied by beak snapping to intimidate nest intruders, a scream used at nest disturbance and 'karr, karr, karr, ... karr, koowook'. Juveniles have four types of vocalization: a cricket-like trill used for contact, 'whoop-whoop' which developed during the first winter, a scream and a conversational note (Barnard 1911; MacGillivray 1914; Le Souëf 1918; Fleay 1940, 1942; Harrison 1973; Van der Weyden & Ginn 1973). The Boobook Owl *N. novaeseelandiae* has at least nine types of adult vocalization. These are the primary call 'more-pork', gruff notes 'more, more, more, ... more', a series of clear, sharp, loud cries 'ow, ow, ow, ... ow', a snore produced while flying, a scream 'airch', 'cree-cree', cat-like mewing when excited, cat-like yowling, and quickly repeated 'por, por, por, ... por', produced by females and a greeting captive bird (Carter 1903; M'lean 1911; Stuart Dove 1922; Fleay 1925; Stidolph 1925; Wilkinson 1927; Fleay 1940; Bryant 1941; Harrison 1973; Van der Weyden & Ginn 1973).

Despite the lack of sonagraphic analysis from these studies, it is possible to comment on the general design of Ninox vocalizations. The minimum set of adult repertoire appears to include the following five types: the primary call, shrieking, screaming, a cat-like sound, and trilling. The primary calls of the three species and the Brown Hawk Owl are produced in a unit composed of two elements. Gradation and variation in physical structure are also found. For example, the Barking Owl varied 'wook-wook' to 'er-wook-wook' (Fleay 1942). The Boobook Owl showed a drop in sound frequency while calling (M'lean 1911), variations in clearness, tempo and number of repetitions (Stidolf 1925) and seasonal changes in tone (Cheney 1915). Primary calls are produced by both male and female birds, and females tend to call at a higher pitch than males. Duetting between the mates of a pair is common. The Powerful Owl duetted out of the nesting season (Ramsay 1919). The Barking Owl performed a coordinated duet in summer (Fleay 1940, 1942; White 1917; Le Souëf 1918). In the Boobook Owl, male primary calls were accompanied by monotonously repeated female calls (Stuart Dove 1922). In the juvenile repertoire, a cricket-like, shrill trill or whistle seems to be in common. Beak snapping is also believed to be shared.

2.6.2. Vocal repertoire of Strigiformes

In the Strigiformes (a total of 133 species over 24 genera), adult vocalizations have been described for 87 species from 21 genera. Only one type of vocalization, generally the primary call, is known in 26 species and two-four types in 35 species (Holman 1926; Favaloro (& Fleay) 1946; Attwood & Attwood 1949; Stillwell & Stillwell 1954; Marshall 1966, 1973; McQueen 1972; Hekstra 1973; Mikkola 1973; Prestt & Wagstaffe 1973; Steyn & Scott 1973; Van der Weyden 1973, 1975; Fitzpatrick 1975; Berggren & Wahlstedt 1977; Kabaya & Higuchi 1977; Barrows 1980; Higuchi & Momose 1980; Scott 1980). In Table 2-6, the size of the vocal repertoire is listed for the 26 species which have at least five types of vocalization. Adult birds have up to fourteen vocal and one - two non-vocal sounds. Nestlings have up to four vocal and one non-vocal sound. In the Japanese Brown Hawk Owl, adults have thirteen vocal and three non-vocal sounds and nestlings have four

Table 2-6. Repertoire size in the Strigiformes

Species	Adult		Nestling		References
	V	NV	V	NV	
Tyto alba	9	2	3	1	Bunn 1974; Bühler & Epple 1980*.
T. capensis	6	1	3	-	Fleay 1949; Hill 1955.
Otus flammeolus	5	-	-	-	Marshall 1939.
O. trichopsis	5	-	-	-	Smith *et al*. 1982; Ligon 1967.
Bubo bubo	9	1	4	1	Leibundgut 1973; König 1972.
B. capensis	6	-	3	1	Gargett 1977, 1978.
B. virginianus	11	1	4	1	Potter 1928; Norton 1928.
Ketupa blakistoni	5	2	2	-	Pukinski 1974.
Scotopelia peli	5	-	-	-	Fogden 1973; Van der Weyden & Ginn 1973.
Nyctea scandiaca	7	1	3	1	Tullock 1968, 1969; Scherzinger 1974*.
Strix aluco	12	1	3	1	Southern 1970; Wendland 1963; König 1972.
S. nebulosa	14	1	4	1	Höglund & Lansgren 1969; Wahlstedt 1969.
S. occidentalis	13	1	3	-	Ligon 1926; Zarn 1974; Forsman *et al*. 1984*.
S. uralensis	14	1	4	-	Scherzinger 1980*; Lundberg 1980.
Asio flammeus	7	2	2	-	Urner 1923; Armstrong & Phillips 1925; Clark 1975.
A. otus	10	1	1	-	Wendland 1957; König 1972.

Table 2-6 (continued)

Species	Adult		Nestling		References
	V	NV	V	NV	
Ninox connivens	7	1	1	-	Fleay 1940, 1942; MacGillivray 1914.
N. novaeseelandiae	7	-	-	-	M'lean 1911; Stuart Dove 1922; Stidolph 1925; Van der Weyden & Ginn 1973.
N. scutulata japonica	13	3	4	1	This study.
Sceloglaux albifacies	9	-	-	-	Harrison 1973; Van der Weyden & Ginn 1973; König 1972.
Surnia ulula	6	-	2	-	Smith 1970.
Athene brama	5	-	-	-	Van der Weyden & Ginn 1973.
A. noctua	7	-	-	-	Haverschmidt 1946; König 1972.
A. cunicularia	14	1	3	1	Thomsen 1971; Coulombe 1971; Martin 1973a*.
Glaucidium passerinum	8	1	2	1	Bergman & Ganso 1965; Schönn 1976.
Micrathene whitneyi	9	-	1	-	Ligon 1967.
Aegolius funereus	9	1	2	-	Kuhk 1941; Van der Weyden & Ginn 1973; König 1972.

Note: V, vocal sounds; NV, non-vocal sounds; *, sonagraphical studies; -, unknown.

vocal and one non-vocal sound. It seems that the upper limit of adult vocal repertoire size is fourteen and that of nestlings is four. Thorpe (1961) presented call vocabularies of a gull, a fowl, a dove and several songbirds. The range of vocabulary size was six - fifteen in adults and one - three in nestlings. It seems that the vocal repertoire size of Strigiformes is not very different from that of other birds. A clear difference between nocturnal and diurnal species is certainly not evident.

Sexual differences in primary calls have been reported for a variety of owls of *Otus*, *Bubo*, *Pulsatrix*, *Strix*, *Asio*, *Ninox*, *Glaucidium*, *Micrathene*, and *Athene*. In general, female calls tend to be higher-pitched than male calls (Marshall 1939, 1966; Van der Weyden 1973, 1975; McQueen 1972; Miller 1930; Miller 1934; König 1972; Hekstra 1973; Emlen 1973; Görner 1977; Leibundgut 1973; Forsman *et al*. 1984; Van der Weyden & Ginn 1973; Bergman & Ganso 1965; Coulombe 1971; Exo 1984). This may be due to smaller syringes in females than in males (Miller 1934). Temporal and tonal features are also different between the sexes in a number of species, although there is no clear overall trend.

3. THE PRIMARY CALL: CIRCADIAN AND SEASONAL PATTERNS OF PRODUCTION

3.1. Introduction

Studies of avian vocal activity have been carried out mainly on the songs of passerine birds. Questions such as when birds begin and end singing during the day (Leopold & Eynon 1961; Armstrong 1973) and seasonally (Saunders 1947, 1948), and how internal and external conditions control the rhythm, have been asked. To understand the function and causation of vocal activity, circadian and seasonal song production has been quantified using a variety of measures. The number of singing males in the forest community reflected the breeding cycle of individual species (Slagsvold 1977). Diurnal and seasonal changes in the number of singing males differed between breeders and non-breeders in the Thrush Nightingale Luscinia luscinia (Sorjonen 1977). Percentages of singing males in a population were used to compare the seasonal activity of two Acrocephalus warblers, and inter-specific differences in the functions of song were suggested (Catchpole 1973). The same measure was also used to demonstrate the late summer singing peak of the Yellowhammer Emberiza citrinella (Hiett & Catchpole 1982). The rate of singing (the number of songs per individual per unit time) has been used to investigate the activity patterns of several songbirds. No clear diurnal pattern was revealed, but seasonal patterns were regarded as reflecting the breeding cycle (Armstrong 1973; Fonstad 1981; Logan 1983). The effects of pairing, intraspecific interactions, and meteorological factors upon the diurnal vocal output of the Reed Bunting Emberiza schoeniclus have also been examined (Åström 1976). The duration of singing period was used to study the effects of temperature and weather upon the song production of the Song Thrush Turdus ericetorum (Higgins 1979). Percentages of time spent singing were used to study interspecific differences in diurnal vocal activity (Catchpole 1973). Factors such as sex, age and mating status were found to be important in the diurnal and seasonal activity of the South Island Robin Petroica australis (Powlesland 1983). Further, Adret-Hausberger (1984) investigated the temporal distribution of whistle types of the

Starling *Sturnus vulgaris* outside the breeding season in an attempt to reveal possible functional differences of whistle types.

Compared with the work on passerine birds there have been very few studies of non-passerine vocal activity. Leopold and Eynon (1961) and Armstrong (1973) gave some accounts of the first and last calls of some species in Ardeidae, Phasianidae, Scolopacidae, Strigidae and Caprimulgidae. Ferrell and Baptista (1982) investigated the diurnal pattern of the number of vocal bouts in the captive Budgerigar *Melopsittacus undulatus* and found a relationship between vocal activity and sensitivity of the pituitary to light. In the Strigidae, nocturnal and seasonal vocal activity has been mainly reported in descriptive accounts (e.g. *Otus flammeolus*: Marshall 1939. *Bubo bubo*: Leibundgut 1973. *Nyctea scandiaca* and *Asio flammeus*: Pitelka *et al.* 1955. *A. otus*: Wendland 1958. *Ninox connivens*: Fleay 1942. *N. novaeseelandiae*: M'lean 1911. *Athene (Speotyto) cunicularia*: Martin 1973b. *Glaucidium passerinum*: König 1965, 1972. *Micrathene whitneyi*: Ligon 1967). There have been only three detailed quantitative studies on owls (*Strix aluco*: Hansen 1952. *S. uralensis*: Lundberg 1980. *Otus bakkamoena*: Higuchi & Momose 1980). Brown Hawk Owls produce primary calls in the two main periods, one at dusk and the other at dawn (*Ninox scutulata lugubris*: Proud 1949. *N. s. hirsuta*: Wait 1931. *N. s. obscura*: Butler 1899b. *N. s. burmanica*: Stanford & Ticehurst 1939; Smythies 1953. *N. s. japonica*: Kawaguchi 1937). More or less continuous call production throughout the breeding season has been mentioned for *N. s. lugubris* (Sálim & Ripley 1969) and *N. s. japonica* (Momiyama & Nomura 1919; Kiyosu 1965). Post-breeding production has been reported from the migratory races, *N. s. japonica* (Ishizawa 1934; Kiyosu 1965) and *N. s. ussuriensis* (Panov 1973). Nothing has been reported about the production of primary calls by migratory races during migration and at their wintering quarters, although the possibility that they call on the way to their breeding grounds cannot be ruled out (Kabaya & Higuchi 1977).

This chapter describes the nocturnal and seasonal production of the primary call of Japanese Brown Hawk Owls at their breeding ground. The temporal and quantitative nature of the production pattern is examined for spontaneity, interactions with conspecific birds in the distance, and effects of environmental factors. Also, vocal activity of an unmated male which replaced a territorial male is compared with that of other conspecific birds and is discussed in terms of the possible functions of the primary call.

3.2. Methods

In 1980, the changes in nocturnal and seasonal vocal activity were monitored at a territory in Zushi. The observation was started from the day following the arrival of a male bird, 4th May, and carried out regularly thereafter. The male permanently disappeared from the territory after a severe storm on 1st July at the early stage of nestling period. A new male replaced the original male and stayed on the territory for the rest of the season. The observation was continued until 17th September. In the present study, the 'day' started in the evening, therefore the quoted date covers two consecutive days, e.g. 4th May means the period from the evening of 4th May to the afternoon of 5th May.

On each monitoring day, the observer occupied a vantage point near the nesting tree in the centre of the territory. A hide was used only while the birds were nesting. Observation started one to half an hour before sunset and continued until half to one hour after sunrise so that the whole active period was covered. The observation period was divided into thirty-second units.

For each territorial male, the number of primary call elements in every bout, other types of vocalization, behaviour, location and orientation were recorded. For the other conspecific birds, their vocalizations, behaviour, location and orientation were also noted. The environmental conditions such as weather, wind strength, and the presence and phase of the moon were recorded for thirty-minute periods. Wind strength was scored as follows (Brainerd 1974):-

Level	Wind speed (m/s)	Level	Wind speed (m/s)
0	0 - 0.5	7	12.5 - 15.2
1	0.6 - 1.7	8	15.3 - 18.2
2	1.8 - 3.3	9	18.3 - 21.5
3	3.4 - 5.2	10	21.6 - 25.1
4	5.3 - 7.4	11	25.2 - 29.0
5	7.5 - 9.8	12	29.1 -
6	9.9 - 12.4		

Dry and wet temperatures were measured every thirty minutes at a fixed point on the hillside, and approximately 8 m above the ground. This is considered to give the most approximate ambient temperature and relative humidity of the owls' environment. Light intensity was measured at dusk and dawn with a photometer at irregular intervals. The light sensitive surface was directed right overhead towards the sky.

The effect of conspecific birds' behaviour upon the primary call production of territorial males was examined for the following time-bins: one-minute, three-minute, ten-minute and thirty-minute periods. For each period the number of primary call elements was obtained and intraspecific conditions classified as follows:

(a) No other conspecific birds produced primary calls.
(b) The mate produced primary calls.
(c) Conspecific birds in the surroundings produced primary calls.
(d) Conspecific males invaded the territory.
Additionally for the replacing male:
(e) The mate of the original male produced primary calls.
(f) The mate of the original male was in a close distance of less than 20 m.
(g) The mate of the original male called 'meeew' (see 2.3.9.).

The number of primary call elements produced in the absence of other conspecific birds' primary calls (condition a) was compared with that of the other intraspecific conditions (b-g). If more than two conditions were found in a period, they were treated independently. A ten-minute period was found to be the most suitable length of unit time. To avoid random effects due to time allocation, two overlapping settings of the ten-minute period were used. One started a period every 10th minute of each hour of Japanese Standard Time, JST (0-setting, i.e. 18:00 - 18:09, 18:10 - 18:19, etc.) and the other at every 5th minute of each hour of JST (5-setting, i.e. 18:05 - 18:14, 18:15 - 18:24, etc.).

In 1981, seasonal vocal activity was monitored for two neighbouring territorial males in Zushi. Each male was observed on one evening a week from its arrival in April until September. From the study of nocturnal vocal activity in 1980, the proportion of primary call production to the total diurnal output was found to be less variable during the first combined period (see 3.3.1., coefficients of variation: 59% for the original male and 83% for the replacing male) than the following combined periods (coefficients of variation: 85-111% for the original male and 63-180% for the replacing male). Consequently, the first two hours after sunset were used. The number of elements produced in each bout, behaviour, and location were also recorded.

3.3. Nocturnal Vocal Activity

3.3.1. Time of day

Circadian patterns of vocal activity during the breeding season of 1980 are shown for the original and replacing males in Appendix C-1 (pp. 240-243). Neither of the males showed an apparent uniform pattern associated with the time of day. However, they appeared to start the activity with primary calls in the early evening, intersperse the night-time with calling, and finally call towards the end of activity at dawn. This is seen more clearly in the generalized circadian patterns (Fig. 3-1), where the activity period was divided into twenty periods. The first period covered from the start of observation to the end of the thirty-minute JST period which commenced within fifteen minutes of sunset. The last period was the thirty-minute JST period in which sunrise took place. The in-between eighteen periods generally followed thirty-minute JST periods.

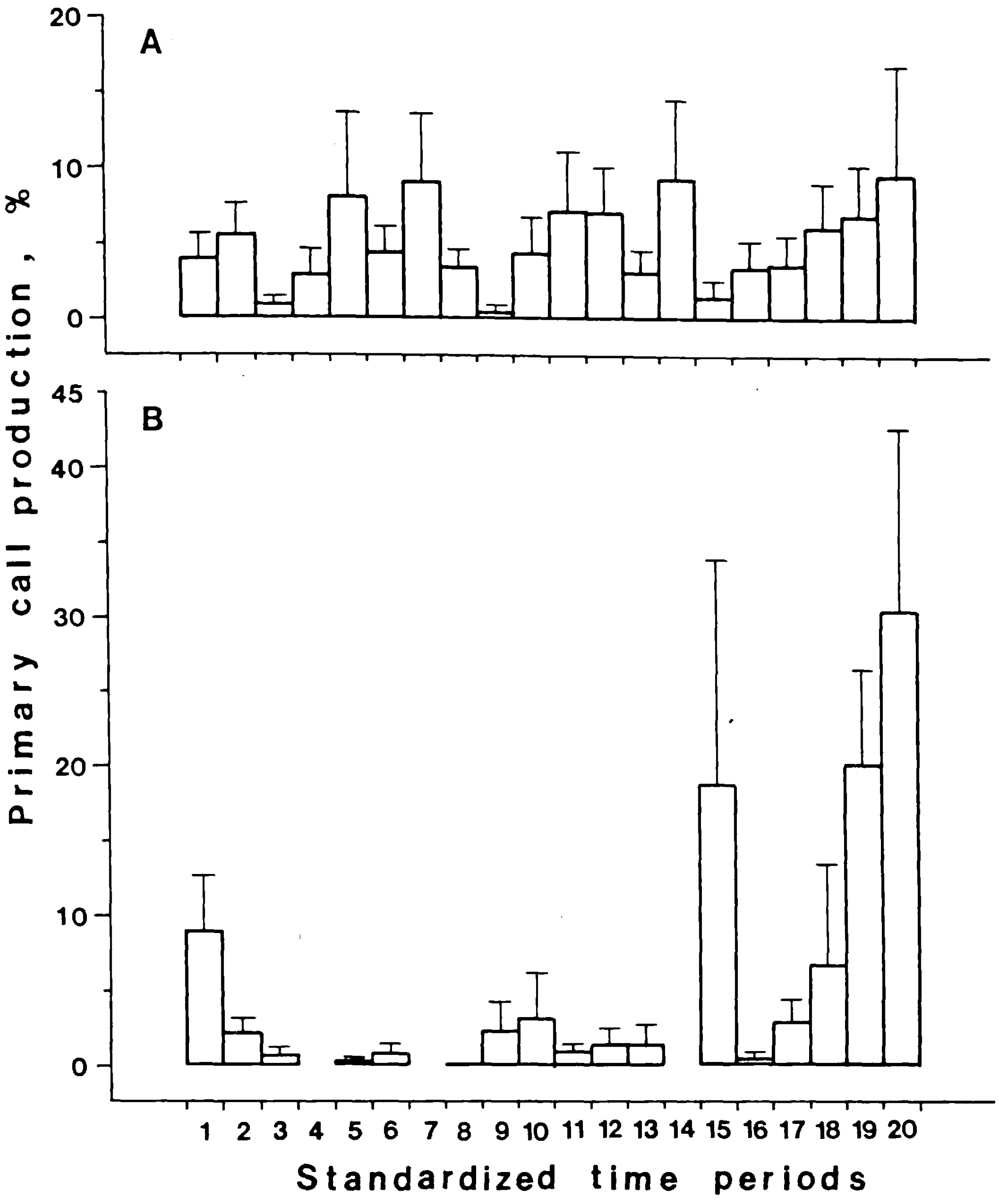


Fig. 3-1. <u>Generalized nocturnal patterns of primary call production at Zushi in 1980</u>. A, the original male's activity between 4th May and 24th June (pre-incubation and incubation stages). B, the replacing male's activity between 7th August and 17th September (fledgling and post-breeding stages). Mean and one standard error are given. For the standardized time period, see the text (p. 87).

However, two adjacent thirty-minute JST periods were combined at midnight, to adjust for the extending night-time length towards the end of season. The vocal output for each period was presented as the mean proportion to the day's total output with its one standard error. For the original male, the vocal activity observed between 4th May and 24th June was used, and for the replacing male between 7th August and 17th September, which excludes the period of vocal accentuation (see 3.5.).

Since variations in the vocal output were high for the twenty periods, four adjacent periods were combined in order to compare the general patterns between the two males. For both males, there was no significant tendency in the vocal production among the five combined periods (Friedman two-way analysis of variance by ranks: the original male, $x_r^2 = 1.325$, $N = 8$, $df = 4$, $0.8 < p < 0.9$; the replacing male, $x_r^2 = 8.900$, $N = 6$, $df = 4$, $0.05 < p < 0.1$). When the first and last combined periods were compared, the original male did not call at dawn significantly more than in the early evening (Wilcoxon matched-pairs signed-ranks test: $T = 11$, $N = 8$, $p > 0.05$), whereas the replacing male produced more calls at dawn than in the early evening ($T = 0$, $N = 5$, $p < 0.05$).

3.3.2. Effects of the physical environment

Sunset and sunrise

From Table 3-1A, it can be seen that the first call tended to occur after sunset. The original male started calling 13.3 ± 5.4 minutes after sunset and the replacing male 16.1 ± 6.0 minutes. Further, they started their activity earlier than or with the emittance of their first calls. The original male started its activity 12.4 ± 5.5 minutes before calling and the replacing male 5.1 ± 4.7 minutes (or 0.4 ± 0.3 minutes if an unusually early value of 43 minutes on 3rd July is removed).

From Table 3-1B, it can be seen that the last call tended to occur before sunrise. The original male stopped calling 8.4 ± 6.0 minutes before sunrise and the replacing male 16.2 ± 3.1 minutes. They concluded their activities with or later than the production of their last calls. The original male stopped its activity 14.3 ± 9.0

Table 3-1. The first and last primary calls of the day

A. The first primary call of the day

Date		Sunset	The first production			FSA	Male
		JST	JST	LI	W	JST	
May	4	18:30	18:41	20	F	18:41	Original
	12	18:36	18:39	30	C	18:36	
	19	18:42	19:26	0	F	18:54	
	27	18:48	18:47	50	F	18:46	
June	4	18:53	19:00	15	F	19:00	
	10	18:56	19:09	0	C	18:42	
	18	18:59	18:59	10	C	18:57	
	24	19:01	19:30	0	F	18:56	
July	3	19:01	19:58	0	F	19:15	Replacing
	8	19:00	19:00	20	C	19:00	
	16	18:57	18:54	20	C	18:54	
	31	18:46	18:49	20	F	18:49	
August	7	18:40	19:02	0	C	19:00	
	14	18:32	18:49	0	F	18:49	
	25	18:18	18:39	10	C	18:38	
September	1	18:09	18:20	10	C	18:20	
	8	17:59	0:15	0	C	?	
	17	17:46	18:03	10	C	18:03	

Note: for abbreviations, see the note under B.

Table 3-1 (continued)

B. The last call of the day

Date		Sunset	The first production			LSA	Male
		JST	JST	LI	W	JST	
May	4	4:45	4:42	30	F	4:42	Original
	12	4:38	4:37	10	R	4:37	
	19	4:33	4:24	20	F	4:24	
	27	4:28	4:16	10-20	F	4:40	
June	4	4:25	4:11	0-10	F	4:13	
	10	4:25	4:50	100	C	4:50	
	18	4:25	4:07	0-4	C	4:22	
	24	4:26	3:51	0	C	5:04	
July	3	4:30	4:09	100	F	4:09	Replacing
	8	4:33	4:33	0	C	4:33	
	16	4:38	4:23	0-5	C	4:46	
	28	4:46	4:36	5	R	4:52	
	31	4:49	22:11	0	C	?	
August	7	4:54	4:26	0-5	C	4:26	
	14	5:00	4:36	30	C	4:36	
	25	5:08	4:53	0-10	C	4:53	
September	1	5:13	5:05	5	C	5:05	
	8	5:19	2:16	0	C	?	
	17	5:26	5:01	0	C	?	

Note: JST, Japanese Standard Time; LI, light intensity (luxes); W, weather; F, fine; C, cloudy; R, rainy; FSA, the first sign of activity; LSA, the last sign of activity. On 8th September the owl could not be seen until the first call was made. On 8th and 17th September the owl could not be visually observed in the end of activity.

minutes after its last call (or 5.9 ± 3.7 minutes if an unusually late value on 24th June is removed) and the replacing male 4.9 ± 3.3 minutes.

Light conditions and the moon

From Table 3-1A, it can be seen that the original male produced the first primary call always at less than 50 luxes and the replacing male at less than 20 luxes. From Table 3-1B, it can be seen that the last call was recorded even over 100 luxes in both males. However, it occurred mostly at less than 40 luxes for the original male, and mostly at less than 10 luxes for the replacing male. In both males there was no significant difference between the light intensity of the first call and that of the last call (median test: $P > 0.05$). There was no significant difference between the two males in the light intensity at which they produced the first or last primary calls (median test: $P > 0.05$). They were occasionally heard emitting primary calls during daytime, when they were perched in the shady woodland or where there was heavy overcast. It was very rare that they called in the bright sunshine. They tended to be less vocal when the moon was present (see Appendix C-1). However, there was no obvious response to moonlight.

Weather

The owls were seen calling in the same manner whether it was fine, cloudy, misty or rainy. However, the replacing male stopped production of primary calls during very hard rain on 31st July, when the activity was severely affected. No significant difference was observed in the time of the first and last primary calls in different types of weather (Mann-Whitney U-test: $p > 0.05$, see Table 3-1). On heavily overcast days they tended to start calling earlier than usual.

Wind

In Table 3-2, the observed and expected numbers of thirty-minute JST periods are given for each category of wind strength and number of primary call elements produced. For the original male, all the periods observed during 4th May - 24th June were used. For the replacing male, the period of accentuated vocal activity (3rd - 28th

Table 3-2. Effects of wind strength upon the vocal activity

A. The original male (May 4 - July 1, 1980)

Number of elements	Wind strength			x^2 test
	1 & 2	3	4 & 5	
0	48 (54.4)	18 (18.7)	14 (6.9)	$x^2 = 15.256$
1-100	49 (44.2)	15 (15.2)	1 (5.6)	$C = 0.284$
101-	22 (20.4)	8 (7.0)	0 (2.6)	$df = 4$
				$0.001 < p < 0.01$

B. The replacing male

(a) During accentuation (July 3 - July 28, 1980)

Number of elements	Wind strength			x^2 test
	1 & 2	3	4 & 5	
0	15 (13.8)	5 (5.0)	1 (2.2)	$x^2 = 0.472$
1-100	5 (5.3)	2 (1.9)	1 (0.8)	$df = 2$
101-	24 (25.0)	9 (9.1)	5 (4.0)	$0.7 < p < 0.8$

(b) After accentuation (August 7 - September 17, 1980)

Number of elements	Wind strength			x^2 test
	1 & 2	3	4 & 5	
0	45 (40.9)	42 (44.4)	6 (7.8)	$x^2 = 4.535$
1-100	11 (11.9)	14 (12.9)	2 (2.3)	$df = 2$
101-	2 (5.3)	7 (5.7)	3 (1.0)	$0.1 < p < 0.2$

Note: For wind strength, see 3.2. Observed and expected (in brackets) numbers of thirty-minute JST periods are given for individual categories.

July) and the post-accentuation period (7th August - 17th September) were examined separately. Generally the wind was not strong during the night and all the strengths recorded in the present study were below level 5. Both males spent large proportions of the observation periods in silence irrespective of the wind strength. The original male emitted significantly fewer primary call elements as the wind strength increased (see Table 3-2 for x^2 test for two independent samples). However, the replacing male did not show any significant correlation. Nevertheless, on the other occasions during the general period of field work, the owls tended to be quiet when the wind strength was over level 6. Even if they had called, it would have been difficult to monitor the vocal activity accurately due to the increased environmental noise.

Temperature

The night temperature varied very little during the period of primary call production. The difference between the maximum and minimum temperatures was 2.9 ± 0.3 degrees for the original male (4th May - 24th June) and similarly for the replacing male 2.4 ± 0.2 (3rd - 16th July) and 2.1 ± 0.4 (7th August - 17th September). There was no apparent relationship between the production of primary calls and temperature (see Appendix C-1).

Relative humidity

Relative humidity during the period of primary call production generally kept high and varied within a narrow range:-

	Maximum (%)	Minimum (%)
May - June	94.1 ± 1.3	75.6 ± 3.2
July	95.7 ± 3.3	89.5 ± 2.8
August - September	87.2 ± 2.9	74.8 ± 2.3

There was no apparent relationship between the production of primary calls and relative humidity (see Appendix C-1).

3.3.3. Effects of conspecific birds

In Appendix C-2 (pp. 244-248), frequency distributions of the number of primary call elements produced in ten-minute periods are shown at the 0-setting. Similar results were obtained for the 5-setting (not shown). Results for the Mann-Whitney U-test are also given for both settings.

The original male produced significantly more primary calls when the mate or other conspecific birds in the surroundings emitted primary calls than when no other birds called. There was no consistent evidence that primary calls of the mate or other birds imposed different effects upon primary call production of the territorial male. Invasion of a conspecific also significantly increased primary call production of the territorial male.

As for the replacing male, different tendencies were observed during and after the accentuated vocal activity. During the accentuated vocal activity, there was no significant increase in the number of primary call elements irrespective of whether other conspecifics or the mate of the original male made primary calls. However, when the mate of the original male came close, the replacing male tended to produce more primary calls. After the accentuated vocal activity, the mode of primary call production became similar to that of the original male. That is, the replacing male called more when the mate of the original male and/or other conspecific birds called. There was no significant association between the number of primary calls and the female's 'meeew' calls.

3.3.4. Discussion

In an introduction to circadian rhythms in birds, Aschoff (1967) wrote that the activity of birds has a distinct temporal organization with a major peak at the beginning and a minor peak towards the end, whether they are diurnal or nocturnal. In many passerine birds, dawn singing is usually more eminent than evening singing (e.g. Thorpe 1961; Armstrong 1973; Catchpole 1973). In non-passerine birds, Budgerigars show a similar bimodal pattern in their calling activity under photoperiod controlled conditions (Ferrell & Baptista 1982).

In the Strigiformes bimodal distribution of nocturnal calling activity has been reported for Eurasian Pygmy Owls Glaucidium passerinum (König 1972), Eagle Owls Bubo bubo (Leibundgut 1973) and Ural Owls Strix uralensis (Lundberg 1980). The last species, however, calls more towards the end of activity than in the beginning. In the present study there are three points to consider.

Firstly, why did Japanese Brown Hawk Owls show neither a bimodal nor any kind of time-related pattern in the circadian production of primary calls? Kacelnik and Krebs (1983) explained the dawn chorus of the Great Tit Parus major in terms of the following three factors:-

(a) physical environment affecting foraging and acoustic communication;
(b) accumulated availability of vacant territories to potential settlers;
(c) efficiency of territorial defence including song against invasion.

The circadian vocal activity of Japanese Brown Hawk Owls can also be interpreted in this way. They may have no strong rhythm as the physical environment is not unfavourable for foraging at particular times, unlike the Great Tit (Kacelnik 1979; Avery & Krebs 1984). They have symmetrical ears with small openings (Dement'ev 1966; Kuroda 1967), and hearing may not be so good as the other nocturnal owls (Payne 1962; Norberg 1970; Knudsen 1981). Yet hearing may play an important role in localizing prey, since they can hunt efficiently even at the lower naturally occurring light levels, where the visual system can only be used to control behaviour with respect to large objects excluding small prey items (Martin 1986). The night-time temperature between April and October in Zushi is high enough to keep prey animals active throughout the night. Also unlike the Great Tit, the Japanese Brown Hawk Owl seems to enjoy optimal acoustic conditions throughout most of the active period. The small night-time temperature gradient is believed to favour sound transmission throughout the night. Also, the general absence of strong winds does not cause turbulence to scatter sound (Wiley & Richards 1982). Being free from the limiting factors of foraging and acoustic communication might be a common factor of more or less uniform vocal activity patterns in other nocturnal owls (Marshall 1939; Fleay 1942; Hansen 1952; Wendland 1958; McClure 1974; Hirons 1976). Theoretically, the accumulation of vacant territories could occur at the beginning of the day, and consequently males could engage in territorial defence at dusk. However, clear evidence of more invasion at the beginning of the day than at other times was not available. While hunting is not incompatible with calling, increased hunting activity at dusk and dawn during the nestling stage (Oba 1986) might influence the output of primary calls of a territorial breeding male.

Secondly, why was day-to-day individual variation high in the pattern of primary call production? This may be largely due to the constantly changing intraspecific environment. Pitelka et al. (1955) and Steffens and Geiler (1975) claim that intraspecific interactions affect vocal activity through population density. Certainly, the birds of highly populated Miyake-jima Island called more than those of Zushi. The presence of strange individuals may trigger an increase in vocal activity as suggested for Boobook Owls Ninox novaeseelandiae (M'lean 1911). It may be beneficial to call when other conspecific males call. If not, it would encourage potential intruders to invade territories (Kacelnik & Krebs 1983). Day-to-day variation may also be partly due to physical factors such as heavy rain, strong wind and sudden drops of temperature which impose adverse effects upon the activity to some extent (M'lean 1911; Alexander 1931; Kuroda 1931; Hansen 1952; Wendland 1958; Ligon 1967; Slagsvold 1973; Higuchi & Momose 1980; Minnemann & Busse 1980). Light intensity can be important only in relation to the beginning and end of daily vocal activity period. This may be primarily endogenous and regulated by the periodical changes of light conditions (Aschoff 1967). Unlike the present study, stimulation by moonlight has been suggested for some Brown Hawk Owls (Robinson 1927; Bartels 1928; Wait 1931; Hoogerwerf 1949; Sálim & Ripley 1969).

Finally, why did the original male tend to produce primary calls evenly throughout the night, while the replacing male produced more at dawn than at dusk? The difference in the nocturnal pattern of primary call production between the two males may be largely due to mating conditions. Prominent dawn calling was shown not only by the unmated replacing male but also by the original male on 4th May when the mate had not arrived (see Appendix C-1a). The early morning period is theoretically freer from invasion than the early evening period, and dawn calling may function in courtship rather than territorial proclamation.

3.4. Seasonal Vocal Activity

3.4.1. Seasonal peaks

In Fig. 3-2, seasonal patterns of primary call production are shown for the two neighbouring territorial males in 1981. Also, that of the original male is presented up to its disappearance in 1980. It appears that there were four common peaks in the seasonal vocal activity of the two males in 1981. The first peak appeared in early May, when most of the owls of the local population had returned and paired. Vocal interactions with their mates and also with other conspecific birds in their surroundings and nest calling were observed. The mid-May trough took place when both males showed less vocal interaction with their mates. They became less responsive to the primary calls of other conspecific birds. The second peak appeared in late May. Vocal interactions with neighbouring males and also with the mate and nest calling took place. When incubation started, both males were vocally less active. The third peak then appeared in late June - early July. This coincided with hatching in both cases. While the nestlings were taken care of by the pairs, vocal activity remained low. The fourth peak happened in late July, when the young birds had fledged and flew about the area away from the nesting tree. Fuboku 1981 did not show any peak after this until the end of observation, whereas Rokudai 1981 had the fifth peak in mid-August, when it accompanied the fledglings and made vocal interactions with the mate. Then Rokudai 1981 became quiet as well until the end of the observation period.

In 1980, the owls returned to the breeding ground later than usual and the population was rather quiet. Rokudai 1980 did not show a clear peak in early May. When vocal activity increased from the

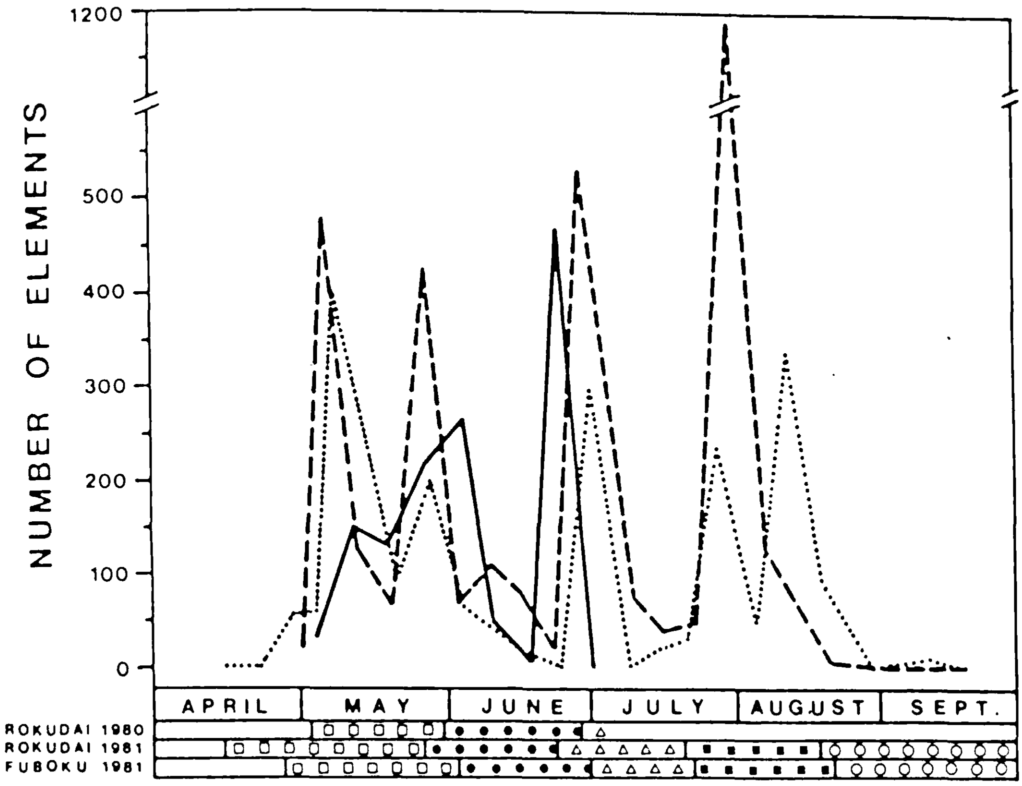


Fig. 3-2. Seasonal patterns of primary call production. The vocal activity of Rokudai 1981 is shown from 15th April to 20th September in 1981 (dotted line). That of Fuboku 1981 is shown from 1st May to 21st September in 1981 (broken line). Also, that of Rokudai 1980, the original male, is shown from 4th May to 1st July (solid line). Breeding stages are indicated individually: □, pre-incubation stage; ●, incubation stage; △, nestling stage; ■, fledgling stage; ○, post-breeding stage.

end of May to early June, the male experienced invasion of another male into his territory. Like the other two males in 1981, it was less vocal during the incubation period. Vocal activity increased in late June before hatching, and the territory was again invaded by another male.

Seasonal fluctuation of vocal activity did not show any association with changes in environmental factors such as temperature, relative humidity, wind or weather. When the day of high vocal output was compared with that of low vocal output in terms of the presence and absence of other conspecifics' primary calls, the result was only partially significant (Fisher test, see Table 3-3). However, primary call production was likely to increase when other conspecific birds also made primary calls. It is notable that when no other birds produced primary calls, vocal output tended to be low for the two males in 1981.

3.4.2. Discussion

Seasonal vocal activity of the Strigiformes can be characterized as a bimodal distribution with one vocal period in spring (breeding season) and the other during autumn and winter (Hansen 1952; Wendland 1958, 1963; König 1965, 1972; Leibundgut 1973; Higuchi & Momose 1980; Lundberg 1980). Earlier descriptive accounts suggested a similar seasonal pattern for Japanese Brown Hawk Owls, spring and early autumn calling. There are two points to consider.

Firstly, why in this study did Japanese Brown Hawk Owls have a vocal period during breeding activity, but none in autumn? Like the seasonal singing activity of most passerines (Thorpe 1961; Arnold 1982), non-passerine vocalizations are closely related to gonadal growth and androgen secretion (Andrew 1969). The reproductive association of primary calls suggests that primary call production is under endocrine control. Towards the end of the breeding season, androgen secretion is much reduced, and the owls are in moult. It is generally believed that birds show reduced vocal activity at this time (Saunders 1947, 1948; Leopold & Eynon 1961). Low vocal output helps to save energy, and gives more time for foraging, both of which help to meet the extra nutritional requirements for feather growth

Table 3-3. Effects of primary calls of conspecific birds upon the seasonal vocal activity of territorial males

A. Primary calls of the mate

Vocal output	Territorial males Rokudai 1980		Rokudai 1981		Fuboku 1981	
	−	+	−	+	−	+
High	2	3	1	5	0	5
Low	2	1	14	2	12	4
Fisher test	$p > 0.05$		$p = 0.004$		$p = 0.006$	

B. Primary calls of the other conspecific birds

Vocal output	Territorial males Rokudai 1980		Rokudai 1981		Fuboku 1981	
	−	+	−	+	−	+
High	3	2	4	2	2	3
Low	3	0	13	3	15	1
Fisher test	$p > 0.05$		$p > 0.05$		$p = 0.027$	

Note: Number of ten-minute periods is shown for each category.
'−' indicates that no conspecific bird produced primary calls.
'+' indicates that conspecific birds emitted primary calls.

(Powlesland 1983). Lack of an autumn vocal period may also be related to the young birds' dispersion and early departure for migration from the natal population. The adult population is free from territorial pressure imposed by additional young birds. This has been suggested as a major cause of the autumn vocal period (Hansen 1952; Wendland 1963; Lundberg 1980).

Secondly, what is responsible for the fluctuation of primary call production during the breeding season? The main factors to cause peaks are suggested as follows:-

(a) to acquire and secure a territory (peaks 1, 2 and 3);
(b) to acquire a mate (peak 1);
(c) to maintain contact with the mate (peaks 1 and 2);
(d) to advertise the nest hole (peak 1);
(e) to guard the mate from other conspecific males (peak 2);
(f) to maintain coherence of the family unit (peaks 4 and 5).

The first peak coincides with the time when territorial males come into intense territorial interactions with conspecifics. Lack of a clear peak in the pattern of the original male in early May is due to less interaction with neighbours in a low-density population (Leopold & Eynon 1961; Steffens & Geiler 1975; Åström 1976). The second peak, and to some extent the third one, are associated with the presence of an invading male or vocal interaction with neighbours. This suggests a general reinforcement of territorial relationships after each quiet period. Also, the second peak appeared just before egg-laying. This is the time when copulation is most likely to lead to fertilization of eggs, and territorial males are less tolerant to the presence of invading males. Since intruders are sometimes successful in approaching residents' mates, copulation between them cannot be ruled out. Consequently, territorial males continue to make primary calls to keep out rivals from their territories. The fourth and fifth peaks may well reflect that special care is necessary to keep all the family members together in the initial few weeks of fledgling life.

There are activities which are incompatible with primary call production. The factors to cause troughs are suggested as follows:-

(g) to maintain and develop the pair-bond and to copulate successfully (trough 1);
(h) to guard the mate and offspring in the nest from predator (troughs 2 and 3);
(i) to feed the mate (troughs 1 and 2);
(j) to feed offspring (trough 3).

Territorial males allocate more time to interact with females after the initial territorial interaction with neighbours (Saunders 1948; Leopold & Eynon 1961). They remain close to their mates for most of the time, and other types of vocalization rather than primary calls are used for communication with their mates. During incubation and nestling stages, breeding males should keep silent so as not to reveal the nest location to possible predators. The males' involvement in feeding their mates in the pre-incubation and incubation stages also reduces opportunities for calling. Low output during the nestling stage is a universal phenomenon in species both male and female birds of which are engaged in feeding offspring (Leopold & Eynon 1961; Logan 1983). Males of Japanese Brown Hawk Owls have little time to make primary calls during the first and last hour of daily activity when most feeding takes place.

3.5 Vocal Activity of a Replacing Male

3.5.1. Results

In 1980, the territory was originally occupied by a mated male, and occasionally invaded by a non-territorial single male. The invader could stay inside the territory as long as it kept silent. However, no sooner did it emit primary calls within the territory than the resident male replied by producing primary calls intensely, approached, and expelled the intruder from the territory.

At dawn of 1st July in the beginning of the nestling stage, the resident male disappeared from the territory after a severe storm. Good weather did not return until 3rd July, and no calling activity had been observed. The female was seen feeding her offspring alone in the evening. The non-territorial single male took over the territory, but its movement was not conspicuous still. It emitted a few awkward primary calls at 19:57, which was rather late for the first call of the day (see Table 3-1).

At midnight, the female cried 'meeew' several times. Abruptly at 1:15 the replacing male started to make low-pitched, emphatically toned primary calls near the nesting tree. The female produced two prolonged bouts of primary calls without showing any sign of coordination with the male's calling. The male kept calling intensely till dawn and often chased the female. The female became quiet and appeared to avoid direct confrontation with the male. Although a neighbour called at dawn, it was not delivered in intense interactions.

In Fig. 3-3, the vocal output of the original and replacing males is shown. As some part of vocal activity could not be recorded, the result is shown separately in the two periods, one from approximately thirty minutes before sunset to 23:59 and the other from 0:00 to approximately thirty minutes after sunrise. The replacing male showed dramatic bursts in primary call production, and maintained it for a month until the offspring of the original male fledged on 31st July. The amount of vocal output was extraordinarily large during accentuation, compared to the general level of the original male. Neighbouring breeding males neither showed any apparent increase in their primary call production at this stage of the breeding cycle. For example, one of them produced only 132 elements for the first period and 780 elements for the second period on 17th July. Also, the breeding males from the 1981 Zushi population vocalized far less elements than the replacing male for the first two hours after sunset during the nestling stage. Rokudai 1981 produced 0-296 elements and Fuboku 1981 called 39-529 elements (see Fig. 3-2), while the replacing male called 2796 elements on 8th July and 1530 elements on 16th July (see Appendix C-1c). The replacing male produced more calls when the female was nearby (see Appendix C-2(3)). The female had some difficulty in rearing her offspring, since the male not only chased her away from the nest but never helped feeding her nestlings. It took 30-31 days for these young birds to fledge, which was exceptionally longer than usual (see 2.4.). The male's disturbance

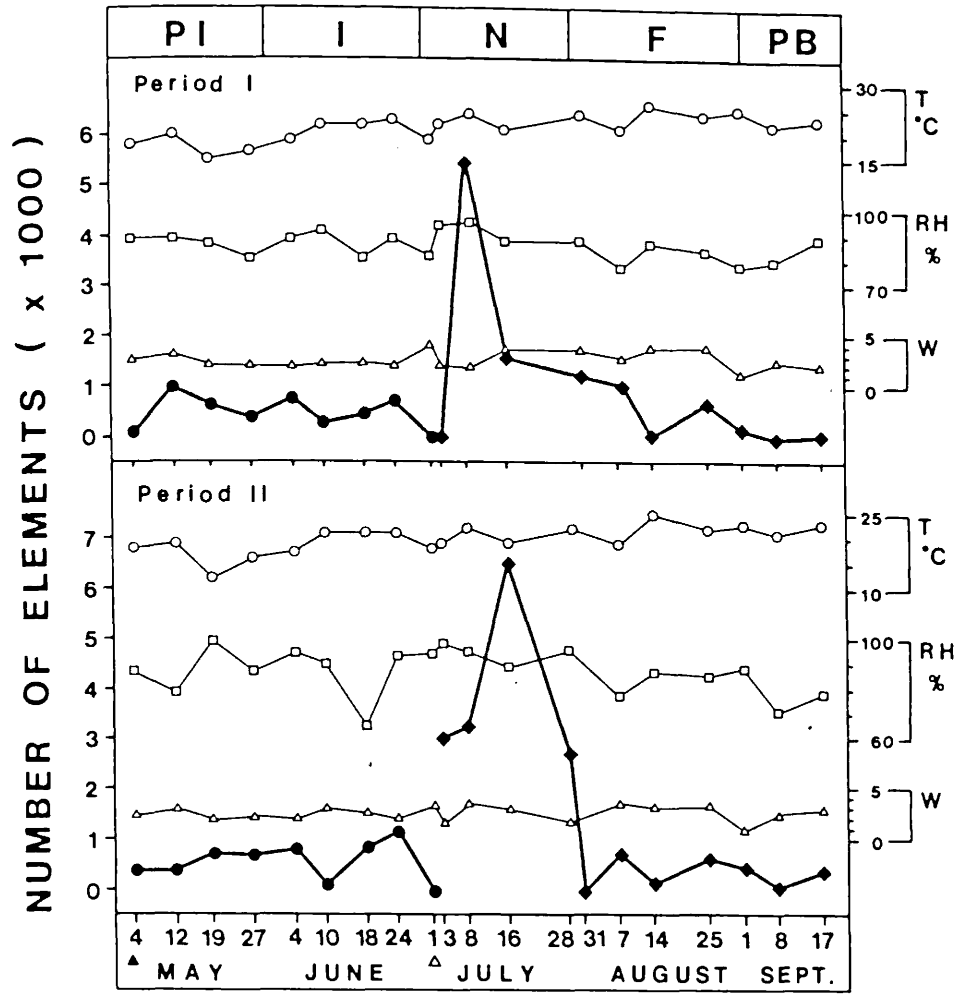


Fig. 3-3. Accentuation of primary call production of the replacing male. The number of primary call elements produced by the original male (●) and replacing male (◆) is shown. Period I covers the time from the beginning of observation at dusk to 23:59, and period II from 0:00 to the end of observation at dawn. ▲, arrival of the original male on 3rd May; △, disappearance of the original male on 1st July; O, temperature (T); □, relative humidity (RH); △, wind strength (W); PI, pre-incubation stage; I, incubation stage; N, nestling stage; F, fledgling stage; PB, post-breeding stage.

was often answered by the female's 'meeew'. However, their relationship became gradually less intense. Neighbouring breeding males made no distinctive response to the vocal burst (see Appendix C-2(3)).

After fledging of the female's offspring, the replacing male reduced his vocal output to distinctively low levels until the end of observation. The neighbouring males also produced primary calls at low levels. His vocal output for the first two hours after sunset during fledgling and post-breeding stages was not significantly different from that of both Rokudai 1981 and Fuboku 1981 (Mann-Whitney U-test: $p > 0.05$). The male no longer increased its vocal output when the female came close to him (see 3.3.3. and Appendix C-2(4)). It stayed away from the nesting tree and moved with the female and her offspring. The relationship with the female was more associative than before. No chasing was witnessed, and the first coordinated vocalization between them was performed on 1st September. From their vocal characteristics (see Chapter 5), it was believed that the replacing male and female returned to the same territory in the following year.

The replacing male started to call earlier in terms of sunset during accentuation than before and after accentuation (Mann-Whitney U-test: $p = 0.012$). However, there was no significant difference in the time of the last call in terms of sunrise (Mann-Whitney U-test: $p = 0.095$, see also Table 3-1). Although the primary call production was not significantly affected by wind, it was less affected during the period of vocal accentuation than after (see Table 3-2).

3.5.2. Discussion

The vocal burst of the replacing male is interesting in terms of the main functions of primary calls, territorial and sexual interactions. There are two points to consider.

Firsly, what triggered the vocal burst of the replacing male? Generally low output during most of the nestling stage does not support the idea of stimulation from neighbours' calling. Rather, it is the disappearance of the resident male. His aggressive response inhibits the intruder from emitting primary calls. Inhibition may even function for some time after, until the absence of the resident male becomes definite, as past territorial encounters are still remembered. The possession of a territory is clearly a prerequisite to produce primary calls, as suggested for the Tawny Owl *Strix aluco* (Hirons 1976).

Secondly, why did the replacing male produce primary calls more frequently than the other conspecific territorial males at this time of the breeding cycle? The replacing male is not likely to start breeding activity in the same year, now that the first half of the breeding season has passed. However, primary call production may be useful investment in future breeding success. Since the owls generally return to the same nesting site every year (Masuda 1974), as indeed happened in this case, it may well be advantageous to claim ownership of the territory long before the actual chance of breeding. Increased singing activity and prolonged vocal production of unmated males is well known in passerines (e.g. Leopold & Eynon 1961; Slagsvold 1973; Åström 1976), but has also been noted for several owl species (Haverschmidt 1946; Thomsen 1971; König 1972; Lundberg 1980). The increased calling rate against the widowed female's approach may also indicate that the primary calls are aimed at the female. The earlier start of daily vocal activity and less influence by wind during vocal accentuation may suggest that the replacing male is sexually stimulated (Åström 1976). Further, the coincidence between the termination of vocal accentuation and pairing with the female suggests a sexual function of the primary call in the unmated male (König 1972). The high calling rate and vocal burst may help to impress other conspecific birds that the new male is capable of establishing and maintaining the territory, and may also permit neighbouring birds to learn the individual characteristics of the new resident's primary call.

4. THE PRIMARY CALL AND AGGRESSION

4.1. Introduction

Birds have developed great variability in their vocalizations, such as the elaborate repertoires of songbirds. Variation can even be found at the lowest level of organization, the element. Physical characteristics of elements such as frequency, amplitude and temporal pattern provide the sender with a capacity to encode different kinds of information in one signal (Marler 1960). Some of the physical characteristics are discrete and others are graded. Discreteness is ideal for information about the identity of a caller, such as species, individual and sex, whereas gradation is more useful in carrying motivational information. Gradation will be much in use when animals are involved in close-range events, where situations are likely to change every moment.

Becker (1982) summarised the possible physical features used to encode motivational information in various bird species such as vocal rate, song length, amplitude, frequency and complexity of sound. He concluded that aggressive excitation often resulted in increased frequency (Hz). However, according to Morton's motivational structural rules (1977), low frequency sounds indicate that the sender is more likely to attack.

In strigidine species, frequency differences within their primary calls may be a widespread phenomenon. For instance, the Great Horned Owl Bubo virginianus altered frequency while hooting (Miller 1934). So did the Boobook Owl Ninox novaeseelandiae (M'lean 1911), which increased the general level of frequency in autumn (Cheney 1915). The primary call of the Boreal Owl Aegolius funereus varied not only in pitch but also in rhythm (König 1972). The Screech Owl Otus asio lowered pitch (Scott 1968) and the Flammulated Owl O. flammeolus and Great Horned Owl turned to a hoarse quality (Marshall 1939), as they became aggressive. The Great Eagle Owl Bubo bubo had longer calls at the peak of courtship (Leibundgut 1973), and the Eurasian Pygmy Owl Glaucidium passerinum called less loud 'dew' with a simplified, subdued ending (König 1972).

The primary call 'k.hoo' of the Japanese Brown Hawk Owl is mainly used in long-distance communication and may contain information about the identity of the caller. It is simple and distinct, and must be discrete enough to reduce the possible degrading effect of the environment. However, it has already been pointed out that there are still large variations in the physical features of primary calls. It is also physically related to 'hoh' and 'guf' to form an acoustic continuum by grading in frequency, tone and temporal patterning. Behavioural contexts of these vocalizations suggest that the physical continuum may correspond with a behavioural continuum in terms of territoriality and aggression as summarized in Fig. 4-1.

In the present chapter, firstly, variations in primary calls are examined in natural conditions, and in particular for frequency changes. Aggressive motivation of territorial males may be affected by their location in the territory, breeding stage and conspecific environment. There are four working hypotheses to be considered:-

1. Territorial males will be more aggressively motivated nearer the boundary of their neighbours.

2. Territorial males will be more aggressively motivated earlier in the breeding season.

3. Territorial males will be more aggressively motivated when they hear other conspecific rivals calling than when they call spontaneously.

4. Territorial males will be less aggressively motivated when their mates approach.

The more aggressive their potential situation gets, the lower-pitched their primary calls will become. Secondly, playback experiments were carried out to simulate aggressive interactions. Not only are the physical features of primary calls and gradation examined but behaviour of territorial males. Also considered are the effect of the speaker's location in the territory and that of the stage of the breeding cycle.

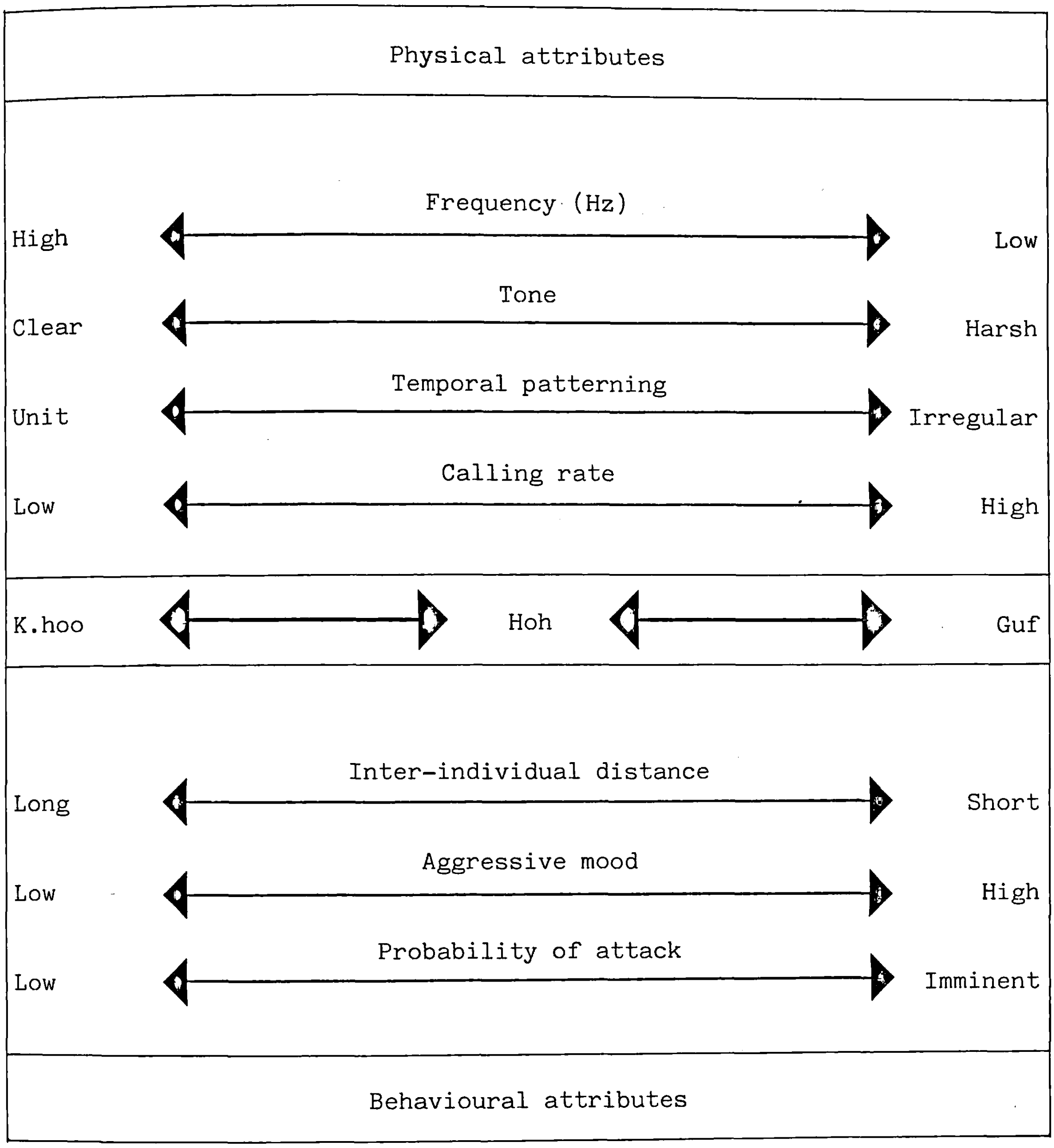


Fig. 4-1. Physical and behavioural continuum of primary call 'k.hoo' and its gradation.

While playback experiments have been widely used as a means of investigating the function of oscine songs during the last two decades (e.g. Bremond 1968; Falls 1969; Catchpole 1973; Krebs 1976), relatively few non-oscine species have been examined in the same way (e.g. Falls & McNicholl 1979; Sparling 1981). As for strigidine owls, only a few descriptions of the territorial male's response to playback of recorded conspecific primary calls are available. Ligon (1967) observed that the Elf Owl *Micrathene whitneyi* occupied the nest hole or dived at the observer attending the speaker. Martin (1973b) reported that mated males of the Burrowing Owl *Athene (Speotyto) cunicularia* called for an extended period after playback. Hirons (1976) noticed that the Tawny Owl *Strix aluco* approached the speaker and produced prolonged bouts of hooting. In addition, the easy imitation of the owls' primary calls has allowed observers to make territorial males approach and call in response (Miller 1930; Marshall 1939; Wendland 1963; Smith *et al*. 1982). The Screech Owl showed aggressive responses to imitation calls with approach and monotonous calls (Miller & Miller 1951; Scott 1968). The Barking Owl *Ninox connivens* (MacGillivray 1914) and Rufous Owl *N. rufa* (MacGillivray 1918) produced softer lower-pitched deep call in response to the imitation call than during spontaneous calling. The Ural Owl *Strix uralensis* interchanged territorial calls with alarm calls in response to the imitation call (Lundberg 1980).

4.2. Frequency of Primary Calls

4.2.1. Methods

Primary calls of territorial males of the Zushi population were recorded at different locations from the centre (i.e. nest) to the boundary of their territory during the breeding season in 1980-1981. Locations of calling birds were measured as the distance from their nest at 10 m intervals on the scale map (1:1875). Primary calls were recorded in the following intraspecific environment:

(a) The solitary caller made primary calls when no other conspecific birds called.

(b) The caller, being accompanied or approached by the mate, made primary calls when no other conspecific birds called.

(c) The solitary caller made primary calls when other conspecific birds called in the distance.

For each recording, up to twenty elements which were produced in succession were measured for their maximum frequency of part B (see p. 36). Either Nagra 4.2 tape recorder or a Sony TC-D5M stereo cassette recorder was coupled with a Uniscan spectrum analyser Model 4500 to analyse the sample calls. The frequency was read digitally at 8 Hz intervals in the range of 1 kHz.

The effect of location in the territory upon the frequency of primary calls was tested by one-way analysis of variance (ANOVA) with regression (Sokal & Rohlf 1973) at the significance level of $\alpha = 0.05$. The effect of the mate's presence and approach and that of other conspecific males' primary calls were also tested by one-way ANOVA. The comparison was always carried out for the same location zones and breeding stages.

4.2.2. Results

When solitary territorial males produced primary calls spontaneously, their frequency changed significantly at various locations in the territory. The results of one-way ANOVA are as follows:-

	Males		
Breeding stage	Rokudai 1980	Rokudai 1981	Sotaiji 1981
Pre-incubation	$p < 0.01$	$p < 0.01$	$p > 0.05$
Incubation	$p < 0.01$	$p < 0.01$	$p > 0.05$

Although the general range of frequency did not seem to vary before and during incubation, the relationship between the location and frequency of primary calls reversed. During the pre-incubation stage, two territorial males, Rokudai 1980 and Rokudai 1981, tended to produce primary calls at lower frequencies as they were farther away from the centre of territory i.e. nest (see Fig. 4-2A). During incubation they tended to emit primary calls at lower frequencies as they approached closer to the centre of territory (see Fig. 4-2B). However, Sotaiji 1981 did not significantly differ in its frequency for the two stages. During the nestling stage, sufficient recordings covering different locations in the territory were not available. However, the same trend as that of the incubation stage was apparent from the limited recordings.

Territorial males tended to reduce the frequency of primary calls when their mates came to perch close to them or even just passed nearby. Some examples are shown in Fig. 4-3. The reduction in frequency happened whether males were vocal at the moment of females' approach or not. However, it happened quite sharply when females approached during a bout of calling. Males usually kept the frequency low while females were close. In some cases, however, they made a quick recovery. Further, the lower frequency was generally observed when females were present rather than absent within 20 m of their calling mates in the central zone (see Table 4-1). For the outer zone, comparisons could not be made due to the lack of recording opportunities as males tended to be alone.

When other conspecific males produced primary calls, territorial males in the absence of their mates produced lower frequencies than when they were making spontaneous and solitary calls (see Table 4-1).

4.2.3. Discussion

The frequency of primary calls changed with location in the territory, but did not always follow the initial hypotheses. Firstly, why didn't males always call at a lower frequency when closer to the territory boundary? This is, after all, where they are supposed to be most aggressive. The hypothesis does not take into account a possible shift in location importance during the breeding season, as the reversed correlation before and after the onset of incubation suggests. In early season, territorial males are likely to clash in establishing and defending their territories. Boundary location is more important in territorial defence against rivals than central location, thus territorial males are likely to be aggressive at the

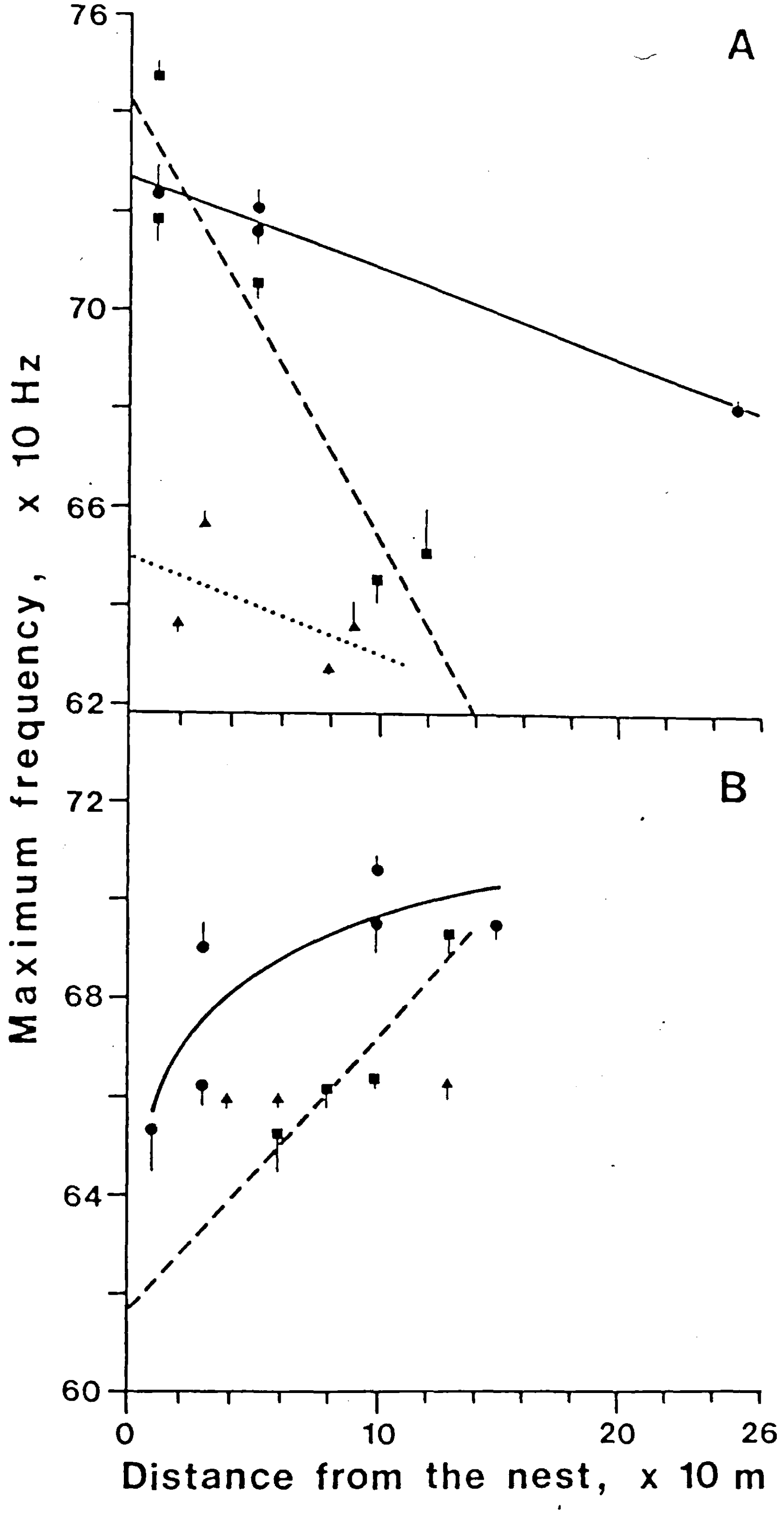


Fig. 4-2. Effects of locations upon the frequency of primary calls. A, Pre-incubation stage: Rokudai 1980 (●), Y = 727.4 - 0.179X, $p < 0.02$; Rokudai 1981 (■), Y = 742.7 - 0.877X, $p < 0.001$; Sotaiji 1981 (▲), Y = 650.8 - 0.198X, $0.05 < p < 0.1$. B, Incubation stage: Rokudai 1980, Y = 618.1 + 39.219 log X, $p < 0.05$; Rokudai 1981, Y = 616.6 + 0.557X, $p < 0.05$; Sotaiji 1981, $p > 0.05$. One standard error is shown in either side of the mean.

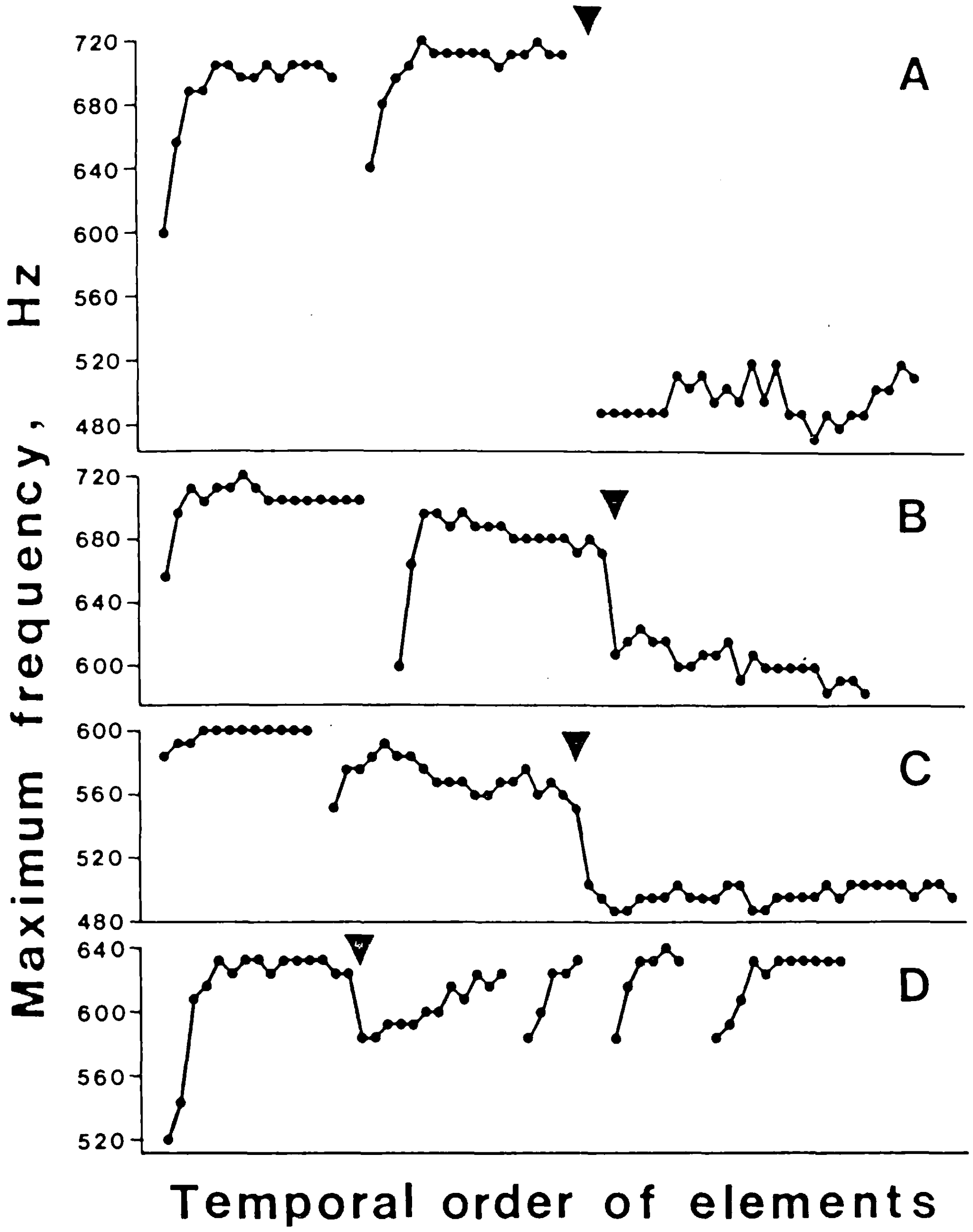


Fig. 4-3. Effects of mate's approach upon the frequency of primary calls. A, Rokudai 1981; B, Fuboku 1981; C and D, Sotaiji 1981; ▼, approach of the mate.

Table 4-1. Effects of mate's presence and conspecific male's primary calls upon the frequency of primary calls

Zone	Breeding stage	Male	Situations A	Situations B	Situations C	ANOVA with replica A vs. B	ANOVA with replica A vs. C
Central	Pre-incubation	Rokudai 1980	717 ± 3 722 ± 4 724 ± 6	660 ± 2 695 ± 7	552 ± 11 649 ± 6	$p < 0.01$	$p < 0.01$
"	"	Rokudai 1981	706 ± 3 719 ± 5 748 ± 4	627 ± 2	694 ± 4	$p < 0.01$	$p > 0.05$
"	"	Sotaiji 1981	628 ± 1 637 ± 5 637 ± 2 657 ± 3	496 ± 1	642 ± 4	$p < 0.01$	$p > 0.05$
Central	Incubation	Rokudai 1980	654 ± 8 663 ± 5 691 ± 5	526 ± 2 584 ± 6 639 ± 6	547 ± 2 587 ± 6 602 ± 6	$p < 0.01$	$p < 0.01$
"	"	Rokudai 1981	653 ± 8 662 ± 4	496 ± 3	-	$p < 0.01$	-
"	"	Sotaiji 1981	660 ± 1 660 ± 2	-	666 ± 1	-	$p > 0.05$

Table 4-1 (continued)

Zone	Breeding stage	Male	Situations			ANOVA with replica	
			A	B	C	A vs. B	A vs. C
Central	Fledgling	Rokudai 1981	554 ± 7	-	688 ± 3 700 ± 2	-	$p < 0.01$
"	"	Sotaiji 1981	656 ± 3	-	577 ± 7 627 ± 5	-	$p < 0.01$
Outer	Pre-incubation	Rokudai 1981	646 ± 4 652 ± 9	-	599 ± 3	-	$p < 0.01$
Outer	Incubation	Sotaiji 19811	663 ± 3	-	598 ± 8 614 ± 9 650 ± 2 652 ± 2	-	$p < 0.01$
Outer	Fledgling	Fuboku 1981	701 ± 3	-	681 ± 3	-	$p < 0.01$

Note: A, spontaneous and solitary calls; B, the mate was nearby; C, other conspecific males were calling.

boundary. As soon as major territorial dispute over the boundaries with neighbours is settled and nesting activity starts, the importance of nest site containing the offspring and mate predominates over that of the other sites in the territory. The centre of defence is now the nest site, so the breeding males are more likely to be aggressive at the centre. The lack of apparent correlation between frequency and location in one of the territorial males, Sotaiji 1981, may be due to less stable territorial status. This bird set up a new territory in 1981 by squeezing in between the three well-established traditional territories, and was under severe territorial pressure from neighbours. The smaller size of territory than the others might also be an important factor.

Secondly, why didn't territorial males produce their primary calls at higher frequency as their mates approached? All other contexts appear to support the relationship between aggressive motivation and frequency: the more aggressive the caller is, the lower the frequency of primary calls will be. Could the territorial males be aggressive towards their mates? When animals vocalize, their sound should be an honest expression of their motivation irrespective of the effect (Morton 1982). Thus the male's motivation at a female's approach is expected to be identical with the motivation in other territorial contexts. Territorial males may not be able to identify an approaching individual instantly, whether it is their mate or a rival. It is more advantageous to express aggressive motivation to deal with the worst possibility.

The low frequency in response to a rival's primary call and also in the artificially simulated aggressive situations (see 4.4.) suggests that the frequency of the primary call is one form of vocal expression reflecting aggressive motivation. In general, the relationship between frequency and aggressive motivation does support Morton's motivational structural rule (1977).

4.3. Aggressive Response to Playback

4.3.1. Methods

Subjects

During the early pre-incubation stage in 1980, experiments were carried out on four birds from Miyake-jima Island and two birds from Zushi. All but one of the test birds had paired with their mates.

Experimental tapes

Test primary calls were recorded at Zushi in September 1979 from a spontaneously calling male which occupied a remote territory approximately 2 km away from the 1980 experimental sites. The three-minute recording contained more or less continuously emitted calls.

Playback system

A Nagra 4.2 tape recorder was placed within the central zone of the territory. It stood or hung at approximately 2 m above the ground on the top of a bush or some other object. The speaker was directed towards the centre of the territory, i.e. the nest. Special care was taken to choose a playback site, so that the owls could be sufficiently well observed with night-time lighting.

Pilot experiments carried out in 1979 showed that sound pressure level of playback calls affected the reaction of owls. Too loud playback calls caused them to retreat quickly after initial aggression. Relatively low playback was ignored, probably because it was not heard. Dabelsteen (1981) also showed the similar tendencies in the Blackbird *Turdus merula*. Thus the playback volume was set at the normal level which the owls spontaneously called at.

Playback schedule

After an initial nine-minute observation period (pre-play period) test birds were exposed to the three-minute recording of test primary calls (play period). Their behaviour was further observed for nine minutes after playback (post-play period). When one of the Zushi birds did not respond to the first exposure, it was given the second exposure after nine minutes and was observed for further nine minutes after the second playback. The experiments were carried out once for each bird in the evening.

Categories of response and statistics

The following measures were suggested by the pilot experiments:-

1. latency of response (seconds), the time period between the start of playback and the first sign of visual and vocal response;
2. number of flights;
3. number of attacks against speaker;
4. distance from speaker (m);
5. number of primary and graded call elements;
6. number of bouts of primary and graded call elements;
7. number of elements per bout.

All statistical comparisons were made by the non-parametric Wilcoxon matched-pairs signed-ranks test (Siegel 1956).

4.3.2. Results

Latency of response

During the pre-play period, all the six subjects regularly produced primary calls. Four of them, which were in sight of the observer and within 30 m from the speaker, also engaged in hunting and associating with their mates. On hearing playback of recorded primary calls of a conspecific stranger which was broadcast from a speaker in their territories, they became alert and showed changes in behaviour. For example, they immediately stopped any current activities. However, primary calls were produced by two of them and another invisible bird without a noticeable delay (mean 6.3 ± 4.5 seconds). Within five seconds or so, the four visible birds orientated towards the speaker, and the next step was flying straight to the vicinity of the speaker. Two of them made an approach within 15 seconds; one bird eventually did when playback nearly came to an end; and the last bird did not move at all. The other two birds moved towards the speaker at 40 and 120 seconds respectively. The three males, which did not make an immediate vocal response, produced graded and primary calls after 25, 45 and 220 seconds respectively.

Number of flights, attacks against speaker, and distance from speaker

In the present experiment, subjects did not fly more than once during playback and one bird, which was close to the speaker from the outset, did not move at all (see Table 4-2). There was no sign of searching behaviour. No test birds flew over the speaker repeatedly nor skimmed over and attacked it with strong pounces and kicks as observed in pilot experiments. Although the number of flights did not vary before and during playback, all the flights made during playback involved shortening the distance between the bird and the speaker (see Fig. 4-4). They tended to stay near the speaker even after playback had ended. Two of them flew away eventually.

Vocal response

Subjects produced graded and primary calls in response to playback. When they were far from the speaker, they tended to respond first with primary calls, 'k.hoo', prior to an approach. In most cases they were initially quiet and made an approach, then became vocal, emitting 'guf', which is the lower end of the frequency continuum and less temporally organized. Calls gradually increased their maximum frequency transforming to 'hoh' and eventually to 'k.hoo', developing the characteristic two-element unit, 'k.hoo-k.hoo'.

(a) **Number of graded and primary call elements**

As can be seen from Fig. 4-5A, subjects produced significantly more elements after playback than before for the following time periods:-

3-minute period ... $T = 1$, $N = 6$, $p < 0.031$
6-minute period ... $T = 1$, $N = 6$, $p < 0.031$
9-minute period ... $T = 0$, $N = 6$, $p < 0.016$

Some subjects increased the number of elements during the play period. However, other subjects just listened to playback, thus the difference between play period (PL) and any one of the three pre-play sub-periods (PR1, PR2 or PR3) was not significant:-

PR1 vs. PL ... $T = 9.0$, $N = 6$, $p > 0.05$
PR2 vs. PL ... $T = 8.5$, $N = 6$, $p > 0.05$
PR3 vs. PL ... $T = 7.5$, $N = 6$, $p > 0.05$

Table 4-2. Number of flights during the playback experiment

Three-minute period	Males					
	1	2	3	4	5	6
Pre-play 1	0	0	0	1	0	0
Pre-play 2	0	1	0	1	0	1
Pre-play 3	0	0	0	0	0	0
Play	1	1	1	0	1	1
Post-play 1	0	0	0	0	0	0
Post-play 2	0	0	0	0	0	0
Post-play 3	0	0	1	0	0	0

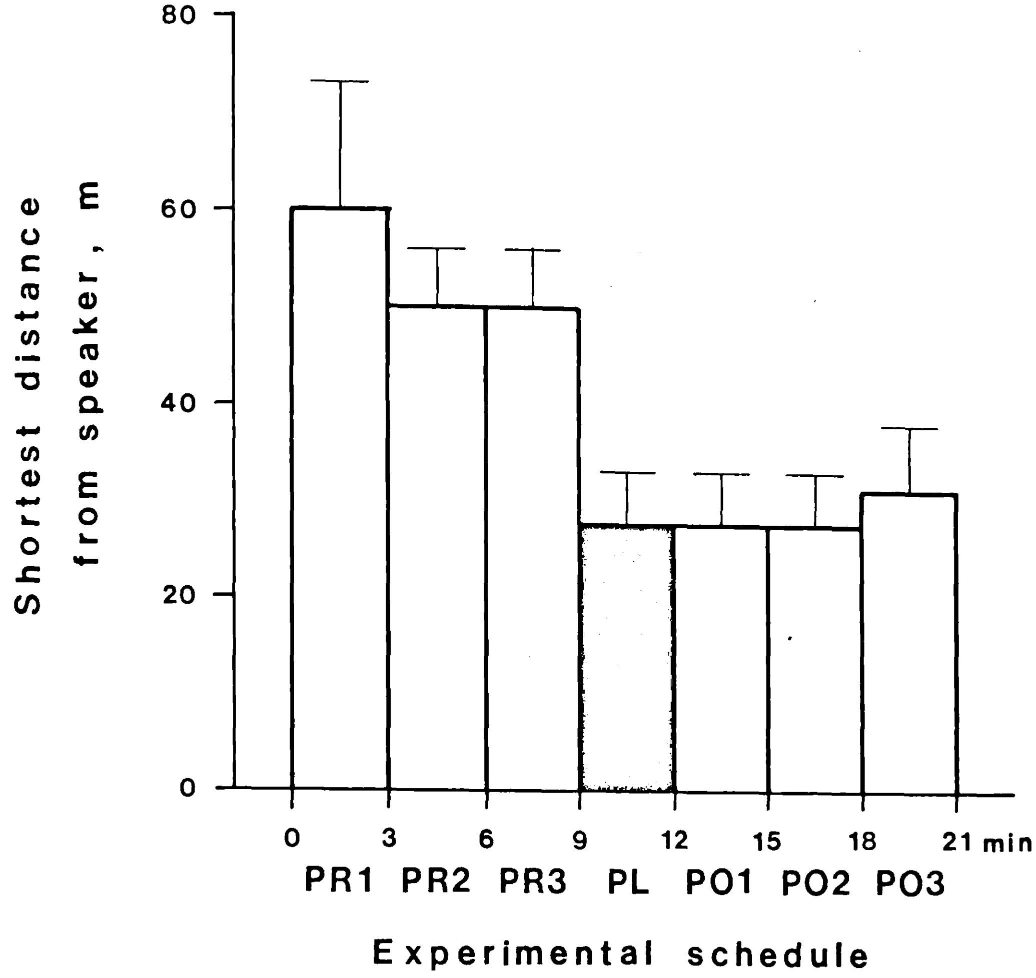


Fig. 4-4. Distance between the test birds and speaker. PR, pre-play period; PL, play period; PO, post-play period. The mean and its one standard error is shown.

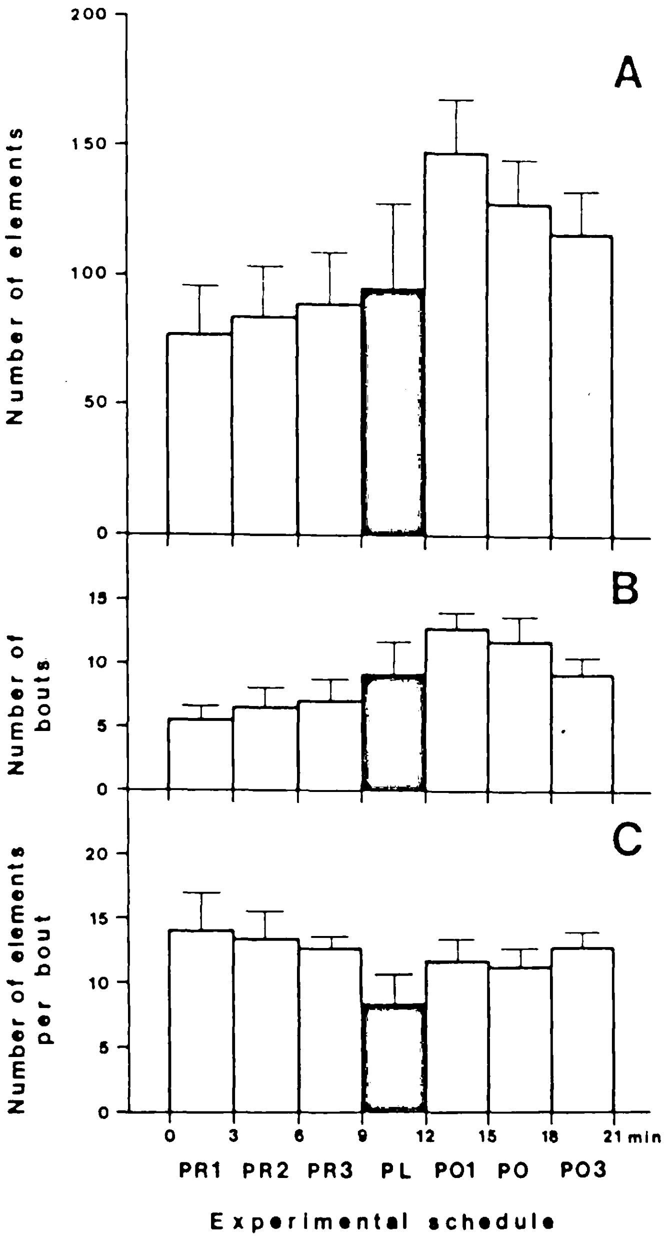


Fig. 4-5. Production of primary and graded calls during the playback experiment. PR, pre-play period; PL, play period; PO, post-play period. The mean and its one standard error is shown.

After playback, the number of elements reached a peak during the first three minutes (P01). The difference between PL and P01 was significant ($T = 1$, $N = 6$, $p < 0.031$). It gradually decreased until there was no significant difference between PL and the rest of the post-play sub-periods (P02 and P03) as follows:-

P01 vs. P02 ... $T = 1$, $N = 6$, $p < 0.031$
P02 vs. P03 ... $T = 1$, $N = 6$, $p < 0.031$
PL vs. P02 ... $T = 5$, $N = 6$, $p > 0.05$
PL vs. P03 ... $T = 8$, $N = 6$, $p > 0.05$

(b) Number of bouts of primary and graded calls

As can be seen from Fig. 4-5B, the number of bouts of primary and graded call elements followed a very similar mode of response to that of graded and primary call elements (see above). Subjects produced significantly more bouts after playback than before:-

3-minute period ... $T = 1$, $N = 6$, $p < 0.031$
6-minute period ... $T = 1$, $N = 6$, $p < 0.031$
9-minute period ... $T = 0$, $N = 6$, $p < 0.016$

There was not always an immediate increase with playback:-

PR1 vs. PL ... $T = 3.5$, $N = 5$, $p > 0.05$
PR2 vs. PL ... $T = 5.5$, $N = 6$, $p > 0.05$
PR3 vs. PL ... $T = 4.5$, $N = 6$, $p > 0.05$

However, after playback the number of bouts reached a peak during P01 ($T = 2$, $N = 6$, $p < 0.047$). Although the number of bouts decreased towards the end of the post-play period, it was not significantly different from the play period:-

P01 vs. P03 ... $T = 1$, $N = 6$, $p < 0.031$
PL vs. P02 ... $T = 3$, $N = 5$, $p > 0.05$
PL vs. P03 ... $T = 8$, $N = 5$, $p > 0.05$

(c) Number of primary and graded call elements per bout

The number of primary and graded call elements per bout significantly decreased during the play period (see Fig. 4-5C):-

PR1 vs. PL ... $T = 2$, $N = 6$, $p < 0.047$
PR2 vs. PL ... $T = 0$, $N = 6$, $p < 0.016$
PR3 vs. PL ... $T = 0$, $N = 6$, $p < 0.016$

However, it was not significantly different during and after playback:-

PL vs. PO1 ... $T = 4, N = 6, p > 0.05$

PL vs. PO2 ... $T = 5, N = 6, p > 0.05$

PL vs. PO3 ... $T = 6, N = 6, p > 0.05$

Some subjects produced more elements in a bout and others less elements in a bout during playback than after.

Effects upon females

Only one of the test males was mated. His mate was not involved in playback responses.

4.3.3. Discussion

If playback experiments are used as evidence in discussion of aggressive motivation and behaviour of territorial males, it is relevant to compare artificially elicited responses with the natural behaviour observed in aggressive situations. Behavioural contexts of aggressive interactions between conspecific individuals, and primary call production in terms of number and frequency, have shown that initial responses to rival males are similar to those observed during playback. Latency of response, distance from the speaker and vocal response seem to be the most useful measures. In particular, the number of graded and primary call elements appeared to be extremely valid measures. The initial quietness and fewer elements per bout during than before playback may partly be due to the result of the test males' perception and assessment of whether a stranger's primary call is a threat or not. The process of locating and approaching the speaker may also partly be responsible for blocking an immediate and full release of primary and graded calls. This conflict between motivational state and motor patterns has been also suggested for the similar playback response of the Cardinal Cardinalis cardinalis (Gottfried & Gottfried 1978). It may be advantageous to produce frequent and short bouts as playback began. In this way the caller could monitor and should transmit attentiveness to the intruder's primary call. Bout formation is possibly influenced by the types of vocalization contained in a bout. Unlike primary calls 'k.hoo', graded calls 'hoh' and 'guf' tend to be produced monotonously with less break. It is possible to comment that the frequency of call elements is also an important measure (see 4.4.2.).

The experimental condition whereby the speaker never changed location during playback only partly represents a natural aggressive encounter. The intruder appears to occupy a site within the territory, which is not uncommon, yet the experimental condition is artificial. Firstly, it lacks visual contact, and one might expect some searching behaviour of test birds. However, they flew over and around the speaker very infrequently and stayed close. This suggests that visual contact is less important than auditory contact. Secondly, components of fighting or escape are missing and a one-way vocal delivery is simply provided. Thus, even if test birds attack the speaker and call in response, the aggression expressed is not complete. At night-time, however, vocal measures are clearly advantageous over visual measures. To some extent, it may be possible to understand the expression of aggressive motivation in nocturnal territorial males by monitoring their vocalizations. However, there is some danger in relying solely upon vocal measures, although for nocturnal owls the difficulty is obvious. Future research may depend more upon the use of radio transmitters. These not only monitor the movement and location of birds accurately in the darkness, but also provide information on the internal condition of animals such as heart rate which may also reflect their motivational state (Zimmer 1982).

4.4. Effects of Speaker's Location in the Territory and Breeding Stage

4.4.1. Methods

Subjects

During the breeding season in 1981, five territorial mated males were used as experimental subjects. They occupied neighbouring territories at Zushi.

Experimental tapes

Test primary calls were recorded from other territorial males (MA, MB and MI) at Miyake-jima Island in late April 1981. They emitted more or less continuous calls spontaneously and solitarily. Experimental tapes were prepared on three-minute endless tapes TDK EC-3.

Playback system

A Sony TC-1160A cassette recorder with a built-in speaker was positioned at approximately 2 m above the ground. It was operated by a remote control switch at the end of a 30-m extension lead. The playback volume was set at the normal level.

Playback schedule

Three different speaker's locations were selected for each territory:-

- Central location was within 20 m from the nest in the central zone.
- Middle location was within the central zone and more than 50 m away from the nest.
- Boundary location was in the outer zone and was 100-250 m from the nest where territorial encounters were observed.

Three different dates were chosen for each test bird during the breeding cycle:-

- between 10th and 30th May during the pre-incubation stage after the territorial relationship had settled;
- between 9th and 26th June during the incubation stage;
- between 21st July and 5th August during the early fledgling stage.

Since the owls were hardly observed in the outer zone from the incubation stage to the early fledgling stage, playback experiments at the boundary location were abandoned. The central location was avoided during the incubation to minimize disturbance to the breeding owls. The final set of experiments to investigate the effect of the speaker's location in the territory and breeding stage are indicated with the source of experimental tape used as follows:-

Speaker's location	Breeding stages		
	Before incubation	During incubation	Early fledgling
Central	MA	None	MA
Middle	MA	MI	MB
Boundary	MA	None	None

After an initial four-minute observation period (pre-play period) test birds were exposed to a four-minute recording of experimental primary calls (play period). Their behaviour was further observed for four minutes after playback (post-play period). For the experiment during the pre-incubation stage, a second exposure was given. It lasted for one minute and was followed by a two-minute observation period. This additional exposure was particularly designed to check the frequency of primary calls. When test birds did not respond to the first exposure at all, the experiment was repeated on a later date. All the experiments were carried out between 23:00 - 3:30. The order of experiments among test birds and locations was basically random.

Categories of response and statistics

The following measures were used for detailed comparison:-

1. latency of response (seconds). The first response can be alerting and flying straight towards the speaker as described before. The problem about using this as a measure was that subjects were not always in sight at the beginning of playback. Therefore, the time from the start of playback to the first approach within 40 m of the speaker was used;
2. number of flights;
3. nearest distance from speaker (m);
4. number of primary and graded call elements;
5. maximum frequency of primary and graded call elements (Hz).

Observed maximum frequency was measured digitally at 8 Hz intervals over the frequency range of 0-1000 Hz, using a Uniscan spectrum analyser Model 4500. The mean maximum frequency of spontaneous primary calls which were produced by each subject at the centre of territory was used as an individual standard maximum frequency. The difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls was obtained. The mean frequency difference was then calculated for every thirty-second sub-period and used as the representative value. When no calls were emitted, the frequency difference was regarded as zero.

For the presentation and analysis of results for measures (1) and (2), the four-minute period was used. However, for measures (3) and (4) the experimental periods were sub-divided into one-minute sub-periods, and thirty-second sub-periods for measure (5), so that the temporal change might be shown. All the statistical comparisons were made by two-way ANOVA with or without replication. The difference between the means was tested by *a priori* and/or *a posteriori* test (Sokal & Rohlf 1973). The significance level was set at $\alpha = 0.05$.

4.4.2. Results

Latency of response

In Table 4-3, latency of response to the first playback (mean with one standard error) is listed for the speaker's different locations in the territory and breeding stages. Regardless of breeding stages, territorial males seemed to come within 40 m of the speaker more quickly when the speaker was closer to the centre of the territory. However, the difference of the means between the speaker's locations was not significant for both pre-incubation and fledgling stages (see Appendix D-1, p. 249). Although the owls appeared to respond more quickly during the pre-incubation stage than the fledgling stage, the difference of the means between the breeding stages was not significant with the speaker at both central and middle locations (see Appendix D-2, p. 250).

Number of flights

In Table 4-4, the mean number of flights at different speaker's locations in the territory and breeding stages is listed with one standard error. Territorial males showed more flights during playback. In the pre-incubation stage, with respect to the first

Table 4-3. Latency of response to the first playback at different locations of speaker in the territory and breeding stages

	Speaker's location in the territory		
Breeding stage	Central	Middle	Boundary
Pre-incubation	17 ± 8 s	25 ± 12 s	34 ± 7 s
Incubation	-	41 ± 23 s	-
Fledgling	30 ± 11 s	46 ± 8 s	-

Table 4-4. Number of flights at different locations of speaker in the territory and breeding stages

A. Before the first playback (four-minute period)

	Speaker's location in the territory		
Breeding stage	Central	Middle	Boundary
Pre-incubation	0.4 ± 0.4	0	0
Incubation	-	0.3 ± 0.3	-
Fledgling	0.3 ± 0.3	0	-

B. During the first playback (four-minute period)

	Speaker's location in the territory		
Breeding stage	Central	Middle	Boundary
Pre-incubation	5.2 ± 1.1	2.4 ± 0.6	2.6 ± 1.1
Incubation	-	2.4 ± 0.5	-
Fledgling	2.8 ± 1.0	1.2 ± 0.7	-

C. After the first playback (four-minute period)

	Speaker's location in the territory		
Breeding stage	Central	Middle	Boundary
Pre-incubation	0.6 ± 0.4	0.8 ± 0.4	0.8 ± 0.4
Incubation	-	0.8 ± 0.2	-
Fledgling	0.6 ± 0.4	0.6 ± 0.4	-

D. During the second playback (one-minute period) and its post-play period (two-minute period) in the pre-incubation stage

	Speaker's location in the territory		
Second playback	Central	Middle	Boundary
During	1.4 ± 0.2	0.4 ± 0.2	2.4 ± 1.5
After	0.2 ± 0.2	0	0.2 ± 0.2

exposure to playback, there were significant individual differences in the number of flights, and the number of flights differed significantly with the speaker's location (see Appendix D-3a, p. 251). Males performed significantly more flights with the speaker at the central location than elsewhere (a priori test: $F_s = 18.940$, df = [1, 8], $p < 0.01$). However, there was no significant difference between the middle and boundary locations (a priori test: $F_s = 0.078$, df = [1, 8], $p > 0.05$). With respect to the second exposure to playback, neither the speaker's location nor individuals had a significant effect upon the number of flights (see Appendix D-3b). In the fledgling stage, there was no significant difference in the number of flights with the speaker's location and also with individuals (see Appendix D-3c). With the speaker at the central location, four out of the five individuals flew more times during the four-minute play period during the pre-incubation stage than the fledgling stage. However, the difference of the means between the breeding stages was not significant (see Appendix D-4a, p. 252). With the speaker at the middle location, the number of flights did not differ significantly with breeding stages (see Appendix D-4b).

Nearest distance from speaker

In Fig. 4-6, the nearest distance of males from the speaker is presented with respect to its locations in the territory. The initial differences among the speaker's locations were large, due to the owls' preference of occupying sites inside the central zone. During the pre-incubation stage, it appears that at the first exposure to playback they were slower to come near the speaker when it was placed at the boundary than elsewhere. However, there was significant evidence of interaction between the individuals and locations of the speaker, suggesting that the speaker's location did not affect the distance of each bird in a consistent manner (see Appendix D-5a, p. 253). For the second exposure, there was no significant difference between the speaker's locations (see Appendix D-5b). During the fledgling stage, the nearest distance from the speaker differed significantly with the speaker's location. However, some individuals came closer at the central location and others at the middle (see Appendix D-5c). In conclusion, there was no simple relationship between distance and the speaker's location.

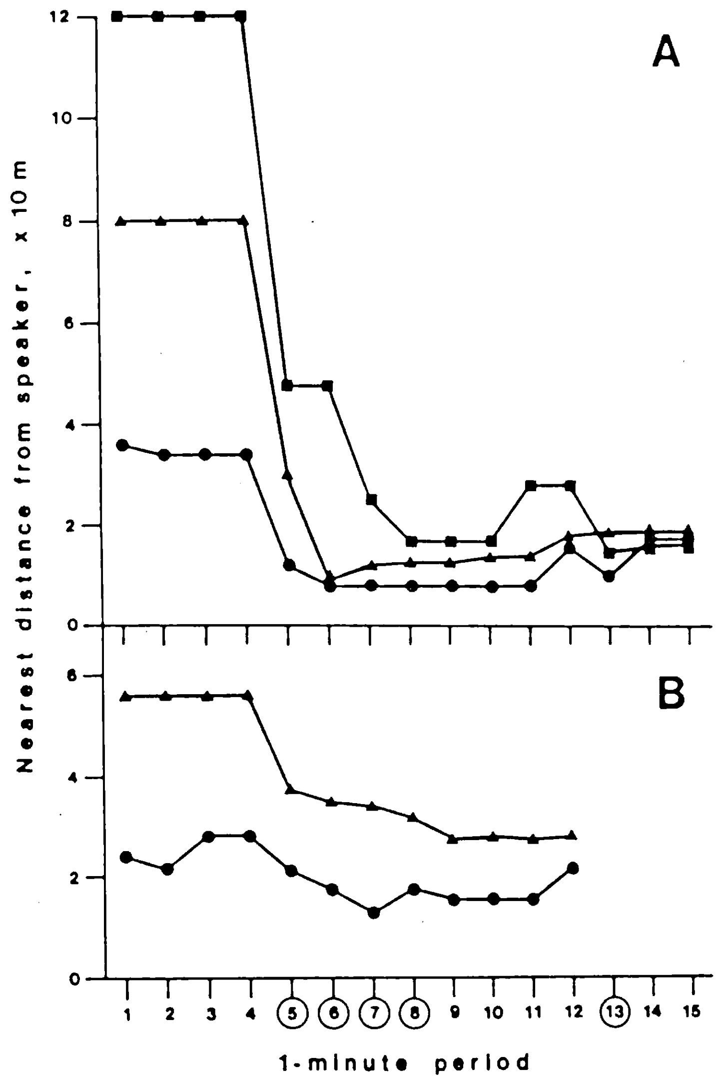


Fig. 4-6. Nearest distance from speaker at different locations in the territory: central location (●), middle location (▲) and boundary location (■). A, pre-incubation stage; B, fledgling stage; ○, play period.

In Fig. 4-7, the nearest distance of males from the speaker is presented with respect to breeding stages. With the speaker at both central and middle locations, it appears that the distance from the speaker was shorter in the pre-incubation stage than later. Although they varied their nearest distance from the speaker with breeding stage, there was significant interaction between the individuals and breeding stages (see Appendix D-6, p. 254). In conclusion, there was no simple relationship between distance and breeding stage.

Number of primary and graded call elements

In Fig. 4-8, mean numbers of primary and graded call elements produced during the experimental periods are presented with respect to the speaker's location in the territory. For both pre-incubation and fledgling stages, the patterns appear to follow the same course of increase and decrease to playback of recorded primary calls of a conspecific stranger. In the pre-incubation stage, the number of elements during the first playback and its post-play period and that of the second playback and its post-play period significantly differed with the speaker's location in the territory (see Appendix D-7 a and b, p. 255). Although with the first exposure a significant difference was recognized among the individuals, no evidence of interaction means that all the individuals produced elements in a consistent way with respect to the speaker's location. Males produced more elements with the speaker at the central location than elsewhere (a priori test: the first play and post-play periods, $F_s = 22.853$, df = [1, 105], $p < 0.01$; the second play and post-play period, $F_s = 16.037$, df = [1, 28], $p < 0.01$). There was no significant difference between the middle and boundary locations (a priori test: the first play and post-play periods, $F_s = 0.889$, df = [1, 105], $p > 0.05$; the second playback and post-pl periods, $F_s = 1.340$, df = [1, 28], $p > 0.05$). In the fledgling stage, however, the number of elements did not differ significantly with the speaker's location (see Appendix D-7c).

In Fig. 4-9, mean numbers of elements produced during the experimental periods are presented with respect to breeding stages. With the speaker at the central location, the number of elements did not differ with breeding stage during playback (see Appendix D-8a, p. 256). However, it did differ significantly after playback (see Appendix D-8b), and males produced more elements during the pre-incubation stage than the fledgling stage (a priori test: $F_s = 68.315$,

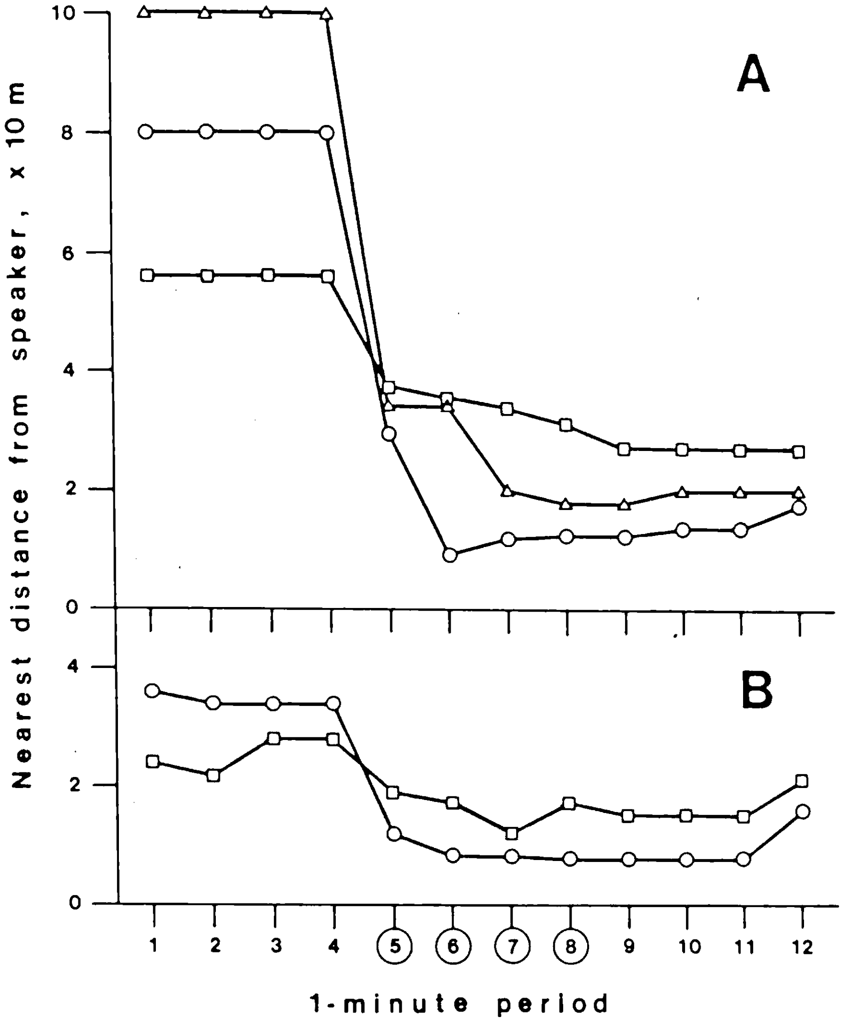


Fig. 4-7. **Nearest distance from speaker at different breeding stages:** pre-incubation stage (o), incubation stage (△) and fledgling stage (□). **A**, middle location; **B**, central location; ○, play period.

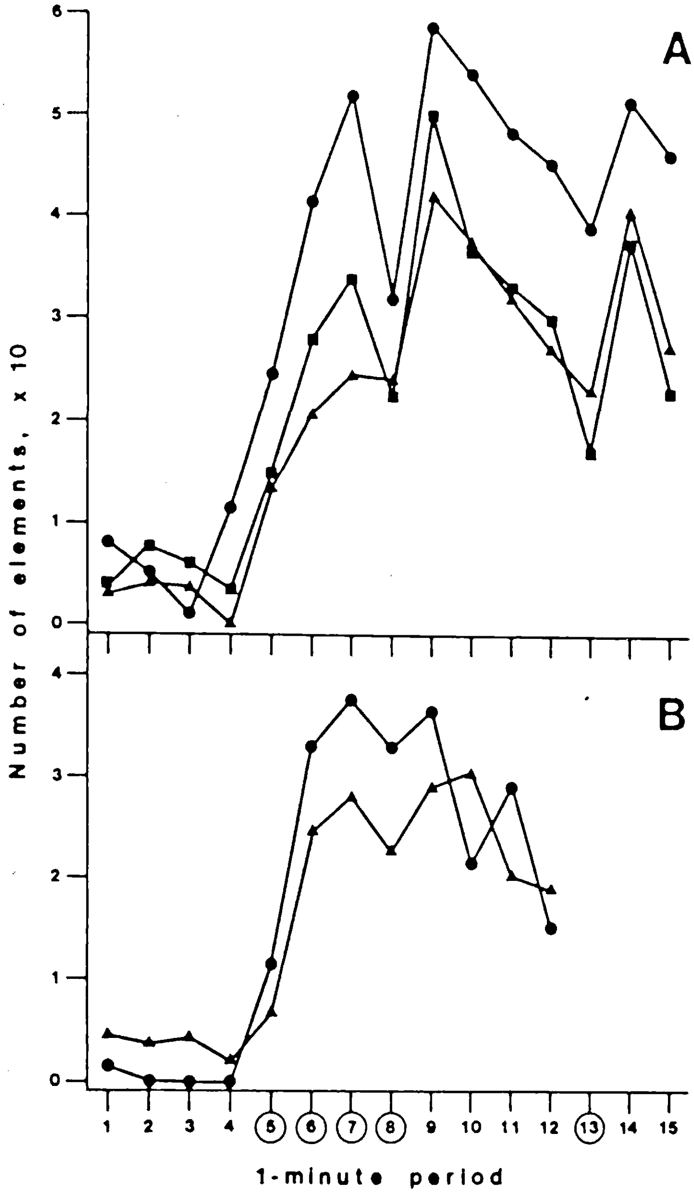


Fig. 4-8. Number of primary and graded call elements at different locations in the territory: central location (●), middle location (▲) and boundary location (■). A, pre-incubation stage; B, fledgling stage; ○, play period.

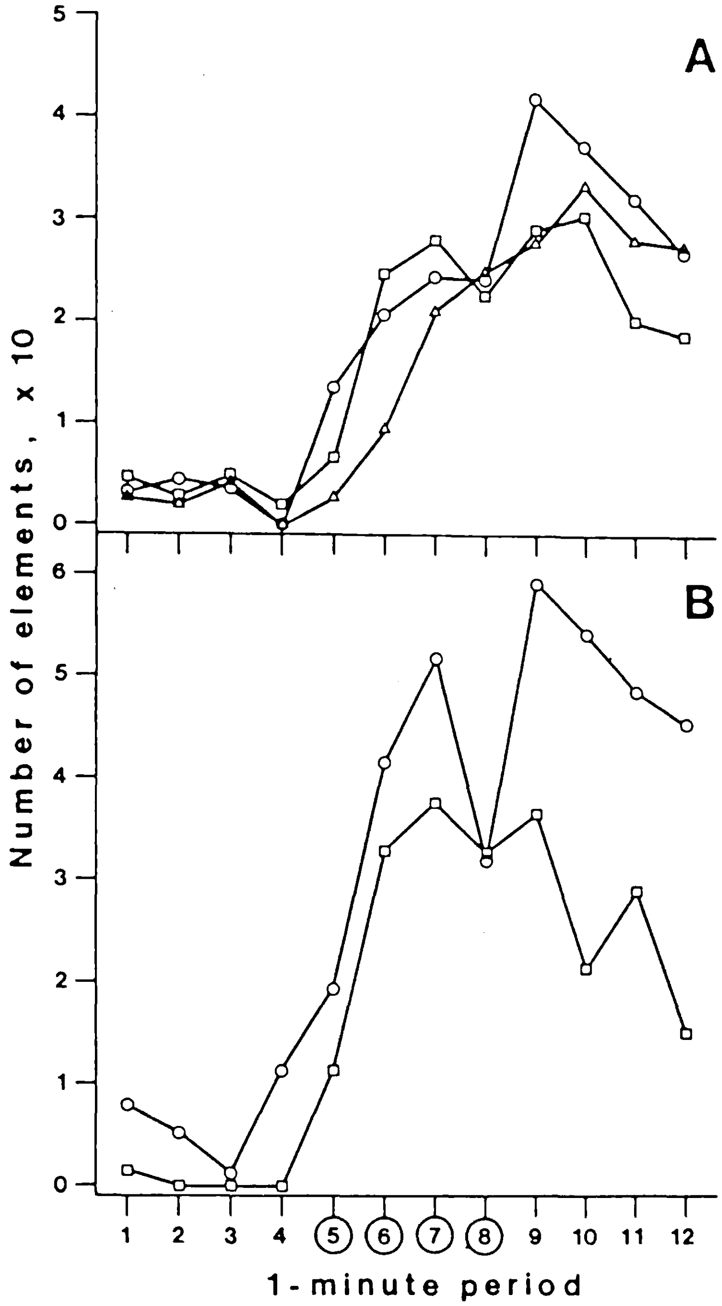


Fig. 4-9. Number of primary and graded call elements at different breeding stages: pre-incubation stage (o), incubation stage (△) and fledgling stage (□). **A**, middle location; **B**, central location; ○, play period.

df = [1, 30], $p < 0.01$). With the speaker at the middle location, the number of elements produced did not vary with breeding stage during playback (see Appendix D-8c). Although it did vary after playback, there was strong evidence of interaction (see Appendix D-8d).

Maximum frequency of primary and graded calls

In Fig. 4-10, changes in the maximum frequency of primary and graded calls with the speaker at the middle location in the pre-incubation stage are given as an example. With the first playback, one bird (■) explicitly showed the frequency drop. It called in the lower frequency range during most of the first play and post-play periods than during the pre-play period by 150-250 Hz. It showed some sign of recovery towards the end of the post-play period. However, the second playback brought the frequency down again, and later there was another sign of recovery. The other three males (▲ , △ , □) presented low frequency calls in response to the first playback and gradually raised the frequency. The last male (●) called at very low frequency 32 seconds after the onset of playback. As it called too close to the speaker, the recording of the initial vocal response was not analysed on the Uniscan. However, the overall pattern of change in maximum frequency with the first playback was similar to the preceding three males. With the second playback, two of the subjects (▲ , ●) did not reduce maximum frequency when they were away from the speaker by 100 m and 30 m respectively. The recording of the calls of one male (△) was not possible for the second playback and following period.

In Fig. 4-11, mean differences between the observed maximum frequency of primary and graded calls and the individual standard maximum frequency of primary calls are shown for the experimental periods with respect to the speaker's locations in the territory. In the pre-incubation stage (see Fig. 4-11A), comparison was made for four subjects, as one bird did not approach close enough to record its calls. Degrees of reduction in maximum frequency differed significantly with the speaker's location during the first playback (see Appendix D-9a, p. 258). However, it is for its initial two minutes that the speaker's location affected all the four equally, for there was no evidence of interaction (see Appendix D-9b). They reduced maximum frequency of their calls significantly more when the

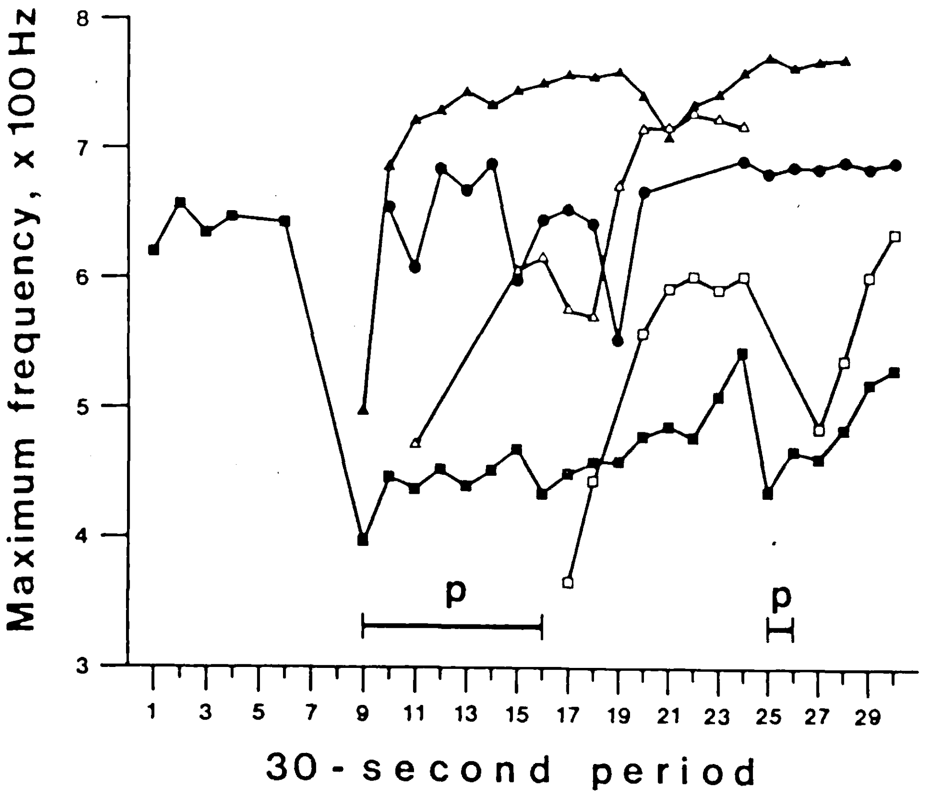


Fig. 4-10. **Maximum frequency of primary and graded calls**: during the playback experiment, with the speaker at the middle location in the territory in the pre-incubation stage. The individual standard maximum frequency is 633 Hz for owl ■, 684 Hz for owl △, 717 Hz for owl ●, 732 Hz for owl □ and 747 Hz for owl ▲. p, play period.

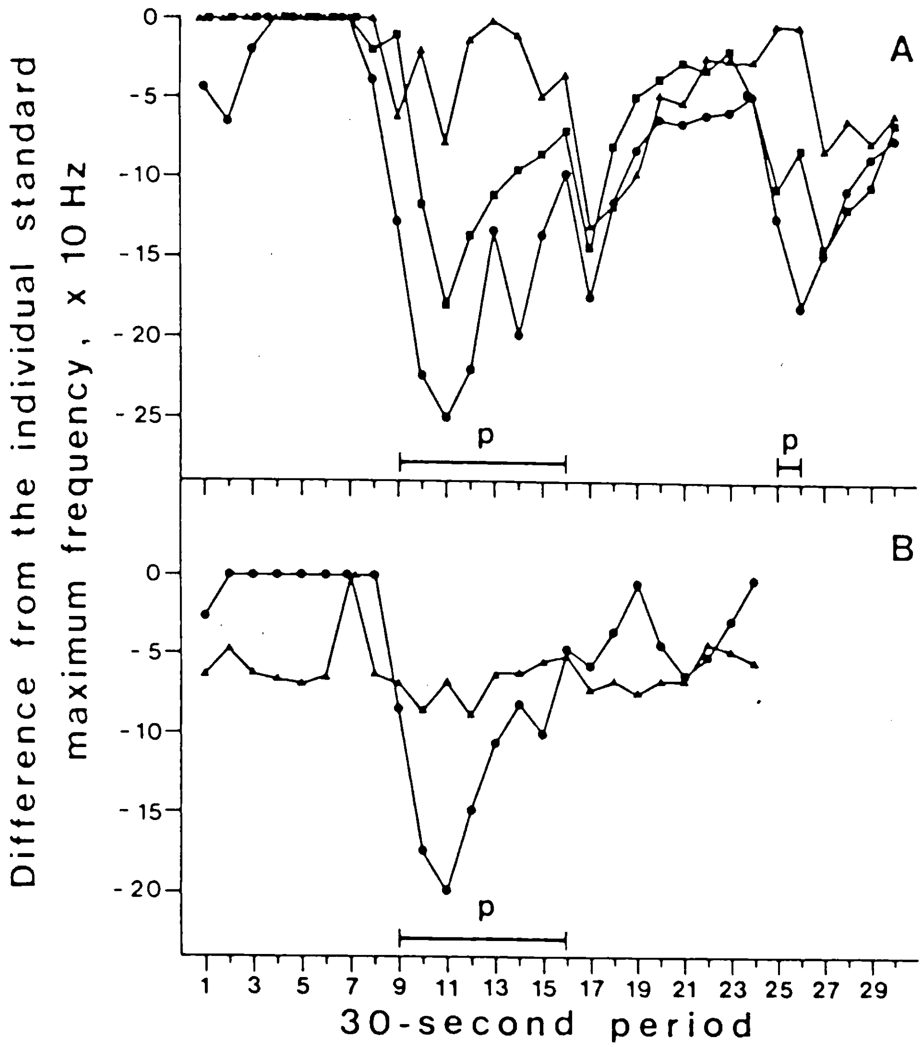


Fig. 4-11. Difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls during the playback experiment with the speaker at different locations in the territory: central location (●), middle location (▲) and boundary location (■). A, pre-incubation stage; B, fledgling stage; p, play period.

speaker was at the central location than elsewhere (a priori test: $F_s = 15.629$, df = [1, 34], $p < 0.01$). There was no significant difference between the middle and boundary locations (a priori test: $F_s = 3.347$, df = [1, 34], $p > 0.05$). After the first playback, there was no significant difference with the speaker's location (see Appendix D-9c). With the second playback they likewise showed the differentiated degrees of frequency reduction (see Appendix D-9d). They reduced maximum frequency of their calls significantly more at the central location than elsewhere (a priori test: $F_s = 10.043$, df = [1, 27], $p < 0.01$). There was no significant difference between the middle and boundary locations (a priori test: $F_s = 4.099$, df = [1, 27], $p > 0.05$). In the fledgling stage (see Fig. 4-11B), although degrees of reduction in maximum frequency varied significantly with the speaker's location, there was strong evidence that the effect of location was not consistent among the five subjects (see Appendix D-9 e and f).

In Fig. 4-12, mean differences between the observed maximum frequency of primary and graded calls and the individual standard maximum frequency of primary calls are shown for the experimental periods with respect to breeding stages. When the speaker was placed at the central location, degrees of reduction in maximum frequency clearly varied with breeding stage during the second half of the first play period (see Appendix D-10 a and b, p. 260). Males reduced maximum frequency significantly more in the pre-incubation stage than the fledgling stage (a priori test: $F_s = 10.885$, df = [1, 30], $p < 0.01$). The effect of breeding stage was still observed in the initial two minutes of the post-play period, but there was significant evidence of interaction (see Appendix D-10c). The difference was not so clear afterwards (see Appendix D-10d). When the speaker was placed at the middle location, only the four birds were available for analysis. Degrees of reduction in maximum frequency did not vary with breeding stage during playback (see Appendix D-10 e and f). Although they did vary after the first playback, evidence of interaction indicated that individuals did not reduce maximum frequency in a consistent manner with breeding stage (see Appendix D-10g).

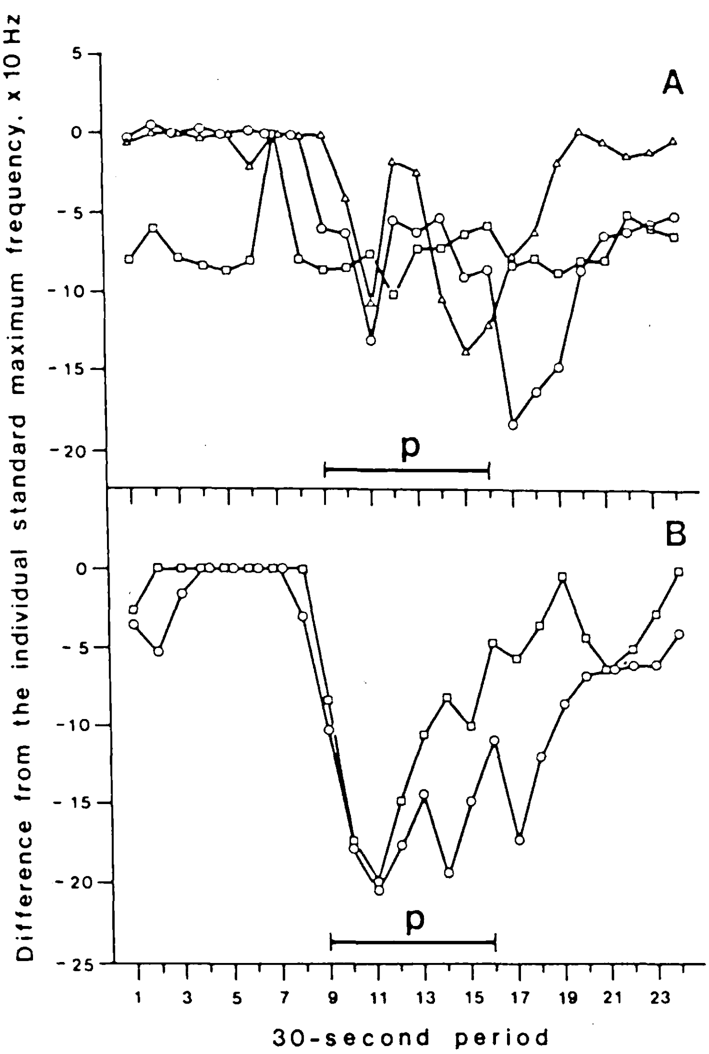


Fig. 4-12. Difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls during the playback experiment at different breeding stages: pre-incubation stage (O), incubation stage (△) and fledgling stage (□). **A**, middle location; **B**, central location; p, play period.

Summary of males' responses

The speaker's location in the territory seems to affect males' response to playback of recorded conspecific stranger's primary calls, and its effect appears to be most conspicuous during the pre-incubation stage. Territorial males responded more aggressively, approaching the speaker more quickly, flying more times and producing more primary and graded calls in a lower range of maximum frequency, with the speaker at the centre than elsewhere. However, there was no graded response between the centre and boundary of the territory. When the speaker was placed at the centre, males appeared to be more aggressive during the pre-incubation stage than other later stages of the breeding cycle.

Effects upon females

The mates of test males sometimes behaved as if they also responded to playback. They approached the speaker after their mates, and produced primary and graded calls (see Table 4-5). In the pre-incubation stage, all the females joined in the response when the speaker was placed at the centre of the territory. In Fig. 4-13, patterns of the mean number of primary and graded call elements are compared between the territorial males and their mates. In general, females produced fewer elements than their mates and showed a delay in vocal production pattern. At the other locations, three of the females stopped responses altogether, while the other two only delayed the approach and were vocal. In the later breeding stages, females' responses declined irrespective of the speaker's location. With the speaker at the middle location, incubating females remained to brood eggs, and in the early fledgling stage, only one of the

Table 4-5. Effects of playback of strange male's primary calls upon the mates of the test males

		Speaker's location in the territory		
Breeding stage	Female	Centre	Middle	Boundary
Pre-incubation	1	A(a)V(abcd)	A(a)V(abcd)	A(a)V(abcd)
	2	A(a)V(bd)	-	-
	3	A(a)V(ad)	-	-
	4	A(a)V(abcd)	A(b)V(ab)	A(c)V(cd)
	5	A(a)V(abcd)	-	-
Incubation	1	*	-	*
	2	*	-	*
	3	*	-	*
	4	*	-	*
	5	*	-	*
Early fledgling	1	A(e)V(abf)	-	*
	2	-	-	*
	3	A(b)V(b)	-	*
	4	-	V(ab)	*
	5	A(a)V(ab)	-	*

Note: A, first approach to the speaker; V, vocal response; a, during the first playback; b, after the first playback; c, during the second playback; d, after the second playback; e, being near the speaker from before the first playback; f, calling 'krrr'; -, no response; *, no experiment.

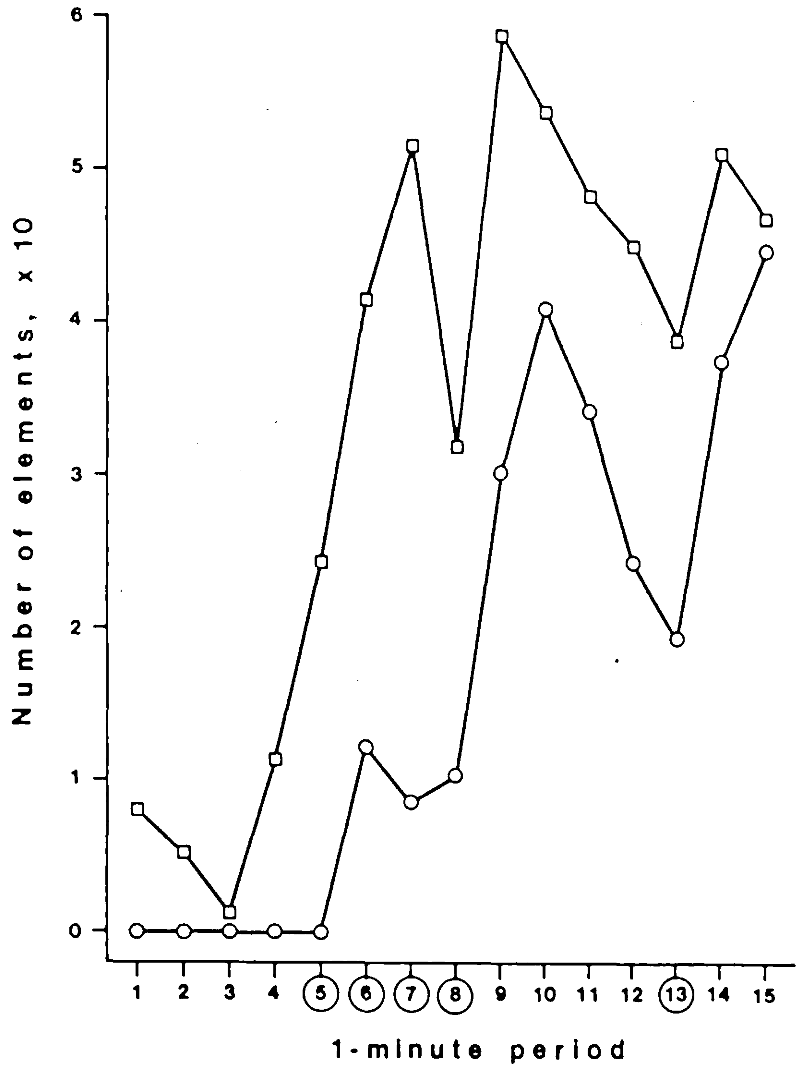


Fig. 4-13. **Comparison between the territorial males and their mates** in the mean number of primary and graded call elements produced during the playback experiment with the speaker at the centre of territory in the pre-incubation stage. □, male; ○, female; ◯, play period.

females called some in the distance as playback terminated. With the speaker at the centre of the territory, three of the females called a much reduced number of elements in the vicinity of the speaker. Two of them positively reduced the distance but were slow to approach. A female produced 'krrr' (see 2.3.7.) during and soon after playback.

4.4.3. Discussion

In playback experiments where intrusion of a conspecific rival is simulated, degrees of response to playback are influenced by the speaker's location. An intruder calling in the centre of the territory must mean a greater threat than one at the boundary. Falls (1969) and Falls and Brooks (1975) showed that male White-throated Sparrows Zonotrichia albicollis responded more strongly at the centre than the boundary. Field Sparrows Spizella pusilla flew more when the speaker was placed at the centre than at the boundary (Goldman 1973). Territorial defence against the intruder does indeed increase at the centre (Hinde 1952; Bremond 1963; Armstrong 1965; Krebs 1971).

Degrees of response are also influenced by seasonal factors. Weedon and Falls (1959) noted that male Ovenbirds Seiurus aurocapillus decreased such responses after pairing. Ickes and Ficken (1970) also reported that male American Redstarts Setophaga rusticilla responded more vigorously at the centre than the periphery before pairing, but equally strongly after pairing. However, in the Japanese Brown Hawk Owl, the noted seasonal decrease in response does not seem to relate to pairing. A lower level of aggression later in the breeding season has been attributed to habituation in response to playback of species song (Falls 1969; Petrinovich & Peeke 1973; Brooks and Falls 1975a). However, it is also likely that seasonal variation in aggressive behaviour is related to underlying hormonal changes (Eisner 1960).

Females' behaviour during and after playback is considered to be aggressive. However, the generally low level and temporal delay in their responses suggests that it is unlikely that their behaviour has an initial influence upon the output of males' responses. Females may be merely stimulated by their mate's aggressive responses rather than triggered by playback. They might have a higher threshold to territorial stimuli than males, as they normally join in a territorial dispute only when it persists. Their strong tendency to stay near the nest may contribute to the higher response with the speaker at the centre of the territory than elsewhere. Presence of offspring may prevent them from making responses to playback (Petrinovich et al. 1976). Wunderle (1978) believed that female Yellowthroats Geothlypis trichas respond to playback only when they are in the process of nest-building and egg-laying.

4.5 Motivational information

The analysis of naturally produced primary calls and playback experiments has shown that some of the physical dimensions of primary calls, such as frequency and rate of production, vary with space, time and the conspecific environment. Intra-individual variation and gradation in vocalizations has been reported from many species of birds and primates. The significance of such variation and gradation may be that every intermediate step represents a particular level of motivation. Smith (1977a) argues that it is advantageous to convey motivational information, as it facilitates mutually beneficial interactions. However, it can also be interpreted as a contest between individuals in order to increase their own inclusive fitness (Trivers 1972).

Many examples of intra-individual variation and gradation so far reported are social interactions between mates and within kin groups in birds like the Kingbird Tyrannus tyrannus (Smith 1966) and Pinon Jay Gymnorhinus cyanocephalus (Berger & Ligon 1977) and also primates (Rowell & Hinde 1962; Green 1975; Marler 1975). Alarm calls are also graded in the Domestic Fowl Gallus domesticus (Konishi 1963), Black Oystercatcher Haematopus ater (E. Miller 1979; Miller & Baker 1980), Avocet Recurvirostra avosetta (Adret 1982), Carolina Wren Thryothorus ludovicianus (Morton & Shalter 1977) and Blackbird (Andrew 1961). Distress calls produced in conflict between escape and aggression are graded in the Common Loon Gavia immer (Barklow 1979) and Guinea Fowl Numida meleagris (Maier 1982).

In the present case, intra-individual variation and gradation are characteristic phenomena in aggressive encounters. It is not unusual to have such behaviour in an agonistic context, and there are similar examples in the Kingbird (Smith 1966), Golden-winged Warbler Vermivora chrysoptera (Ficken & Ficken 1973) and also in primates (Rowell & Hinde 1962). But what does intra-individual variation and gradation mean to the receiver in aggressive contexts? Dawkins and Krebs (1978) have discussed the evolution of graded signals in the context of aggression. From the viewpoint of game theory, it is not always advantageous for the sender to give away information about intentions. It could help the receiver to take advantage of the available information and act to reduce the inclusive fitness of the caller. Thus selection pressure would lead the sender to fake or even stop advertising its aggressive motivation. Van Rhijn (1980) has criticised the game theory approach to signals, in that it hardly takes account of individual recognition. Grading may well be a successful strategy in which increasing or decreasing probability of attack is shown before a real attack occurs.

Territorial males of Japanese Brown Hawk Owls do appear to express aggressive motivation in changes in the physical characteristics of primary call. Varying features, such as quick reduction and gradual recovery of frequency with the mate's approach and the dynamic response on hearing a conspecific neighbour's calling or playback of recorded primary calls, seem to provide evidence for momentary changes in aggressive motivation. These variations can be perceived and acted upon by the receiver in relation to the possible consequences of the particular vocal behaviour.

5. THE PRIMARY CALL AND INDIVIDUAL RECOGNITION

5.1. Introduction

The ability for individual recognition is important and necessary in interactions between individuals of social animals (Beer 1970). Activities like defending a territory, mating, maintaining the pair-bond and bringing up offspring all depend upon this ability. Failure to recognize individuals will reduce efficiency in interactions by wasting time and energy, and have adverse effects upon reproductive success. Individual recognition is possible if the following conditions are satisfied:-

- There are perceptible features which are individually distinct.
- They remain consistent within individuals.
- They are highly variable between individuals.

In birds, visual acuity aids recognition (Guhl & Ortman 1953; Thorpe 1968; Buckley & Buckley 1970), and it is still possible for nocturnal owls to use visual cues even in poor light conditions ([Tansley] Erichsen 1985). The frequency and temporal resolution of birds is comparable to that of humans (Dooling 1982), suggesting that birds may be able to distinguish individual differences in calls and songs which human observers also notice (Saunders 1924; Beer 1970). Although owls' power of frequency and temporal resolution has not been well studied, it should be good enough to cope with the normal variations in their frequency and temporal features, as demonstrated in other avian auditory systems (Dooling 1982). Individually characteristic calls have been noted in some owl species (*Otus*: Marshall 1939; Van der Weyden 1975, *Bubo*: Van der Weyden & Ginn 1973, *Ninox*: M'lean 1911, *Strix*, Wendland 1963; Hirons 1976).

Examination of individual consistency in a particular signal is an important step in the investigation of individual recognition. It is necessary to study how much variation within individuals is present in both short and long terms. Several studies have demonstrated the short-term consistency of calls in non-oscines (Jouventin 1972; Derenne *et al*. 1979; White & White 1970; Bailey, 1978; Wooler 1978; Hutchinson *et al*. 1968). James (1985) reported relatively stable physical features within individuals in the call of Manx Shearwaters Puffinus puffinus over seven years. However, long-term consistency (i.e. daily, seasonal and annual) has not been thoroughly examined, which leaves some ambiguity in the demonstration of individual variation. Seasonal changes in call characteristics are not uncommon even when year-to-year variation is little (Beightol & Samuel 1973; Thomas & Dilworth 1980; Wooler 1978).

The next step is to examine the individual variation of the signal. Sonagrams may provide a means of first-hand comparison of different individuals' vocal signals in visually presented forms. This has been done not only in songbirds (Marshall 1964; Bertram 1970; Chew 1981; Lein 1981; Mamman & Nowicki 1981) but also non-oscines, such as colonial seabirds (Jouventin 1972; Jouventin et al 1979; Jouventin & Roux 1979; Derenne et al. 1979; White & White 1970; Wooler, 1978; Hutchison et al. 1968; Stevenson et al. 1970; Moseley 1979), Phasianidae (Bailey 1978; Miller 1978), Rallidae (Huxley & Wilkinson 1979) and Scolopacidae (Beightol & Samuel 1973; Thomas & Dilworth 1980). Hirons (1976) gave sonagraphic evidence for clear individual differences in the primary call of Tawny Owls Strix alco. Visual inspection of sonagrams nevertheless depends upon the identifying ability of a view and may not be objective by itself. Alternatively, physical features of vocalizations, i.e. frequency, time and amplitude are measured and statistically analysed. Different statistical values have been used: coefficient of variation, CV (e.g. Hutchison et al. 1968; Jouventin et al. 1979), information measure, H (e.g. Bailey 1978; Beecher 1982) and variance ratio, F (e.g. Wooler 1978; Thomas & Dilworth 1980; Mamman & Nowicki 1981). Duncan's multiple range test (Thomas & Dilworth 1980), multivariate analysis and graphical plotting (Bailey 1978) have also been applied. As the alternative to the feature analysis, difference index (Bertram 1970) and profile matching analysis (White & White 1970) have been developed.

Following the demonstration of a physical basis for recognition, behavioural evidence can be given by playback experiments. Recorded vocalizations are broadcast to see if test birds change their behaviour. In species which defend territory, territory owners tend to respond more aggressively to a playback of a stranger's voice than that of neighbours. So far most of the results have been obtained in songbirds (Troglodytidae: Wiley & Wiley 1977, Paridae: Krebs 1971; Järvi et al. 1977; Emberizinae: Falls 1969; Lemon & Harris 1974; Brooks & Falls 1975a; Harris & Lemon 1972; Kroodsma 1976; Searcy et al. 1981; Goldman 1973; Cardinalinae: Emlen 1971; Ritchison 1983a, Parulidae: Weedon & Falls 1959; Wunderle 1978, Icteridae: Yasukawa et al. 1982, Falls & d'Agincourt 1981; Falls 1982, Fringillidae: Pickstock & Krebs 1980, Cracticidae: Falls 1969). The only non-oscine species which has been demonstrated to have neighbour-stranger discrimination is the Blue Grouse Dendrogapus obscurus (Falls & McNicholl 1979). Hirons (1976) attempted playback experiments on the Tawny Owl only to obtain inconclusive evidence due to the difficulty in observing in the dark. Similar examination was carried out for the non-vocal drumming noises of the Ruffed Grouse Bonasa umbellus, only giving inconclusive evidence for aural recognition of individuals (Aubin 1972).

In species which develop the pair-bond for a period of reasonable length, mates may be able to recognize each other using their vocalizations. In cardueline finches, mates of a pair imitate the partner's flight calls to develop pair-specific calls, and are believed to use them as a naming system (Mundinger 1970; Marler & Mundinger 1975). In other species, however, birds seem to use individual variations as an auditory clue to recognize their own mates. Individual variations can be superimposed upon sexual dimorphism if any (e.g. Jouventin 1972; Derenne et al. 1979; Brooke 1978; Huxley & Wilkinson 1979; Ritchison 1983b; Beletsky 1983a). In the strigiformes females' primary calls tend to be higher in pitch, shorter in duration, softer and less clear in tone, and less regular in temporal delivery than males' (see 2.6.2.).

The possibility of mate recognition has been noticed for gulls (Tinbergen 1953; Beer 1970; Falls 1972) and quails (Ellis & Stokes 1966; Stokes & Williams 1968) from field observation that mates responded to the partner's vocalizations. Playback experiments have been carried out and discriminative responses to the mate's vocalization have been observed in different groups of birds.

1. Colonial seabirds - Spheniscidae (Jouventin et al. 1979; Derenne et al. 1979), Procellariidae (Brooke 1978), Hydrobatidae (James

1984), Laridae (Wooler 1978; Moseley 1979).

2. Other non-oscines - Phasianidae (Williams 1969), Rallidae (Huxley & Wilkinson 1979), Psittacidae (Saunders 1983), Picidae (Falls 1982).

3. Oscines - Muscicapidae (Watson 1969), Cardinalinae (Ritchison 1983a), Icteridae (Beletsky 1983a), Carduelinae (Mundinger 1970; Marler & Mundinger 1975), Estrildidae (D. Miller 1979), Sturnidae (Bertram 1970), Cracticidae (Berger & Ligon 1977).

The primary call 'k.hoo' of the Japanese Brown Hawk Owl shows audible differences among individuals and sexes, and might be expected to be important in recognizing neighbours or mates. In the present chapter, the first half describes the physical basis for individual recognition, and behavioural evidence for individual recognition is given in the second half. The physical basis is approached firstly by examining the consistency of each individual's calls within a series of consecutive bouts recorded on one day. In addition to the visual inspection of sonagrams, separate physical parameters of the calls of two neighbouring territorial males are treated by cumulative analysis to reveal similarities and differences. The analysis is also designed to derive the minimum sample number for the study. Secondly, the extent of individual consistency during the breeding cycle is studied for two territorial males by visual inspection of sonagrams and physical feature analysis. Thirdly, inter-individual variations are investigated in local populations. Primary calls of both male and female birds are studied for their sonagrams and respective features. Behavioural evidence is obtained by investigating the responses of territorial males to two series of playback experiments. Series I demonstrates discrimination between a male neighbour and a male stranger. Experiments are also designed to check the locational clue in individual recognition. Series II concerns discrimination between own mate and other females i.e. neighbour and stranger. Experiments also test whether there is sexual discrimination. All primary calls which were analysed and used in the experiments had been recorded from birds in a normal motivational state, since gradation (see 4.2-3.) might obscure the individual characteristics. Southern (1970) noted that in the Tawny Owl excitation made their primary calls less individually unique.

5.2. Physical Basis of Individual Recognition by Primary Calls

5.2.1. Comparison of primary calls between two individuals

5.2.1.1. Methods

Primary calls were recorded from two neighbouring territorial males at Zushi in 1980. In order to control for the effect of motivational states upon the physical features of primary calls, recordings were only made when the birds were calling spontaneously at the centre of the territory after midnight during the early fledgling stage. They were not accompanied by their mates and all the neighbouring birds were quiet.

For each bird, 130 elements which were produced in consecutive bouts during approximately three minutes were analysed using a Kay Sonagraph 6061B and studied for the following physical features:-

(a) duration of part A;
(b) duration of part B;
(c) minimum frequency of element (= minimum frequency of part A);
(d) maximum frequency of element (= maximum frequency of part B);
(e) harmonics structure;
(f) duration of short interval between the two elements of unit;
(g) duration of long interval between units in bouts.

For the temporal features, the range of 80-8000 Hz and wide-band setting were used. The unit of measurement was 10 ms. For the frequency features, the range of 40-4000 Hz and narrow-band setting were used. The unit of measurement was 20 Hz. The means, their one standard error and coefficients of variation (CV) were obtained for these features at every five cumulative samples. The last mean is considered to be most approximate to the true individual mean. If earlier cumulative means are not significantly different from the last mean by t-test at the significance level of $p < 0.05$, the sample number to give the earliest cumulative mean is the minimum requirement for the analysis of individual features. This cumulative analysis was carried out separately for the first elements and the second elements. If the CV is less than 10%, it is considered to be fairly stable.

5.2.1.2. Results

Sonagrams

Primary calls of the two neighbouring territorial males were easily distinguishable by human ears. Sonagrams made the audible differences visually recognizable. Scanning the sonagrams of the respective birds easily convinced the researcher that in spite of some degrees of intra-individual variations each bird showed individuality in its time-frequency traces. In Fig. 5-1, examples of sonagrams are presented for the two types of preparation, one in the range of 80-8000 Hz at wide-band setting (A) and the other in that of 40-4000 Hz at narrow-band setting (B). It can be seen that the difference between the two birds' calls was clear. In particular, the second preparation threw a better light upon the differences in frequency modulation than the first one. For instance, the first bird showed squarish part B, while the second bird had roundish part B.

Statistical portraits

Statistical portraits of primary calls were drawn, using the last means of measured physical features and supplementary data of the maximum frequency of part A and minimum frequency of part B. In Fig. 5-1C, the first unit and the first element of the second unit are shown. The two birds' calls are overlapped to facilitate comparison. Although the portraits did not show the frequency modulation which was the prominent feature in distinguishing the two birds, the duration, interval and frequency range of primary calls still remained to show differences between the callers.

Similarities between the two males

In Fig. 5-2, results of the cumulative analyses are given. It

Fig. 5-1. Sonagrams and statistical portraits of the primary calls of two neighbouring territorial males, X and Y. **A**, wide-band sonagrams; **B**, narrow-band sonagrams; **C**, statistical portraits of primary calls are shown using three elements. The left and middle elements form a unit separated by a short interval. The right element follows them after a long interval to be the first element of the next unit. In sonagrams shown in **A** and **B**, elements, particularly those of male Y, show tails after part B. They are not the essential part of call, and are believed to be reverberation due to atmospheric or topographical conditions. Thus these shadows are ignored in the portraits (male X in white and male Y in black).

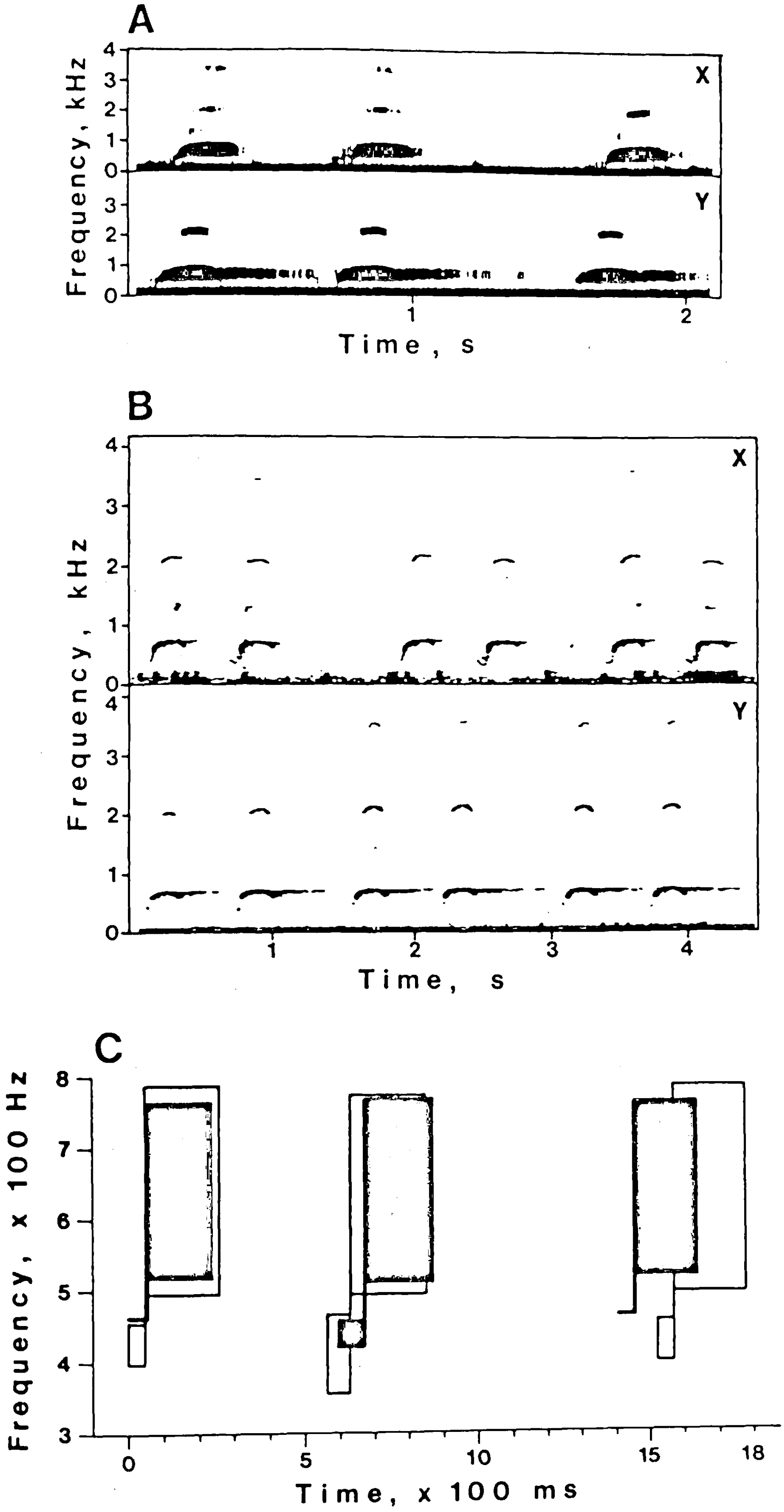
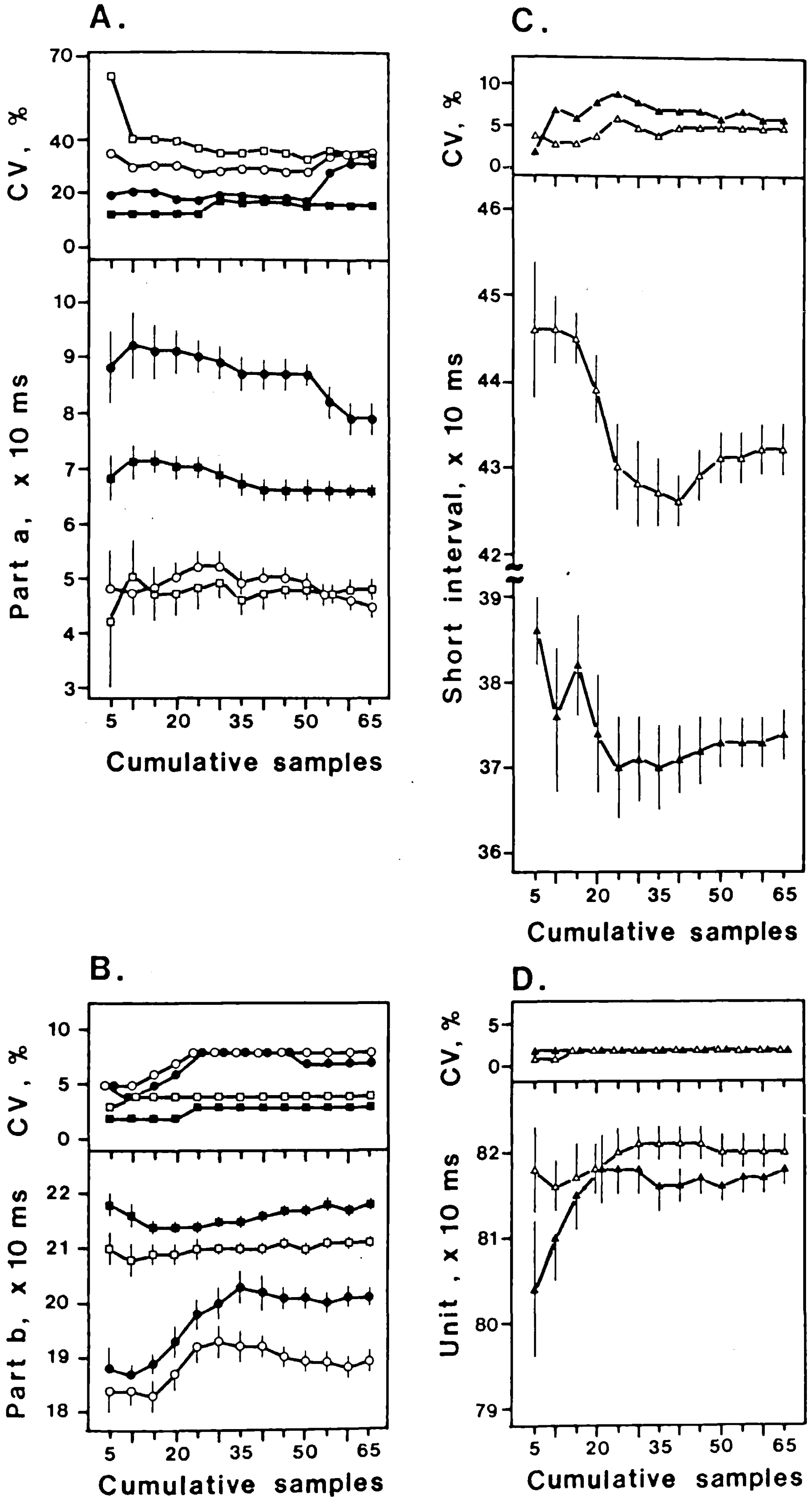

A
X
Y
Frequency, kHz
0
1
2
3
4
Time, s
1
2
B
X
Y
Frequency, kHz
0
1
2
3
4
Time, s
1
2
3
4
C
Frequency, x 100 Hz
3
4
5
6
7
8
Time, x 100 ms
0
5
10
15
18

Fig. 5-2. Cumulative analyses of the physical features of the primary call. The mean, its one standard error, and coefficient of variation are shown at every five cumulative samples for two individuals. One standard error of the mean may be shown on either or both directions. **A,** duration of part A; **B,** duration of part B; **C,** duration of short interval between the elements of unit; **D,** duration of unit; **E,** duration of long interval between units; **F,** maximum frequency of element; **G,** minimum frequency of element. Owl X: □, the first element of unit; ■, the second element of unit; ▲, intervals. Owl Y: ○, the first element of unit; ●, the second element of unit; △, intervals.


A.
CV, %
70
40
20
0
Part a, x 10 ms
10
9
8
7
6
5
4
3
5
20
35
50
65
Cumulative samples
B.
CV, %
10
5
0
Part b, x 10 ms
22
21
20
19
18
5
20
35
50
65
Cumulative samples
C.
CV, %
10
5
0
Short interval, x 10 ms
46
45
44
43
42
39
38
37
36
5
20
35
50
65
Cumulative samples
D.
CV, %
5
0
Unit, x 10 ms
82
81
80
79
5
20
35
50
65
Cumulative samples

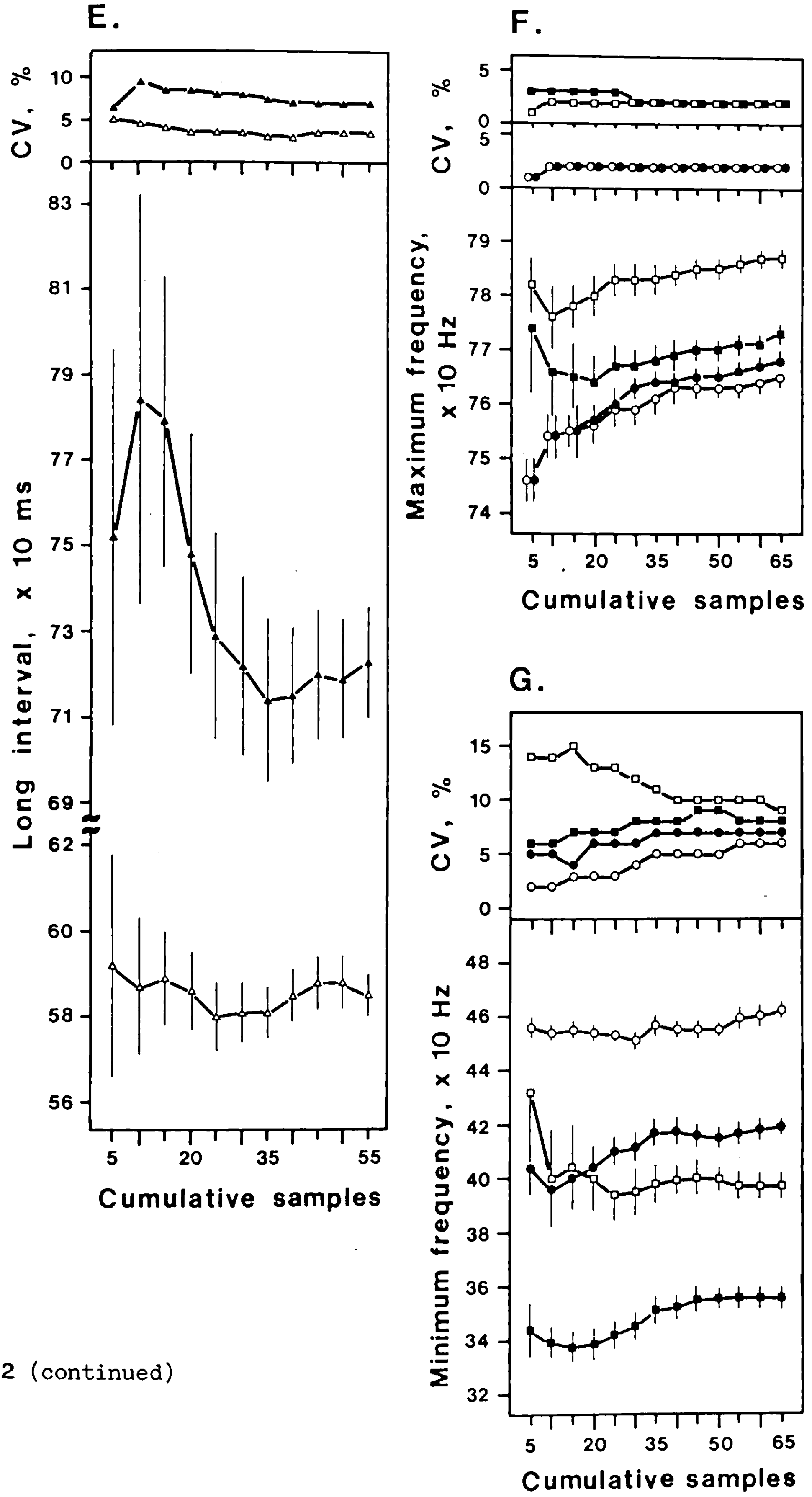


Fig. 5-2 (continued)

can be seen that the two males shared a similar extent of variation in the respective physical features. The duration of part A was highly variable, showing CV's generally between 10-40% (A), while that of part B was fairly stable, showing CV's of less than 10% (B). The duration of short interval between the elements of unit was stable, showing CV's of less than 10% (C), while that of long interval between units was not as stable as the former (E). The duration of unit (D) and maximum frequency of element (F) were very stable, showing CV's mostly of 2%. The minimum frequency of element generally showed CV's of less than 10% (G).

The overall range of fundamental frequency mostly overlapped between the two birds: Owl X in 310-810 Hz, and Owl Y in 350-810 Hz. However, only the maximum frequency of the second element was significantly similar between them (t-test: $p > 0.05$ for $n = \sum_{k=1}^{13} 5k$). The first element was significantly higher in the minimum frequency than the second element ($p < 0.01$ in Owl X and $p < 0.001$ in Owl Y, for $n = \sum_{k=1}^{13} 5k$). Harmonics were observed up to the eighth with the odd-numbered emphasized. The temporal features which were similar between them were the duration of part A of the first element ($p > 0.05$ for $n = \sum_{k=1}^{13} 5k$) and that of unit ($p > 0.05$ for $n = \sum_{k=1}^{13} 5k$). The first element was significantly shorter than the second element in the duration of both part A ($p < 0.01$ for $n = \sum_{k=2}^{13} 5k$ in Owl X, and $p < 0.001$ for $n = \sum_{k=1}^{13} 5k$ in Owl Y) and part B ($p < 0.02$ for $n = \sum_{k=6}^{13} 5k$ in Owl X, and $p < 0.001$ for $n = \sum_{k=7}^{13} 5k$ in Owl Y).

Differences between the two males

The two males had significantly different primary calls in terms of most of the physical features (t-test):-

- duration of part A of the second element ($p < 0.01$ for $n = \sum_{k=1}^{13} 5k$);
- duration of part B of both elements ($p < 0.001$ for $n = \sum_{k=1}^{13} 5k$);
- duration of short interval between the elements of unit ($p < 0.001$ for $n = \sum_{k=1}^{13} 5k$);
- duration of long interval between units ($p < 0.02$ for $n = \sum_{k=1}^{11} 5k$);
- maximum frequency of the first element ($p < 0.01$ for $n = \sum_{k=2}^{13} 5k$);

- minimum frequency of the first element ($p < 0.01$ for $n = \sum_{k=2}^{13} 5k$);
- minimum frequency of the second element ($p < 0.001$ for $n = \sum_{k=1}^{13} 5k$).

The maximum frequency of the first element was significantly higher than that of the second element in Owl X ($p < 0.02$ for $n = \sum_{k=4}^{13} 5k$), while it was as high as the latter in Owl Y ($p > 0.05$ for $n = \sum_{k=1}^{13} 5k$).

Number of samples

As can be seen in the cumulative analyses of various physical features (see Fig. 5-2), the individual mean and CV tended to vary initially but settle eventually. In Table 5-1, the minimum number of sample is listed for the respective physical features in the first and second elements for the two males. The trends were shared between the two males. Although in some cases over twenty-five and up to forty samples were required for each individual in order to have the mean which was significantly similar to the last mean (t-test, $p < 0.05$), significant differences between the two birds were detectable even from only five or ten samples.

5.2.2. Physical features of primary calls during the breeding season

5.2.2.1. Methods

In 1980, primary calls were regularly recorded from a territorial male from arrival to the beginning of nestling stage when it was replaced by another male. The replacing male's primary calls were recorded thereafter until the middle of August. The following physical features were studied:-

(a) part A - duration, maximum and minimum frequency;
(b) part B - duration, maximum and minimum frequency;
(c) duration of short interval;
(d) duration of long interval;
(e) duration of unit.

Frequency features were measured up to 20 Hz from successive twelve

Table 5-1. Minimum number of samples required to obtain individual means (*t*-test, $\alpha = 0.05$)

Physical feature	Owl X	Owl Y
Duration of part A	5^f, 5^s	5^f, 5^s
Duration of part B	5^f, 40^s	5^f, 25^s
Duration of short interval between the elements of a unit	5	5
Duration of long interval between units	5	5
Duration of unit	10	5
Maximum frequency of element	5^f, 25^s	5^f, 25^s
Minimum frequency of element	5^f, 5^s	25^f, 30^s

Note: f, the first element; s, the second element.

elements, the sonagrams of which were obtained in the range of 40–4000 Hz at narrow-band setting. Temporal features were measured up to 10 ms from successive twenty elements, the sonagrams of which were obtained in the range of 80–8000 Hz at wide-band setting. However, as part A had low frequency, it was obscured by the background noise in 80–8000 Hz traces. The sonagrams prepared in the range of 40–4000 Hz at wide-band setting were used for its temporal measurement. The unit was thus 20 ms. The traces in which part A was too obscure were eliminated from the analysis and mean sample number for each recording was about six.

5.2.2.2. **Results**

In Fig. 5–3, sonagrams of the primary calls recorded from a male from arrival to incubation stage (A) and those recorded from another male from nestling stage to fledgling stage (B) are presented. Temporal and frequency traces appeared fairly constant for each bird during the breeding cycle. The first male had part B in short, roundish crescents, while the second male tended to have part B in long, flat shapes. Most of the physical features, however, showed significant intra-individual variation (Table 5–2). For example, as can be seen from the duration of part A and that of part B in Fig. 5–4, these variations were not apparently related to the breeding stage. However, the first male appeared to increase the duration of long interval between units ($F_s = 11.040$, df = [1, 8], $p < 0.025$) and the maximum frequency of part B ($F_s = 6.443$, df = [1, 8], $p < 0.05$) from arrival to incubation stage. Yet there were significant deviations from the regression, suggesting the large amount of random heterogeneity in the duration of long interval between units ($F_s = 2.592$, df = [8, 102], $p < 0.025$) and also in the maximum frequency of part B ($F_s = 60.355$, df = [8, 148], $p < 0.01$). Each male appeared to make use of wide ranges of respective physical dimensions. Staying within the particular individual range, there were significant individual differences between the two males, except for the duration of long interval between units (see Table 5–2).

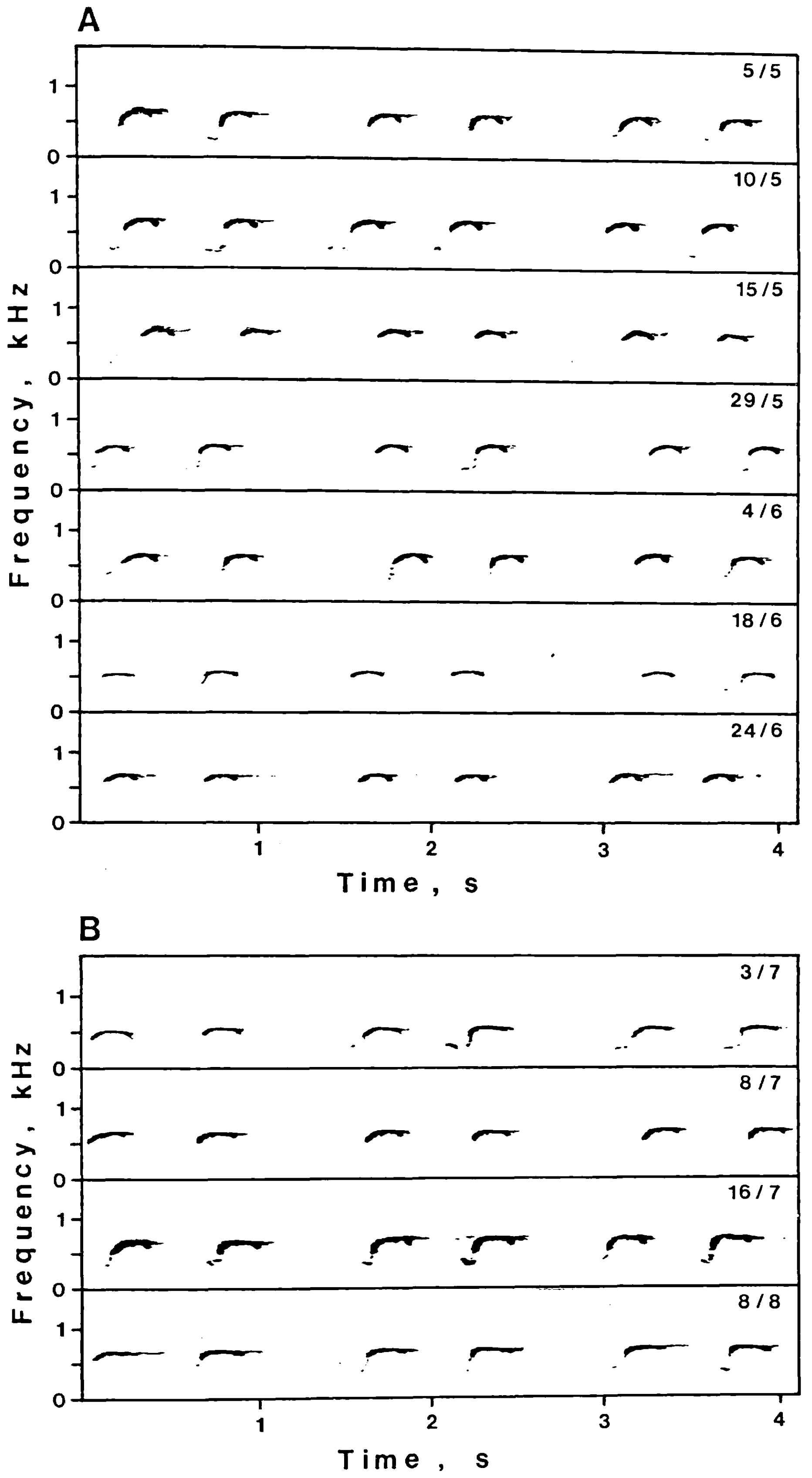


Fig. 5-3. Sonagrams of primary calls during the breeding cycle. **A**, the original male; **B**, the replacing male. Sonagrams are prepared at narrow-band setting in the range of 40-4000 Hz.

Table 5-2. Intra-individual and inter-individual variations in the physical structure of primary calls during the breeding season

Physical feature	Intra-individual variation		Inter-individual variation
	The first male from arrival to incubation stage	The second male from nestling to fledgling stage	
Part A - duration	6.76 [8, 54]***	1.48 [2, 26] ns	66.96 [1, 80]***
- minimum frequency	6.89 [8, 55]***	2.88 [2, 27] ns	59.46 [1, 82]***
- maximum frequency	69.18 [8, 53]***	11.47 [2, 25] ***	40.23 [1, 78]***
Part B - duration	7.37 [13, 233]***	12.46 [3, 76] ***	508.58 [1, 309]***
- minimum frequency	26.94 [14, 143]***	6.84 [3, 38] ***	7.05 [1, 181]***
- maximum frequency	60.16 [14, 143]***	61.37 [3, 38] ***	108.07 [1, 181]***
Duration of interval between the two elements of unit	8.71 [13, 109]***	21.40 [3, 36] ***	44.71 [1, 145]***
Duration of interval between units in bouts	3.65 [13, 98]***	0.09 [3, 36] ns	2.14 [1, 134] ns
Duration of unit	5.98 [14, 61]***	1.85 [3, 17] ns	23.98 [1, 78]***

Note: One-way analysis of variation was used at the significance level of $p < 0.05$. For the inter-individual variation, a priori test was applied. F_S values, degrees of freedom in brackets and significance levels (***, $p < 0.01$; **, $p < 0.025$; *, $p < 0.05$; ns, $p \geq 0.05$) are given.

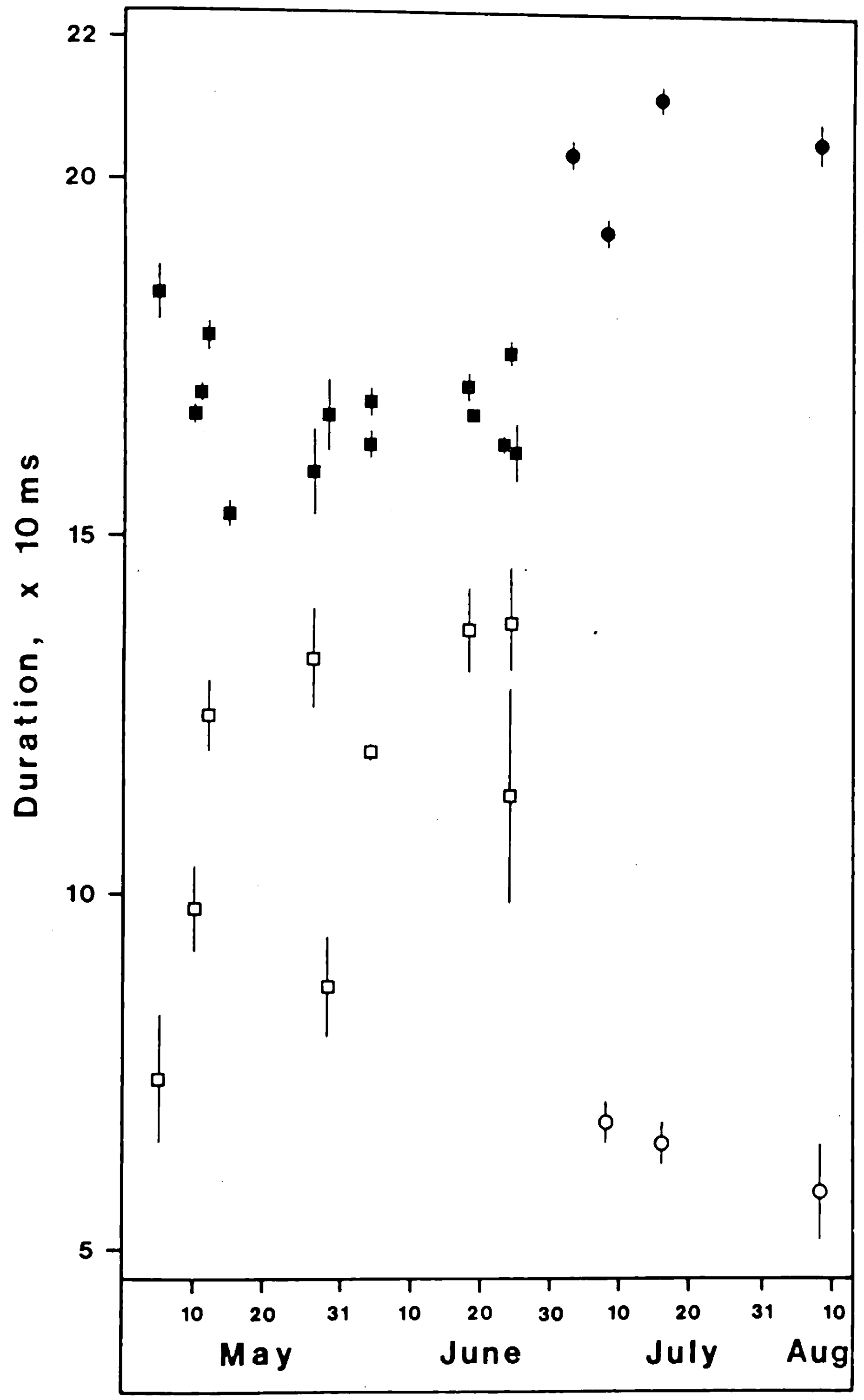


Fig. 5-4. Duration of parts A and B during the breeding cycle. Part A: □, the original male; ○, the replacing male. Part B: ■, the original male; ●, the replacing male.

5.2.3. Discussion

5.2.3.1. Consistency within individuals

No bird produces primary calls in an exactly identical form within an individual, and there are always some variations. Yet, somehow a bird's own individuality appears to remain intact, whilst allowing intra-individual variation to certain limited degrees. Firstly, variations observed in sonagrams are sufficient for identification. Wooler (1978) suggested that in view of the variation between individuals, visual inspection of sonagrams suffices to demonstrate the consistent individuality of calls. Secondly, temporal and frequency features are consistent within an individual. Regardless of the size of the coefficient of variation, the mean of respective physical feature was significantly similar to its last mean from the early stage of the cumulative analysis. This suggests that individuality is available even with a small number of elements. The later analyses by one-way ANOVA also confirmed this. It is particularly important if listeners can identify the caller without hearing a great many number of elements. This saves time and secures the probable gain obtained by quick recognition. Thirdly, despite significant variation during the breeding cycle without a clear seasonal trend, each individual is likely to maintain individuality in the physical features of their primary calls.

Intra-individual variation may be caused internally and externally. Internal variation is partly due to the changeable performance of the vocal organs. Bailey (1978) noticed amplitude-related variations of fundamental frequency modulation of individual separation calls in the Bobwhite Quail Colinus virginianus. The possibility of amplitude effect upon the fundamental frequency modulation of the owls' primary calls is unknown. Changes in motivational state is another possible factor to influence the physical structure of primary calls, although it is considered to be minimal in the present study based upon samples collected in controlled conditions. Physiological and endocrinological factors might also be involved. Wooler (1978) suggested the effects of hormonal level upon tonal differences. However, the lack of seasonal trends do not support this mechanism.

External variation takes place once primary calls are produced into the sound field. The acoustic environment differs with the topographical features and vegetation. Sound characteristics of a bird's primary calls heard inside the wooded valley system were slightly different from the same calls heard outside. Atmospheric conditions and weather are never constant. The primary calls which were emitted on a very hot and humid night lacked clarity, sounding dull compared with the regular calls of the same bird. While these external factors are operative in the field, their effects are only minimal.

Some intra-individual variation may not be enough to confuse listeners with the identity of the caller, and others may be learnt by the listeners. In particular, variations due to the topographical and vegetational features may be associated with locations, since the owls occupy the same territories. Individuality of primary calls is considered to be contained in a relatively flexible range of physical dimensions. This flexibility may ensure transmission of the information of individual identity to receivers, while simultaneously sending other kinds of information (e.g. motivational state).

5.2.3.2. Differences between two individuals

In the comparison of primary calls between the two neighbouring territorial males, the different sonagrams immediately separated them. Most of the physical features were significantly different between them, but temporal features may be better than frequency features to separate the two. There were some differences in the physical features which separated two individuals between the first pair for the short-term comparison and the second pair for the seasonal comparison. The first pair did not differ in the duration of the unit, while the second pair did not differ in the duration of the long interval between units.

5.3. Inter-individual Differences in Primary Calls

5.3.1. Methods

In 1980, primary calls were recorded from ten different individuals of the Zushi population and nine of the Miyake-jima Island population during the breeding season. The former group consisted of six neighbouring territorial males from the main study area, two territorial males from a separate area in the north-east and two mated females. The latter group included eight neighbouring territorial males and one individual which was believed to be a female. Recordings were further supplemented with the primary calls of different individuals: one new territorial male and three mated females of the 1981 Zushi population and one female of the 1979 Zushi population.

For each individual, sonagrams were prepared for twelve successive elements at both narrow and wide-band settings in the range of 40-4000 Hz. Firstly, the temporal-frequency profile of primary calls was visually examined to compare the individuals. Secondly, the sonagrams of the nine males and six females of the Zushi population were used to measure the duration, maximum and minimum frequency, form of frequency modulation and harmonics structure of both parts of elements, and the duration of short and long intervals (see 2.2.6.). The units of measurement were 20 ms for temporal feature and 20 Hz for frequency feature. One-way analysis of variance (ANOVA) was applied to see the inter-individual differences in the temporal and frequency features. Forms of frequency modulation and occurrences of harmonics were analysed by the binominal test. The level of significance was $\alpha = 0.05$.

For the eight territorial males of the 1980 Zushi population, the part B and unit structure were re-examined applying the more accurate measurement. For temporal features, wide-band sonagrams were prepared for twenty successive elements in the range of 80-8000 Hz. The unit of measurement was 10 ms. For the maximum and minimum frequency, the elements were measured digitally at 8 Hz intervals in the range of 0-1000 Hz, using a Princeton Applied Research 4512 FFT real-time spectrum analyser and a Unigon UB-1 visual display unit.

5.3.2. Results

Sonagrams of individuals' primary calls

In spite of simple structures of primary calls, it was not impossible to distinguish calling birds solely by their voices. Here are the sonagrams of wide-band trace, which are the representative units of primary calls of fifteen Zushi birds and nine Miyake-jima Island birds (Fig. 5-5). In spite of some intra-individual variations there were temporal-frequency profiles which were typical to individuals. Individuality and inter-individual differences can visually be noticed by scanning the sonagrams. The profiles were recognized in various forms between the neatly roundish crescent and straight squarish band. The profile of the first and second elements was almost identical within an individual. However, some birds presented a set combining two distinct profiles. .

Physical features

Physical features of individuals' primary calls measured at 40-4000 Hz in the first analysis are listed in Appendices A-1 - A-5 (pp. 208-212). In Fig. 5-6, examples of the individuals' distributions of physical features are given for the eight territorial males used in the second analysis. In all the physical features, individuals' distributions appeared different from one another to various extents. In Appendix E-1 (see pp. 263-267), the results of one-way ANOVA are shown for the first and second analyses. For every physical feature, there was a significant added variance component among individuals ($p < 0.01$). Regardless of the sexes, different individuals clearly produced their primary calls with significantly different temporal and frequency features.

In Fig. 5-7, individual means obtained in the first analysis are plotted for the following four pairs of physical features:-

A. (duration of part A) x (duration of part B);
B. for part A, (maximum frequency) x (minimum frequency);
C. for part B, (maximum frequency) x (minimum frequency);
D. (duration of short interval) x (duration of long interval).

The range of one standard error is also shown. It can be seen that

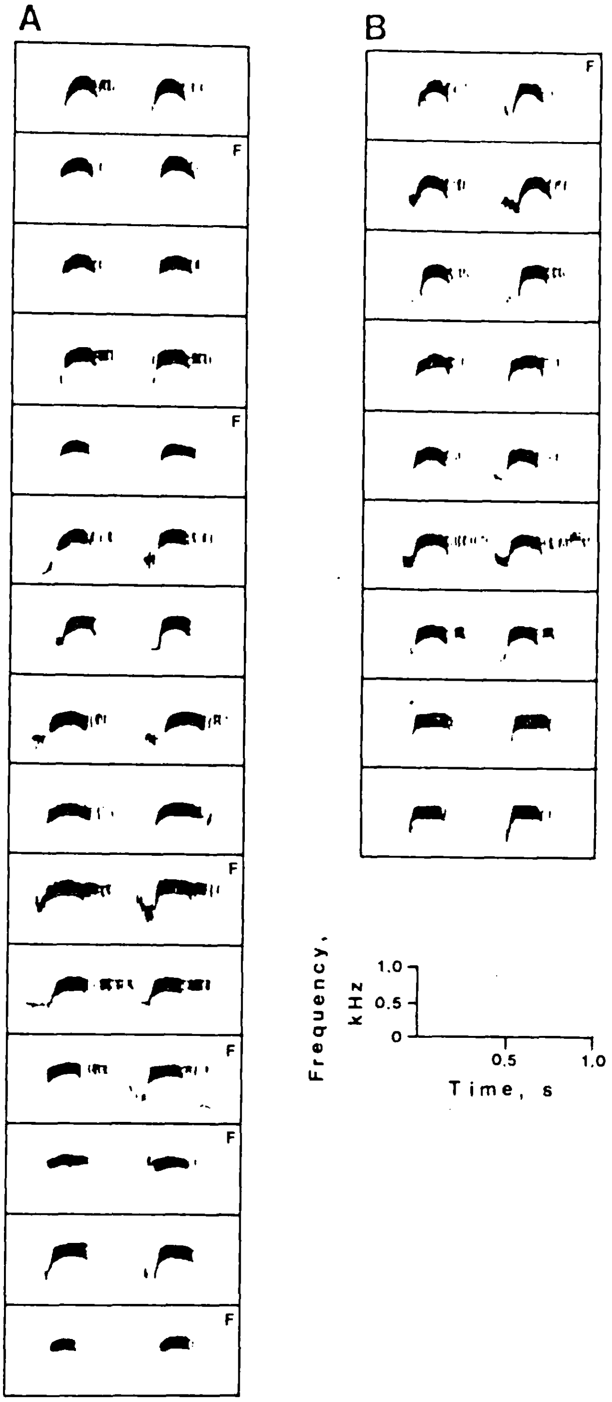


Fig. 5-5. Sonagrams of primary calls of the individuals of the two local populations: **A,** the Zushi population; **B,** the Miyake-jima Island population. Sonagrams are prepared at wide-band setting in the range of 40-4000 Hz. Individual calls are arranged according to the shape of part B between neatly roundish crescent and straight squarish band. F, female.

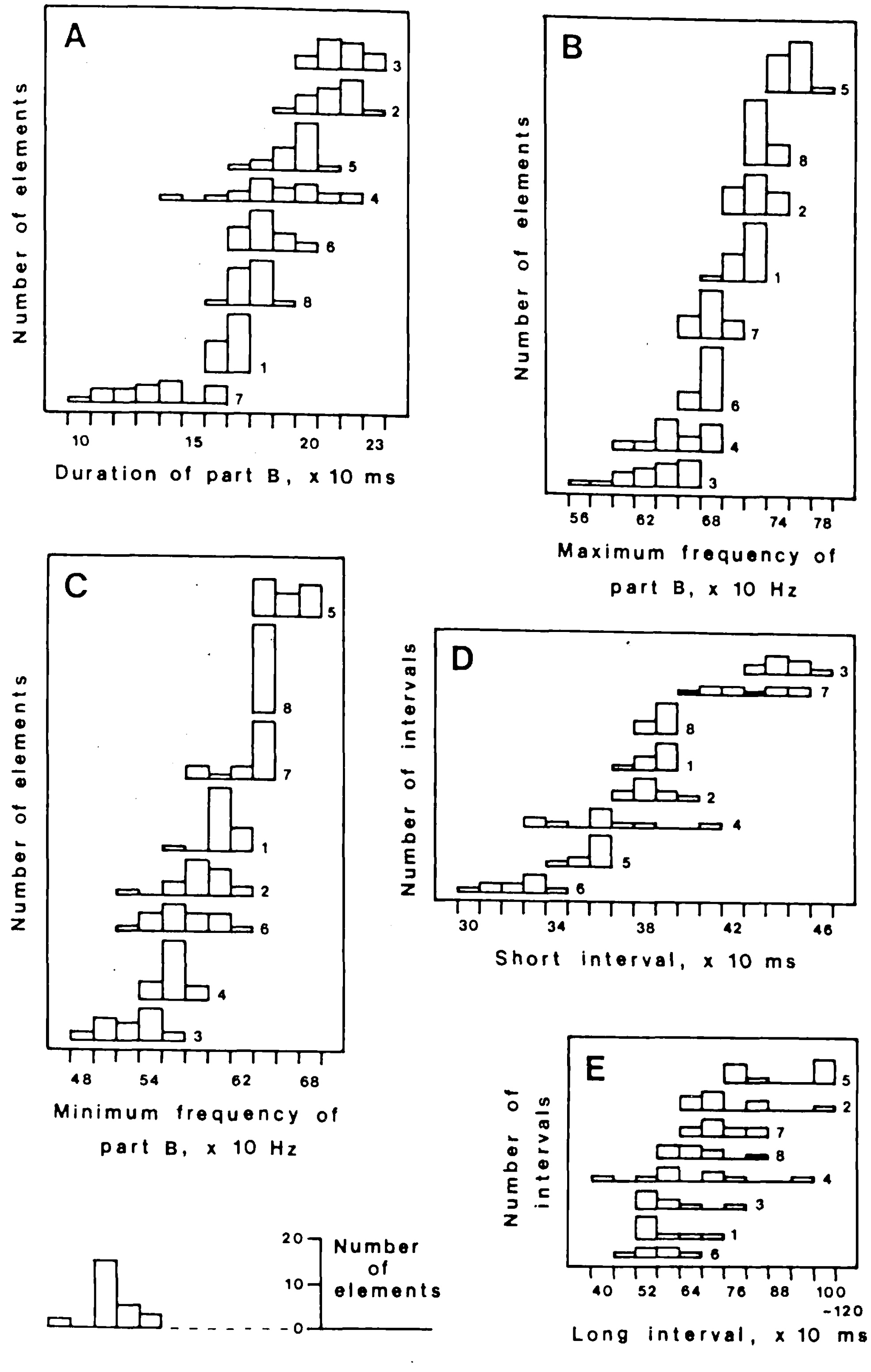
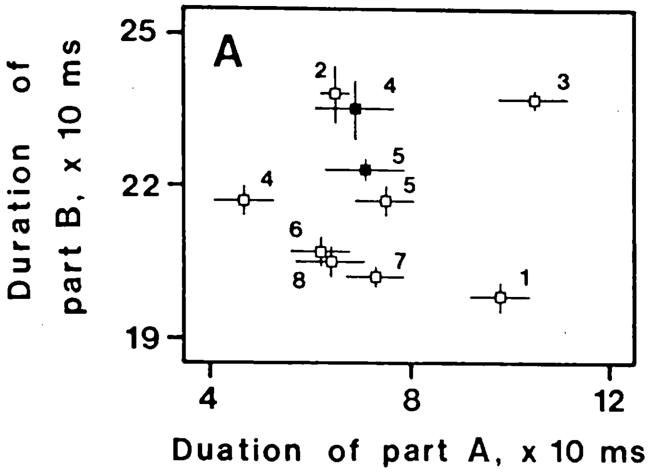
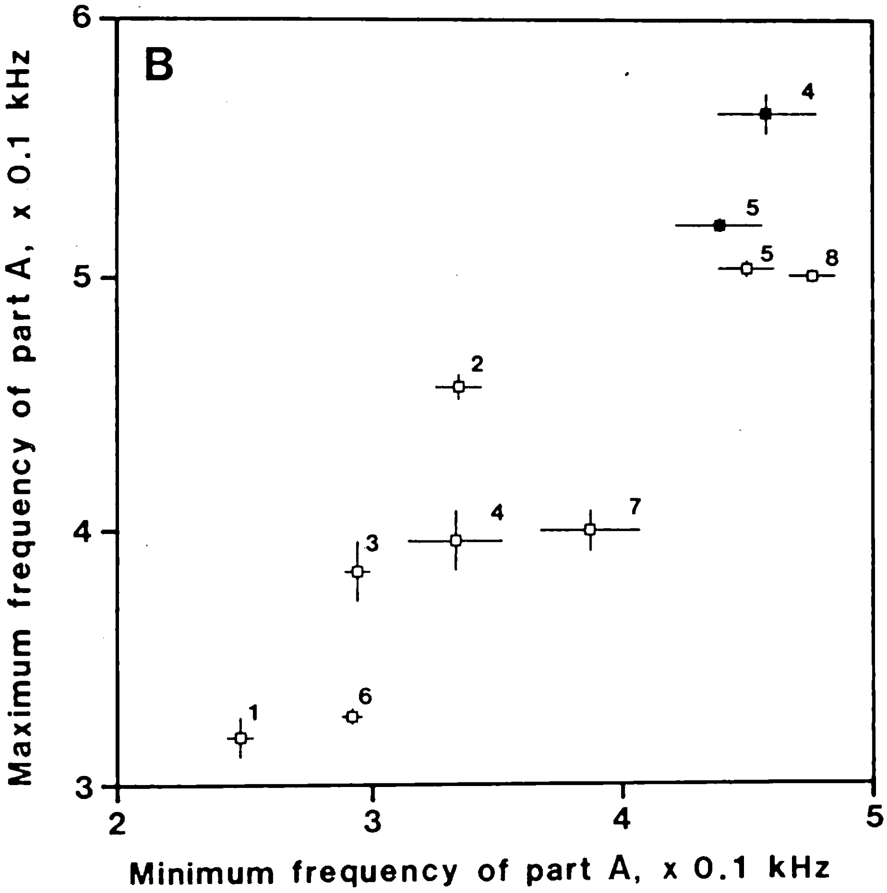


Fig. 5-6. Individuals' distribution of the physical features of primary calls. **A**, duration of part B; **B**, maximum frequency of part B; **C**, minimum frequency of part B; **D**, short interval between the elements of unit; **E**, long interval between units. Results are shown for eight territorial males, and figures to the right of each histogram indicate individuals.

Fig 5-7. **Inter-individual differences of the physical features of primary calls** in terms of combination of two features. **A,** (duration of part A) x (duration of part B); **B,** (minimum frequency) x (maximum frequency) for part A; **C,** (minimum frequency) x (maximum frequency) for part B; **D,** (duration of short interval) x (duration of long interval); □, male; ■, female. Individual identity is indicated by numbers. The range of one standard error of the mean is shown on both or either direction.


A
Duration of part B, x 10 ms
25
22
19
4
8
12
Duation of part A, x 10 ms
1
2
3
4
4
5
5
6
7
8


B
Maximum frequency of part A, x 0.1 kHz
6
5
4
3
2
3
4
5
Minimum frequency of part A, x 0.1 kHz
1
2
3
4
4
5
5
6
7
8

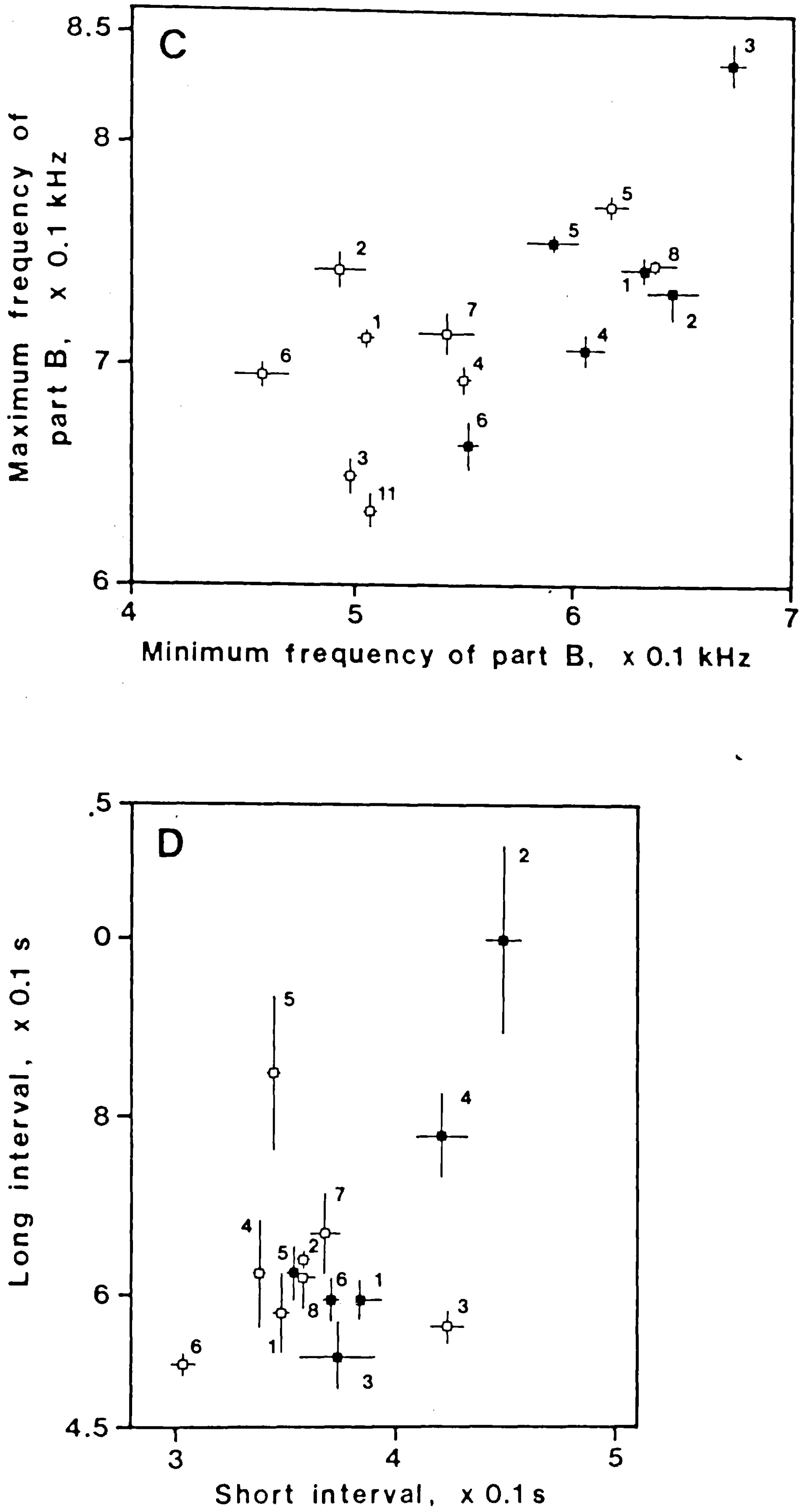


Fig. 5-7 (continued)

some plots form clusters or are close to each other, but that others occupy isolated locations. For example, in terms of pair A, three birds (males 6, 7 and 8), two birds (male 2 and female 4) and two birds (male 5 and female 5) respectively form close groups, whereas males 1, 3 and 4 are respectively apart from the rest. However, the individuals of the former three groups were different from one another in terms of the other pairs, B, C and D. Similar observations can be made for any clusters in other figures.

From the study of the eight birds, males 4, 6 and 7 had two similar elements in a unit in terms of the duration and frequency of part B, while the other birds differentiated the first element from the second in one or more of the physical features of part B (see Appendix E-2, p. 268). In male 2, for example, part B of the first element was significantly shorter in the duration and higher in the maximum frequency than that of the second element.

Forms of frequency modulation were shared among the different individuals to various extents. However, some individuals used particular forms more frequently than expected (see Appendix A-4, p. 211). For example, male 2 tended to produce part A in the category of DA and part B in that of right-biased AFD & AD, while male 8 did not have any prevailing forms for part A but tended to produce part B in the left-biased AFD & AD. Harmonic patterns seem to be less different among individuals, having the third and fifth harmonics significantly more than expected. However, one of the females (5) emphasized the second harmonic (see Appendix A-3, p. 210).

5.3.3. Discussion

Visual inspection of sonagrams to identify individuals can be difficult if the number of individuals increases (Beightol & Samuel 1973). In the comparison of primary calls recorded from the two distant populations, however, individual differences are still visually noticeable within populations. Such differences in the neighbouring individuals' primary calls are important as a physical basis for neighbour and mate recognition. The analysis of frequency modulation further demonstrated individual trends in the sonagrams, and harmonic patterns also seem to aid individuality.

It is important to assess the sound complex of primary calls in various ways and study each physical domain separately. One-way ANOVA is believed to be appropriate for this task in spite of a criticism by Thomas and Dilworth (1980). That variation between individuals is significantly higher than variation within individuals has been used as part of evidence for the individual recognition of vocalizations by many authors (e.g. Marler & Isaac 1960; Borror & Gunn 1965; Hutchison et al. 1968; Beightol & Samuel 1973; Miller 1978; Mamman & Nowicki 1981). The obtained result for primary calls seems to support individual differences in every physical feature. This does not mean that each individual's primary calls differ significantly from those of the rest of the local population for every physical feature (Mamman & Nowicki 1981). Some features can be shared by some birds in a population, and others are quite separated between them. The latter is supposed to be the relevant clue for individual identification. In some species, temporal structure is believed to be an important carrier of individual identity (Derenne et al. 1979; Jouventin et al. 1979; Huxley & Wilkinson 1979; Bertram 1970), and amplitude pattern in others (White & White 1970). However, in Japanese Brown Hawk Owls no single feature is a self-sufficient clue for individual identity. Rather, with a reservation over amplitude, it is different patterns of sound as a composite structure of time and frequency that are considered important. This type of individual variation does not seem to be unusual and has been reported in other species (Hutchison et al. 1968; Bailey 1978; Wooler 1978).

Are the observed variations in the physical features of primary calls detected by listeners? Birds can detect 10-20% change in duration and 1% change in frequency (Dooling 1982). Suppose the mean duration of part B is 200 ms in a bird and 10% of the mean is 20 ms. Any birds which have their means between 180 and 220 ms would not be registered different from it. Fifteen individuals were studied to see how different from all the other individuals of the population they were in terms of five physical features (duration, maximum and minimum frequencies of part B, duration of short interval between the elements of a unit, and duration of long interval between units). Primary calls of an individual were found to be different from those of 2.1 ± 0.4 owls by all the five physical features; similarly, 5.5

± 0.7 owls by any four features, 3.7 ± 0.6 owls by any three features, 2.4 ± 0.6 owls by any two features and 0.3 ± 0.1 owls by any one feature. Similarly, with regard to the three physical features of part A studied for ten individuals, primary calls were found to be different from those of 5.4 ± 0.5 owls by all three features and 3.6 ± 0.5 owls by any two features.

It is important to note that sonagrams prepared in the range of 40–4000 Hz can be measured only up to 20 ms in duration and up to 20 Hz in frequency. The expected accuracy of the owls' detection of change in duration at the level of 10% are 5–11 ms for part A, 18–25 ms for part B, 30–45 ms for the short interval between the elements of a unit, and 52–100 ms for the long interval between units. The expected accuracy of their detection of change in frequency at the level of 1% are 3–6 Hz for the maximum frequency of part A, 2–5 Hz for the minimum frequency of part A, 6–8 Hz for the maximum, and 5–7 Hz for the minimum frequency of part B. Apart from the duration of the two intervals, the present measurement may not be comparable with the owls' ability of detecting the differences in the other physical features. Certainly, the second analysis with an improved accuracy of measurement of up to 10 ms in duration and up to 8 Hz in frequency revealed that more individuals' calls can be separated by every single physical feature. The rates of detection of the difference between every two individuals among the eight males were 67.9% for the duration of part B, 92.9% for part B's maximum frequency, 100.0% for part B's minimum frequency, 58.9% for the duration of short interval between the elements of the unit and 75.0% for that of the long interval between units in the second analysis, while in the first analysis they were respectively 28.6%, 89.3%, 96.4%, 48.2% and 55.4%. The relatively high rates of detection in frequency are due to the birds' supposed power of frequency resolution.

Primary calls are used in long-range communication, and to human ears the owls could be heard in the distance only with part B. The loudness and relatively small variation in the physical features of part B seem to satisfy the conditions necessary to be a carrier of individual information over a long distance. The low amplitude and large variation of part A may mean that it is constrained by the acoustic environment in which it has to travel. The relevance of part A as a source of individual identification may be small in long-range communication. However, the significant individual differences of part A should still function in short-range communication. This leaves the possibility that part A functions in individual recognition and this can be tested by playback experiments.

5.4. Behavioural evidence for individual recognition by primary calls

5.4.1. Methods

Subjects

During the breeding season in 1981, experiments were carried out on five territorial males from the Zushi population.

Experimental tapes

The test primary calls were recorded from the following males and females:-

(a) spontaneously calling neighbouring territorial males;
(b) spontaneously calling strange males of the Miyake-jima Island population in 1981;
(c) mated females which were performing duets with their mates (for the experimental tape, only the female calls were extracted).

Experimental tapes were prepared on 3-minute endless tapes, TDK EC-3.

Playback system

See 4.4.1. for details.

Playback schedule

Two series of experiments were carried out. Series I investigated the male primary calls and Series II examined the female primary calls. In Series I, each bird was exposed to a set of three experiments as follows:-

(a) A recording of a neighbouring territorial male's primary calls was played at the middle location of the territory, i.e. within the central zone and more than 50 m away from the nest, on the side of the neighbour's territory (normal location).

(b) A recording of stranger's primary calls was played at the middle location of the territory.

(c) The same recording as used in (a) was played at the middle location of the territory on the other side of the neighbour's territory (opposite location).

To determine whether individual differences are detected by the subjects, the experiments were done during the incubation stage in May (Experiment I) and were repeated during the fledgling stage in July-August (Experiment II), when territorial relationships among territory owners were firmly established. In Series II, each territorial male was exposed to a set of four recordings as follows:-

(d) primary calls of his own mate;
(e) primary calls of neighbouring territorial male's mate;
(f) primary calls of a strange female;
(g) primary calls of strange males (control).

All the experiments were carried out at the centre of territory, i.e. within 20 m from the nest, during the late nestling and early fledgling stages in July-August. Further details of the playback schedule have been described in 4.4.1.

Categories of response and statistics

See 4.4.1. for details.

5.4.2. Individual recognition by male primary calls

In Experiment I, which was carried out during the incubation stage, all the five territorial males responded to playback in aggressive manners as described earlier in 4.3.2. In Experiment II, which was undertaken during the early fledgling stage, one of the test birds did not show noticeable response to playback of neighbour's primary calls regardless of repeated trials. Even with playback of stranger's primary calls it produced merely six primary call elements at fifty seconds after the start of playback at the distance of 50 m from the speaker. However, all the others did respond. The results were compiled from these responsive individuals.

Latency of response

In Fig. 5-8, latency of response observed in Experiment I and Experiment II is shown to compare three playback conditions. In both experiments, the different conditions clearly had a significant effect upon latency of response ($p < 0.01$ and $p < 0.025$ respectively, see Appendix F-1, p. 270 for two-way ANOVA tables). Territorial males significantly more quickly approached within 40 m of the speaker or produced primary calls, when stranger's calls were broadcast than when neighbour's calls were played back at the normal location (Experiment I: $p < 0.01$, Experiment II: $p < 0.025$). However, the same recordings of neighbour's calls induced significantly swifter response when they were broadcast at the opposite location than when they were played back at the normal location ($p < 0.01$ for both experiments). Latency to neighbour's calls at the opposite location was not significantly different from that to stranger's calls ($p > 0.05$ for both experiments).

Number of flights

In Table 5-3, mean number of flights during the playback experiment is listed with one standard error. Territorial males tended to fly during playback. In Experiment I, as can be seen from Appendix F-2a (see p. 271) they flew more times when stranger's calls were broadcast than when neighbour's calls were played back at the normal location ($p < 0.01$). Although number of flights shown during playback of neighbour's calls was higher at the opposite location than at the normal location, the difference between the means was not significant ($p > 0.05$). However, number of flights shown during playback of stranger's calls was not significantly different from that shown during playback of neighbour's calls at the opposite location ($p > 0.05$). In Experiment II, there was no significant effect of the playback conditions upon number of flights during playback (see Appendix F-2b), and there were significant variations among the individuals.

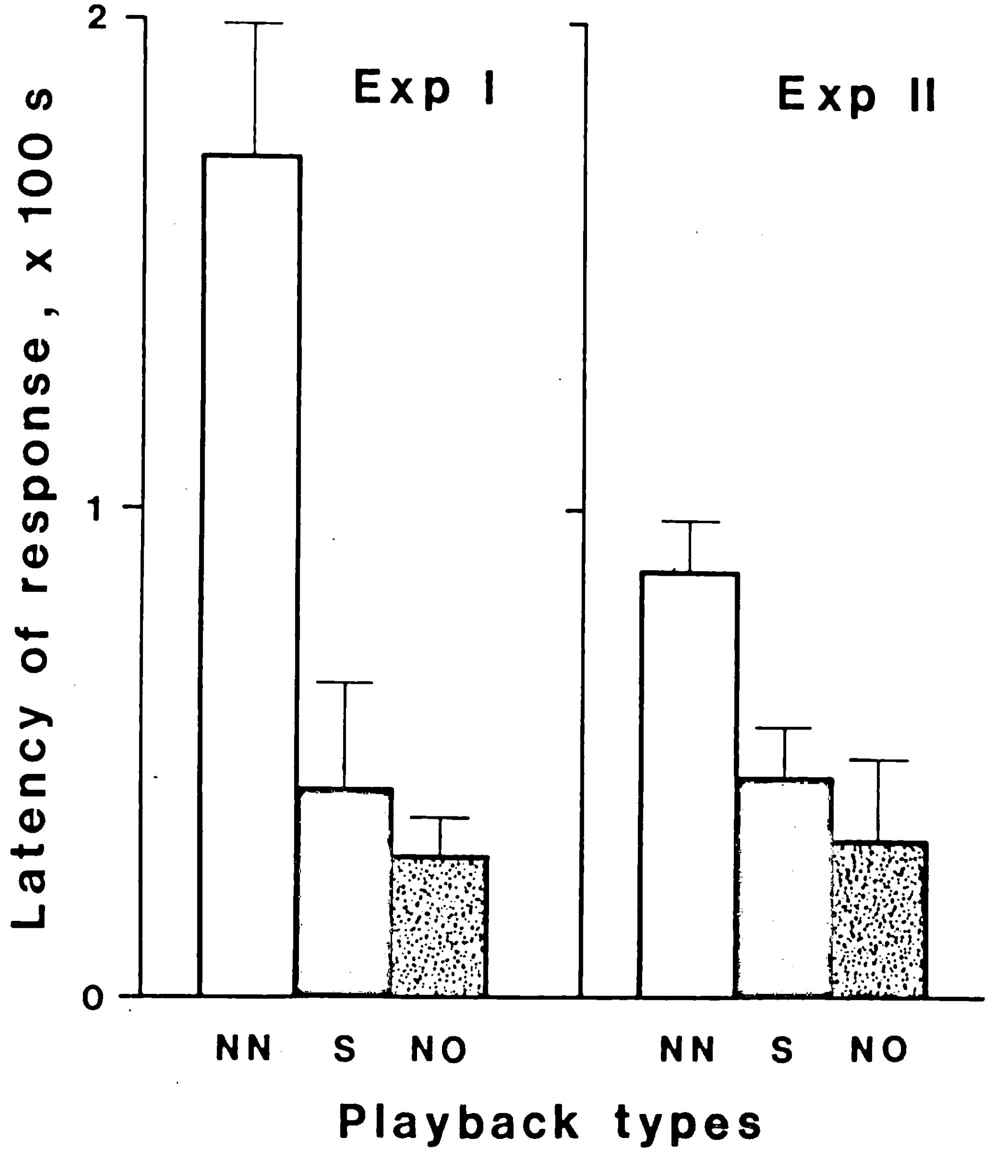


Fig. 5-8. Latency of response to playback of primary calls of strange and neighbouring territorial males. NN, neighbour's calls broadcast at the normal location; S, stranger's calls; NO, neighbour's calls broadcast at the opposite location. The mean and its one standard error are shown.

Table 5-3. Number of flights during the playback experiment of primary calls recorded from strange and neighbouring territorial males

A. Experiment I (5 males)

Period	Playback calls (location)		
	Stranger	Neighbour (Normal)	Neighbour (Opposite)
Before playback	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2
During playback	2.8 ± 0.4	1.2 ± 0.4	1.8 ± 0.2
After playback	0.6 ± 0.2	0.2 ± 0.2	0.8 ± 0.2

B. Experiment II (4 males)

Period	Playback calls (location)		
	Stranger	Neighbour (Normal)	Neighbour (Opposite)
Before playback	0	0	0
During playback	1.5 ± 0.9	1.0 ± 0.7	1.8 ± 0.6
After playback	0.5 ± 0.5	1.5 ± 0.5	0.8 ± 0.6

Nearest distance from speaker

In Fig. 5-9, mean nearest distance of test birds from the speaker is shown to compare different playback conditions. In Experiment I, it seems that they approached closer to the speaker when stranger's calls were broadcast than when neighbour's calls were played back at the normal location. However, when the same recording of neighbour's calls was broadcast at the opposite location, the distance from the speaker was as short as that recorded with playback of stranger's calls. Again in Experiment II, it appears that the distance was shorter with the stranger's calls than with the neighbour's calls broadcast at the normal location. However, it does not seem that the location at which neighbour's calls were broadcast had a clear effect upon the distance of test birds from the speaker.

Two-way ANOVA (see Appendix F-3, p. 272) made it clear that there were significant differences in the distance from the speaker among playback conditions in both experiments ($p < 0.01$). However, there was highly significant evidence of interaction between playback conditions and test birds ($p < 0.01$). The study of individual means for different playback conditions revealed that Owl 4 in Experiment I and Owl 3 in Experiment II did not somehow approach closer to the speaker which was playing back stranger's calls than the speaker which was broadcasting neighbour's calls at the normal location. Yet they showed positive responses in other measures, i.e. latency and number of call elements. Owl 5 in both experiments and Owl 2 in Experiment II did not shorten the distance from the speaker with playback of neighbour's calls at the opposite location. They, however, responded more quickly at the opposite location than at the normal location.

Number of primary and graded call elements

In Fig. 5-10, mean numbers of primary and graded call elements produced during the playback experiment are shown. In both experiments, playback triggered test birds' primary and graded calls. In Experiment I, they appeared to produce more elements during and after playback of stranger's calls than during and after that of neighbour's calls at the normal location. When recordings of neighbour's calls were broadcast at the opposite location, they seemed to produce far more elements than they did at the normal location.

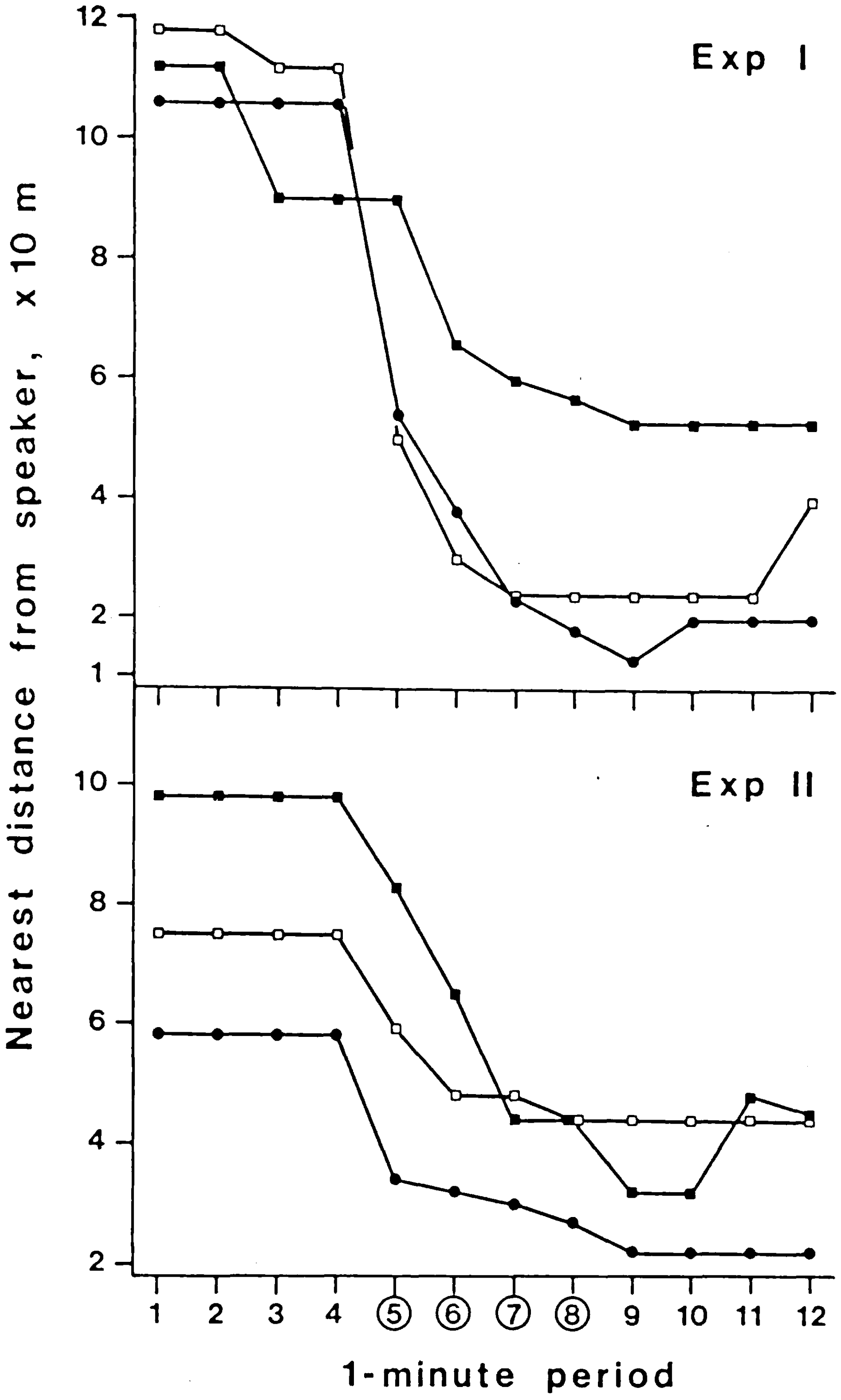


Fig. 5-9. Nearest distance from speaker during the playback experiment of primary calls recorded from strange and neighbouring territorial males. ■, neighbour's calls broadcast at the normal location; ●, stranger's calls; □, neighbour's calls broadcast at the opposite location; ○, play period.

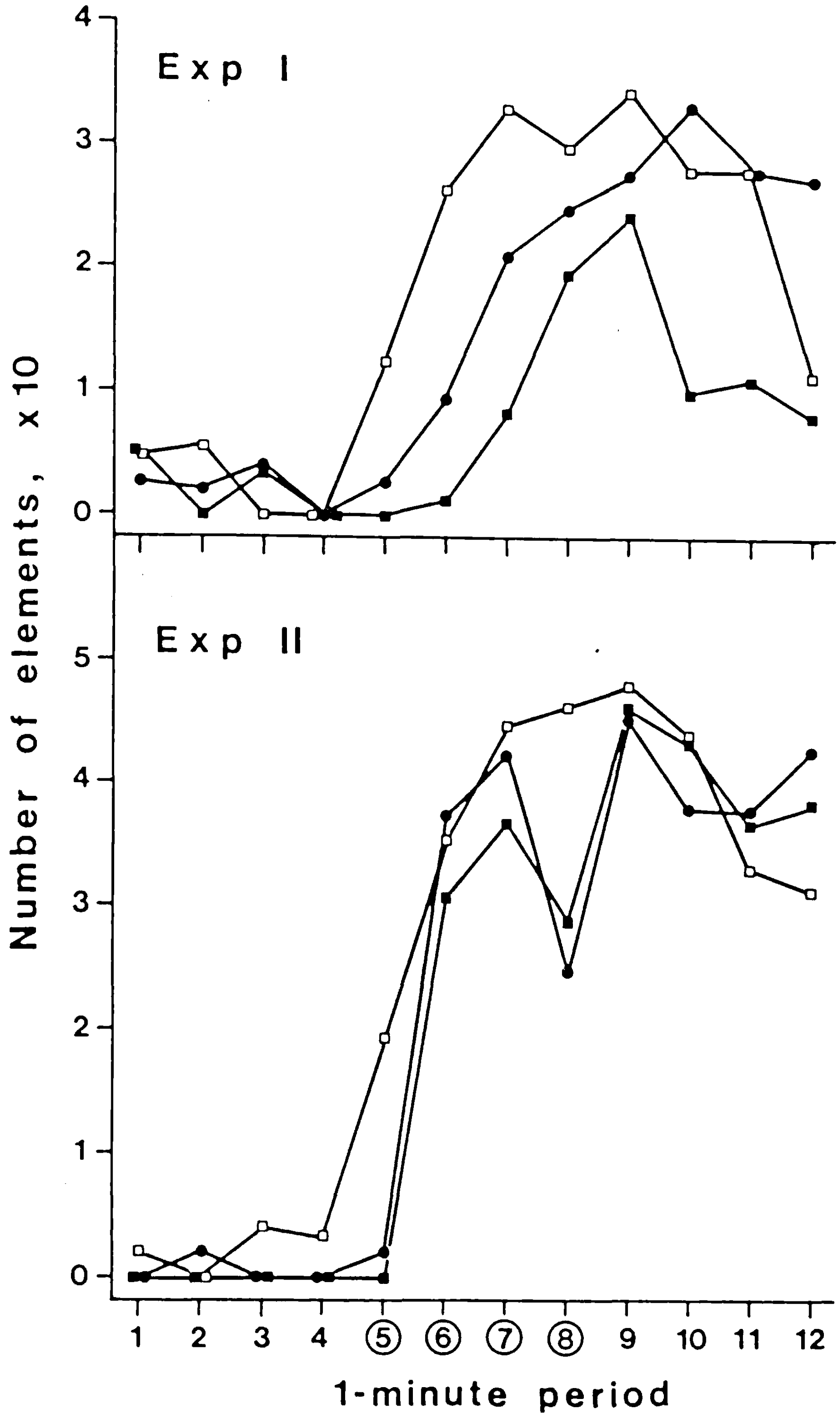


Fig. 5-10. Number of primary and graded call elements during the playback experiment of primary calls recorded from strange and neighbouring territorial males. ■, neighbour's calls broadcast at the normal location; ●, stranger's calls; □, neighbour's calls broadcast at the opposite location; ○, play period.

Two-way ANOVA (see Appendix F-4, p. 273), however, gave sufficient evidence of interaction between playback conditions and test males over a number of elements during and after playback. Some of the test birds produced elements in different manners with different playback conditions. In Experiment II, the difference between playback conditions was not clear whether it was during or after playback. Test males did not produce significantly more elements to playback of stranger's primary calls.

Maximum frequency of primary and graded calls

In Fig. 5-11, the mean difference between the observed maximum frequency of primary and graded calls produced during the playback experiment and the individual standard maximum frequency of primary calls is presented for each playback condition. In Experiment I, the negative difference increased as playback continued and decreased after it ceased. However, there was no apparent neighbour-stranger difference in the pattern of frequency reduction. Two-way ANOVA (see Appendix F-5 a and b, p. 274) showed that there was no significant neighbour-stranger discrimination in the extent of frequency reduction, whereas the study of individual means showed that some of the males decreased frequency lower in response to stranger's calls than to neighbour's calls. From Fig. 5-11, it appears that reduction of frequency might be larger when neighbour's calls were broadcast at the normal location than when they were played back at the opposite location. However, two-way ANOVA (see Appendix F-5 c and d) failed to show statistical significance ($p > 0.05$). Two males decreased frequency more when neighbour's calls were broadcast at the opposite location than when they were played back at the normal location. In Experiment II, similar insignificant results were obtained.

Effects upon females

In Experiment I, females did not respond to playback of primary calls of both neighbouring and strange males, except for the mate of male 3. This female approached her mate, while he was still producing primary calls after playback of stranger's calls had ceased. In Experiment II, the mates of males 2 and 4 respectively produced a bout

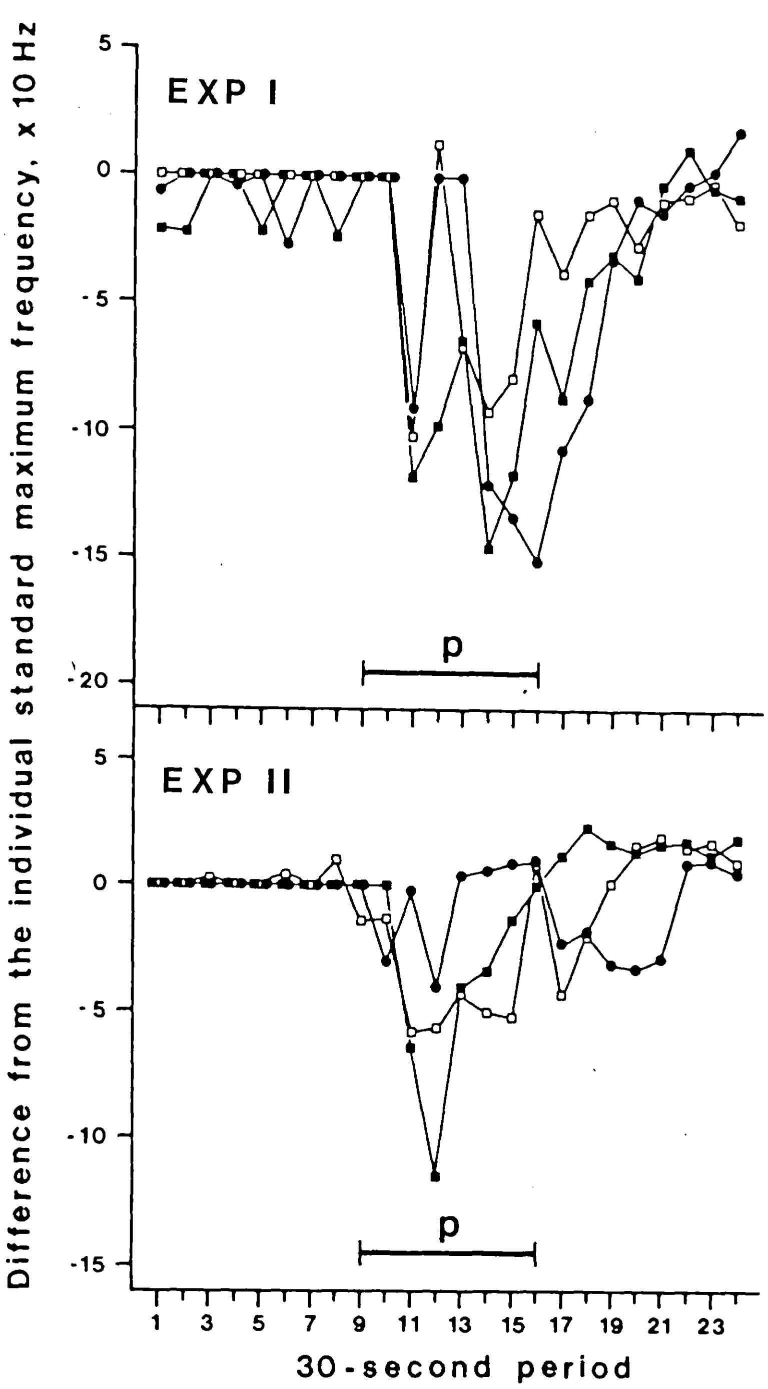


Fig. 5-11. **Difference between the observed maximum frequency** of primary and graded calls and individual standard maximum frequency of primary calls during the playback experiment of primary calls recorded from strange and neighbouring territorial males. ■, neighbour's calls broadcast at the normal location; ●, stranger's calls; □, neighbour's calls broadcast at the opporite location; p, play period.

of only eight primary call elements as they joined in their mates' vocal responses after playback of neighbour's calls at the normal location had finished. The mate of male 4 also produced a bout of twelve elements towards the end of playback of stranger's calls and another bout of four elements afterwards. However, no female approached the playback site.

5.4.3. Individual recognition by female primary calls

Latency of response

In Fig. 5-12, latency of response is compared among different playback conditions. Although the mean latency to playback of female's calls is slightly longer than that of control male's calls, there was no significant difference between sexes in terms of approach within 40 m (A) and production of primary and graded calls (B). It is apparent that there was no clear difference among different types of female calls.

Number of flights

In Table 5-4, number of flights recorded during the playback experiment of female primary calls with a control of strange male's calls is listed. Although the mean number of flights is slightly lower during playback of female's calls than during that of control male calls, there was no significant sexual difference. There was also no significant difference in the mean numbers among different females' calls (see Appendix G-1, p. 276).

Nearest distance from speaker

In Fig. 5-13, temporal patterns of the mean nearest distance of test males from the speaker are presented for the three types of female primary calls and control male stranger's calls. It is clear that males approached the speaker as playback of females' calls began and tended to stay close thereafter, as they did on hearing the control male calls. It appears that they were slower to approach the speaker which broadcast the recording of mate's primary calls than that of the other females' calls and control. Two-way ANOVA (see Appendix G-2, p. 276), however, revealed that there was no significant

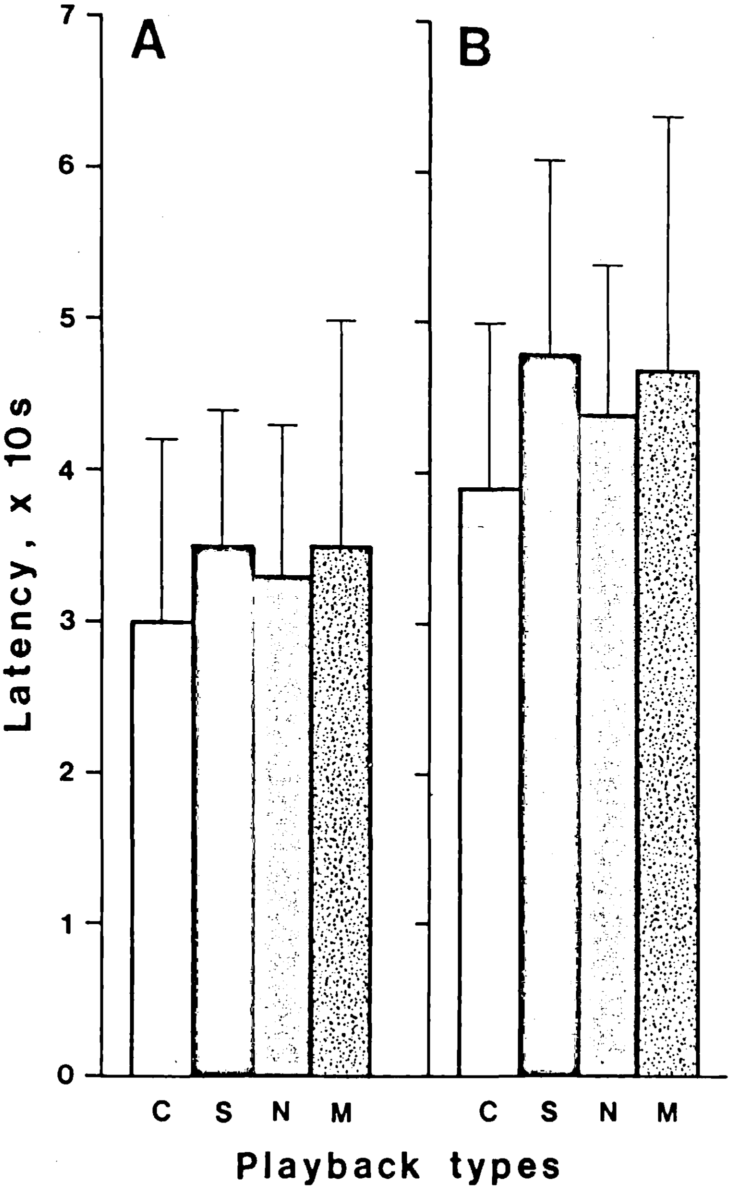


Fig. 5-12. Latency of response to playback of female primary calls recorded from a stranger, neighbour, and mate. **A**, approach within 40 m of the speaker; **B**, production of primary and graded calls; **C**, control calls of a male stranger; **S**, strange female's calls; **N**, neighbouring female's calls; **M**, mate's calls.

Table 5-4. Number of flights during the playback experiment of female primary calls recorded from different individuals

Period	Playback calls			
	Strange male (Control)	Strange Female	Neighbouring female	Mate
Before playback	0.3 ± 0.3	0.2 ± 0.2	0.4 ± 0.4	2.0 ± 0.4
During playback	2.8 ± 1.0	2.0 ± 0.6	1.8 ± 0.4	1.8 ± 0.5
After playback	0.6 ± 0.4	0.4 ± 0.2	0.4 ± 0.2	0.4 ± 0.2

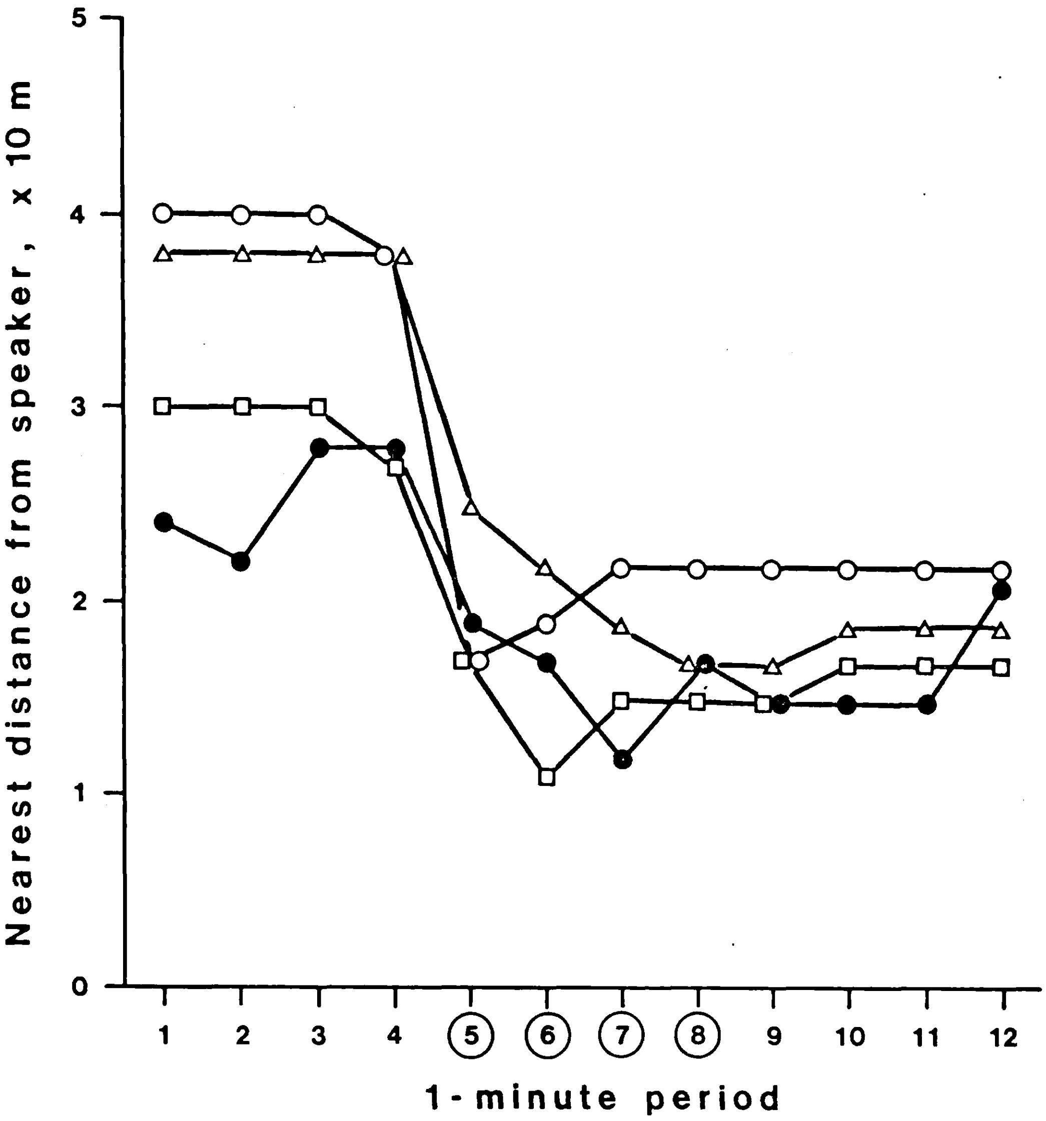


Fig. 5-13. Nearest distance from speaker during the playback experiment of female primary calls recorded from a stranger, neighbour and mate. ●, control calls of a male stranger; ○, strange female's calls; □, neighbouring female's calls; △, mate's calls; ◯, play period.

difference among the four playback conditions during the initial two one-minute periods of playback. Yet as far as the nearest distance in the initial two-minute period of playback was concerned, males did approach closer when control calls were broadcast than that of mate's calls (non-parametric Friedman two-way ANOVA: $x_r^2 = 5.0$, df = 1, $p < 0.05$). There was no significant difference among recordings of female primary calls in the initial two-minute period of playback (non-parametric Friedman two-way ANOVA: $p > 0.05$). In the following experimental periods, there was no apparent intra and inter-sexual difference.

Number of primary and graded call elements

In Fig. 5-14, temporal patterns of the mean number of primary and graded call elements are shown for the three types of female primary call and control male calls used for playback. It is clear that playback of female calls triggered the vocal response of territorial males as did that of male calls. The number of elements produced during playback of female stranger's calls and that of female neighbour's calls was not significantly different from that of control male calls ($p > 0.05$, see Appendix G-3a, p. 277). However, there was a significant difference between playback of mate's calls and that of control male calls ($p < 0.01$).

After playback, males still showed the different levels of call production among playback conditions ($p < 0.01$, see Appendix G-3b). The most extraordinary point was that four out of the five males were hardly vocal after playback of the mate's calls. There was sufficient evidence of interaction between playback conditions and test males ($p < 0.01$), suggesting that types of playback call affected birds differently during the four one-minute periods after playback. In Appendix G-3c, the result of two-way ANOVA applied for the whole four-minute period after playback is given. Territorial males produced significantly more elements after playback of female stranger's calls ($p < 0.05$) and significantly less after playback of mate's calls ($p < 0.01$) than they did after playback of control male calls. There was no significant difference between playback of female neighbour's calls and that of control male calls ($p > 0.05$). The number of elements after playback of mate's calls was significantly lower than after

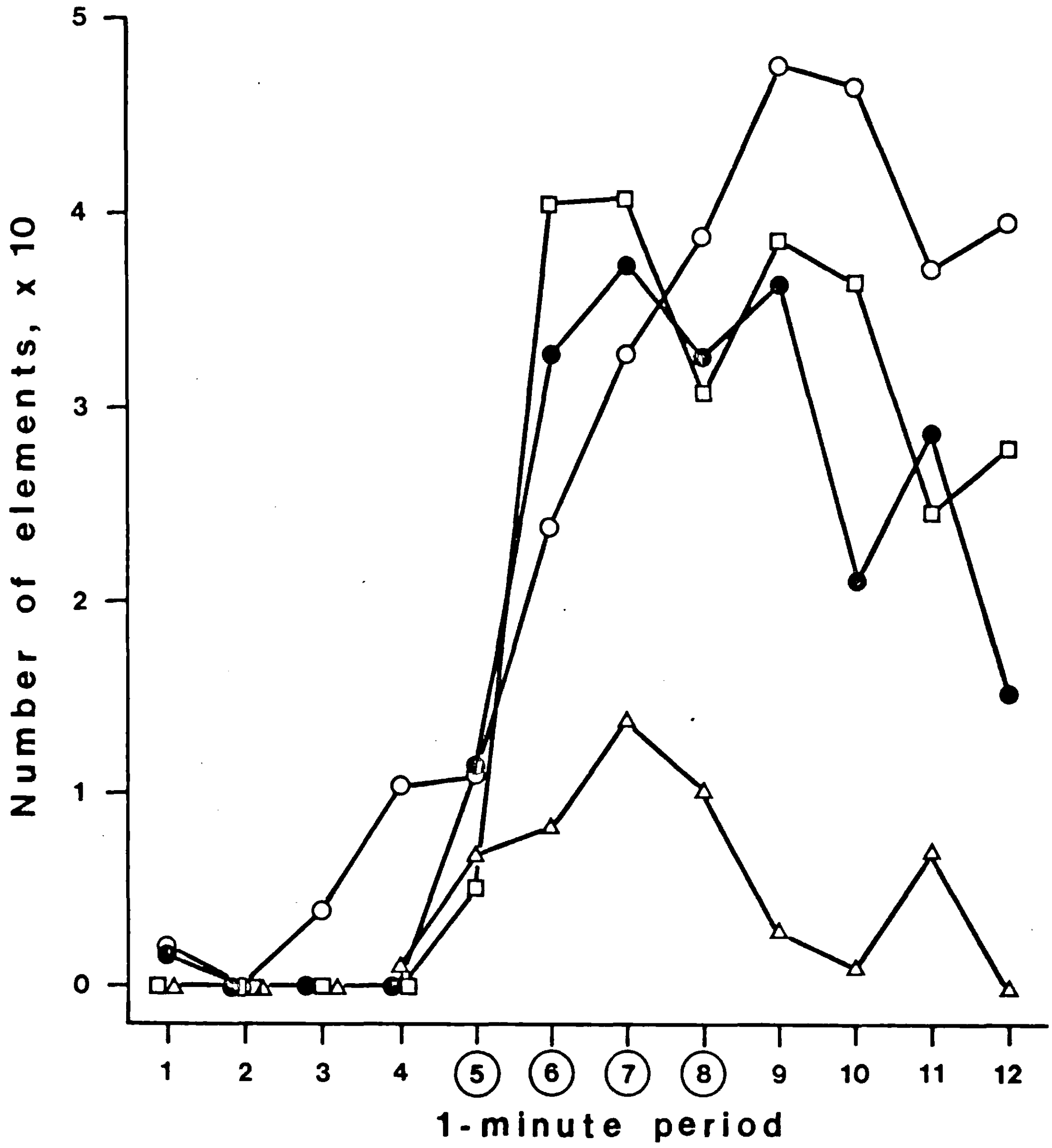


Fig. 5-14. <u>Number of primary and graded call elements</u> during the playback experiment of female primary calls recorded from a stranger, neighbour, and mate. ●, control male stranger's calls; ○, strange female's calls; □, neighbouring female's calls; △, mate's calls; ◯, play period.

playback of the other female calls ($p < 0.01$).

Maximum frequency of primary and graded calls

In Fig. 5-15, temporal patterns of the mean difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls are presented for the three types of female primary call and control male calls used for playback. In the control experiments, the negative difference increased during the initial 1.5 minutes of playback and then gradually decreased during and after the rest of playback. Similar patterns were observed in the other experiments using female stranger and female neighbour's calls. Playback of mate's primary calls induced smaller initial reduction and slightly earlier beginning of recovery than that of the other types of call.

The differences in the extent of frequency reduction among these playback conditions are particularly noticeable during the first half of playback. Two-way ANOVA (see Appendix G-4a, p. 278) revealed that a significantly different response was found between different sexes of playback calls ($p < 0.01$). However, there was no significant difference among playback experiments using female calls ($p > 0.05$). During the second half of playback there was sufficient evidence for interaction between playback conditions and tested males ($p < 0.01$, see Appendix G-4b), suggesting that playback conditions did not affect birds in a consistent manner. However, it appears that playback of female stranger's calls induced a similar level of frequency reduction to that of control male calls ($p > 0.05$). Playback of female neighbour's calls and that of mate's calls induced smaller reduction than that of control male calls ($p < 0.05$ and $p < 0.01$ respectively). In response to playback of female stranger's calls, the frequency was reduced as much as that in response to playback of female neighbour's calls ($p > 0.05$), but it was a greater reduction than that seen in response to playback of mate's calls ($p < 0.01$). There was no significant difference in frequency reduction between playback of female neighbour's calls and that of mate's calls ($p > 0.05$).

Effects upon females

The mates of males 1, 3 and 5 showed low levels of vocal

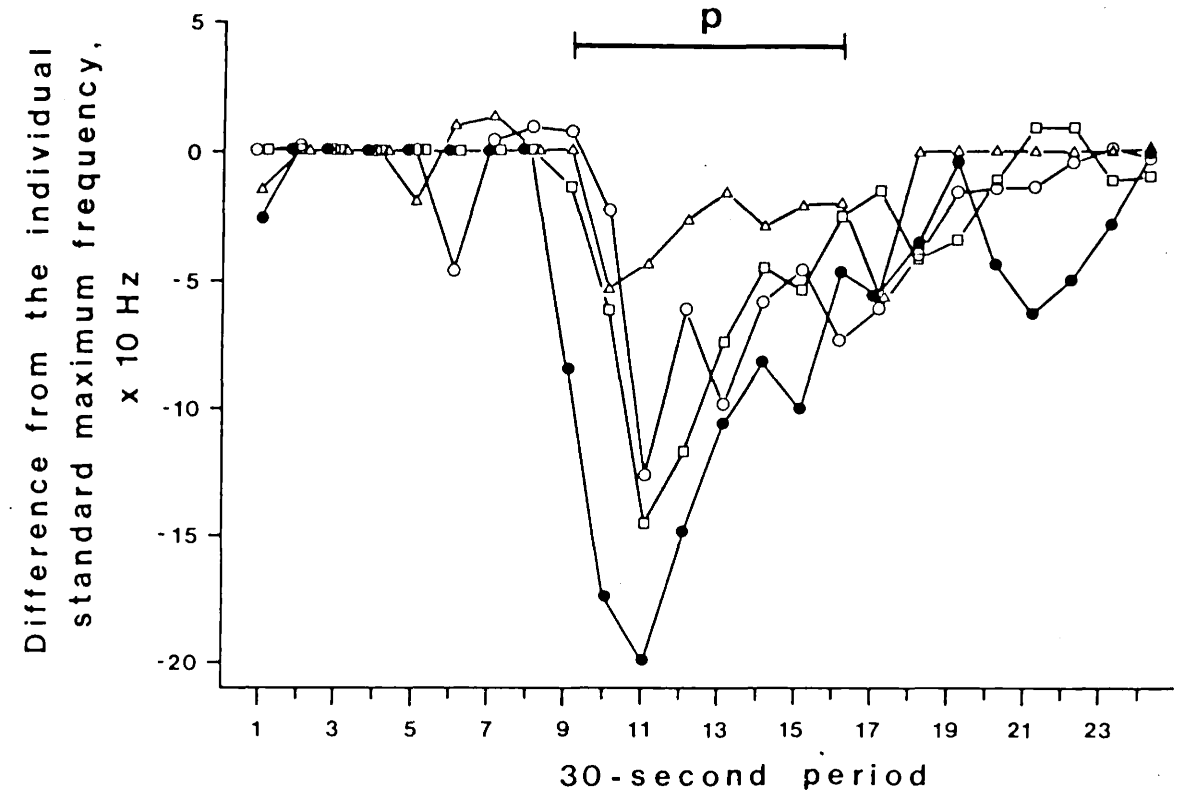


Fig. 5-15. Difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls during the playback experiment of female primary calls recorded from a stranger, neighbour, and mate. ●, control male stranger's calls; ○, strange female's calls; □, neighbouring female's calls; △, mate's calls; p, play period.

production in the vicinity of the speaker which broadcast control male calls. Two of them also showed a low level of vocal production nearby mainly after playback of strange female's primary calls, while their mates, males 1 and 5, were emitting calls. 'Krrr' (see 2.3.7.) was also heard from both birds during and/or after playback. No female showed noticeable changes in behaviour during the playback experiment of neighbouring female's primary calls. The mate of male 4 did produce up to 118 elements of primary calls after playback of self primary calls, after her mate had already finished vocal response, and she called from afar. Females were busy attending their offspring in most cases.

5.4.4. Discussion

5.4.4.1. Neighbour-stranger discrimination

If territorial males recognize individuals by their primary calls, their response to neighbours' calls should be different from that shown to strangers' calls. Once territorial relationships are established between males, known neighbours' calls may not impose so much of a threat as strangers' calls. Thus territorial males may respond more aggressively to playback of stranger's calls than that of neighbour's calls. From the earlier observation and playback experiments documented in Chapter 4, it was speculated that territorial males should respond more quickly, approach the speaker more closely, fly more frequently, and produce more elements of primary and graded calls in lower frequency (Hz) as they became more aggressive.

The results of playback experiments (Series I), in which the territorial male's response to playback was compared between neighbour's primary calls and stranger's calls, provide some evidence that male Japanese Brown Hawk Owls are capable of discriminating neighbours from stranger. In Experiment I, which was carried out during the incubation stage, males responded with a stronger intensity to playback of stranger's calls than neighbour's calls, as has previously been demonstrated for several oscine and one non-oscine species (Weedon & Falls 1959; falls 1969; Emlen 1971; Krebs 1971; Harris & Lemon 1972; Goldman 1973; Lemon & Harris 1974; Brooks & Falls

1975a; Kroodsma 1976; Jarvi et al. 1977; Wunderle 1978; Falls & McNicholl 1979; Pickstock & Krebs 1980; Falls & d'Agincourt 1981; Searcy et al. 1981; Falls 1982; Yasukawa et al. 1982; Ritchison 1983a). Latency of response and number of flights indicated significant neighbour-stranger discrimination. However, there was some variation in response in terms of nearest distance from the speaker as well as number and maximum frequency of primary and graded call elements. One of the males approached closer to the speaker but did not call more during playback of stranger's calls. The other bird called more elements at lower pitch but did not approach closer to the speaker. Another bird approached the speaker closer and called more elements, but the maximum frequency of calls was not lower. Similarly in Experiment II, which was carried out during the fledgling stage, territorial males showed significant neighbour-stranger discrimination in terms of latency of response. The males responded more quickly to stranger's calls than to neighbour's calls. However, they again showed variable behaviour in terms of the other four measures. It can be seen that demonstrating neighbour-stranger discrimination by using only one of these measures is not feasible (Falls & McNicholl 1979). The introduction of a scaling system using combined measures as described by Emlen (1971) and Emlen et al. (1975) may be more useful in future work. Nevertheless, different behavioural measures should be studied separately as much as possible in order to understand individual variation in response.

In these experiments, responses to neighbour's calls were smaller than to stranger's calls. This may be due to habituation to neighbour's calls (Falls 1969; Petrinovich & Peeke 1973; Armstrong 1973). Neighbours generally concentrate their activity within their territory and do not present an imminent threat to territory owners. Strangers persistently attempt to invade and squeeze in between territories at any time during the breeding season, which imposes an immediate threat to the established territory owners. Therefore it is time and energy-saving to respond to stranger's calls more quickly and aggressively than to neighbour's calls. From the analysis of physical features of individuals' primary calls, individual identity of calls appears to remain throughout the breeding season and may last for life. If based upon long-term memory, then neighbour's calls will always evoke less response than stranger's calls when the owls re-establish territories after every spring migration. Neighbour-stranger discrimination may be important in a population composed of the same individuals occupying the same site in each year (Falls 1982).

5.4.4.2. Recognition of neighbours

Beer (1970) pointed out that discriminative response of territorial males to vocalizations between neighbours and strangers does not necessarily mean that males recognize their neighbours individually. They may merely distinguish familiar vocalizations from unfamiliar ones. In territorial species, like Japanese Brown Hawk Owls, neighbours are located in fixed directions throughout the breeding season, and individual calls may be associated with these locations. It follows that the owner of a territory should respond more aggressively to a neighbour's calls when heard from a different location. The results of playback experiments (Series I), in which the response to neighbour's calls was compared between the normal and opposite locations, support this view. In both experiments, the males responded to playback with a stronger intensity when the speaker was at an opposite location, demonstrating individual recognition of neighbours by both primary calls and location. Falls and Brooks (1975), Wiley and Wiley (1977) and Wunderle (1978) showed this at the opposite side of a territory boundary, while Ritchison (1983a) did so at both the centre and edge of territory. In the present study, the location used was neither the centre nor the boundary but half-way between the centre and boundary. This location is considered to be more sensitive than the boundary in testing response to playback, and invading birds were also seen there. Wiley and Wiley (1977) have cast some doubt upon responses to playback of neighbour's calls at the wrong location as the birds only infrequently and temporarily move to unusual locations. In the present species, however, deep invasion was not necessarily infrequent nor temporary throughout the breeding season. No sooner did an invading neighbour produce primary calls than territorial males responded aggressively. Since there was no significant neighbour-stranger discrimination at the opposite location, it is concluded that primary calls alone may not be sufficient for recognition of neighbours.

5.4.4.3. Speed of recognition

The results of playback experiments in Series I suggest that discrimination occurs quickly. Latency was significantly shorter when stranger's calls were played back than when neighbour's calls were presented. It was also significantly shorter when neighbour's calls were played back at the opposite location than at the normal location. In Experiment I, in particular, the first response in these playback conditions had been made before the first bout of ten - twenty elements was completed. This behavioural evidence supports the physical evidence given earlier that the individuality of primary calls is achieved within the physical features of a small number of primary call elements. In Experiment II, more elements were broadcast before the first response. This may be due to the seasonal decline in territorial aggression which has been discussed earlier. In view of the adaptive significance of recognizing individuals vocally, it seems unlikely that the birds' efficiency of recognition decreases with season.

5.4.4.4. Sexual discrimination and mate recognition

If territorial males recognize the sex of the caller by its primary calls, their response to female calls must also be different. The impact which females impose upon the territorial and reproductive strategy of males should vary from that of males. Females of Japanese Brown Hawk Owls play an assisting role in territorial defence and also use primary calls. However, in general, their primary calls appear more in interaction and integration with their mates. It is speculated that territorial males may respond to female primary calls with a weaker intensity than they do to male calls.

Similarly if territorial males recognize their own mates by primary calls, their response to the mate's calls must be different from the response to other females' calls. For territorial males which are well-established and occupied in the care of offspring, interest in their mates is much more than in other females. Time for new mating with other females has passed, and so territorial males regard the primary calls of a female stranger as much as that of a male stranger. Although territorial males may be habituated to the primary calls of a female neighbour, the unusual location from which they hear them may affect the intensity of response. The mate's primary calls heard at the centre of territory may induce the least aggressive response. There may also be stronger responses to a female stranger's calls than to a female neighbour's calls.

The results of playback experiments in Series II, however, were not straightforward. Sexual and mate discrimination did not emerge in a unified manner with the five behavioural measures. The main source of evidence for male-female discrimination was given by the maximum frequency during the first half of playback. Frequency is considered to encode information about aggressive motivation as discussed in Chapter 4. Less reduction of maximum frequency in response to playback of female calls than that of male calls may mean that female calls are less provocative than male calls.

The best evidence for mate discrimination was provided by the number of call elements. During playback, territorial males produced significantly less calls in response to the mate's calls than to other calls, while there was no discrimination among the latter. After playback, mate discrimination was still observed and also discriminative reduction in calling emerged among the other calls (i.e. mate's calls < female neighbour's calls < female stranger's calls). Maximum frequency also showed significant mate discrimination during the second half of playback. Playback of mate's calls produced the least frequency reduction, and that of female stranger's calls as much as that of control male calls. Finally, neighbour's calls produced less reduction than the latter. More evidence of mate discrimination is given by the nearest distance from the speaker. Territorial males did not approach the speaker broadcasting the mate's calls as closely as they did the speaker broadcasting control male calls and also the other female calls.

In these experiments, latency of response and number of flights showed no discrimination, in spite of speculation that territorial males should respond slower and fly less often when female calls were broadcast. Since test males tended to stay near the nest site in the centre of territory, they were already situated close to the speaker. Short distance might have obscured differences in latency and number of flights among playback conditions. In the experiments of Series I, where the initial distance between the males and speaker was long, clear differences were found in these two measures.

Why did males produce a lower number of call elements in response to the mate's calls? In vocal interaction between mates, it is very unusual that females initiate calling and produce their primary calls as insistently as presented in the playback experiment. It is also unusual for females to call in this way in the late nestling and early fledgling stage, when they are busy caring for young. Territorial males may well be puzzled by such an unusual vocal activity. It is remarkable that most of the males stopped calling immediately after playback of their mate's calls had finished. This suggests a non-aggressive nature of the males' response, and must be understood in the context of interactions with the mate. It is unlikely that the presence of the mate had an effect upon the males' response. No females produced their primary calls during playback, so there was no chance for territorial males to listen to and compare playback and live calls.

In view of the number of call elements, the nature of territorial males' response to playback of other females' calls is similar to the responses to other males' calls. It is evidently territorial. Not only does this suggest that territorial information is encoded in the number of call elements, but also that female primary calls can function as a territorial signal.

Males of Japanese Brown Hawk Owls are clearly capable of discriminating sexes and recognizing their own mates by listening to the females' primary calls. Several factors might encourage this vocal recognition to develop. Firstly, the owls are morphologically similar between sexes. Secondly, they are crepuscular and nocturnal, and live in a habitat where vision is restricted by the dense vegetation. Thirdly, they are long-lived and form the pair-bond for life.

5.4.4.5. Female responses

The observed intensity and manner of females' responses did not suggest that there was any strong influence upon the territorial male's response to playback. In species where females also respond to primary calls or songs, it is helpful to control female response in order to examine the territorial males' response. This was achieved by choosing incubation, late nestling and fledgling stages for the playback experiment. Female Japanese Brown Hawk Owls showed fairly vigorous responses during some of the pre-incubation stage. Petrinovich et al. (1976) also reported that the female's aggressive response to playback depends upon the breeding cycle. He believed that responsive females are in the process of nest-building or egg-laying. In this species, there was no sign of female responses specially aimed at conspecific females as reported by Beletsky (1983b).

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APPENDICES

Part A. Physical Structure of Vocalizations of the Japanese Brown Hawk Owl

For temporal features, the mean and one standard error (SE) are given in the unit of ms, and the coefficient of variation (CV) is provided in percentages. For frequency features, the mean, one standard error, and standard deviation (S) are given in the unit of Hz. Harmonic patterns are indicated by the mean strength of each harmonic. For the scoring method, see 2.2.6. For types of frequency modulation, the number of occurrences in a sample is shown. See Table 2-1 (p. 31) for categories of frequency modulation. (A), part A; (B), part B; x, absent; xx, few samples.

A-1. 'K.hoo' (the primary call): temporal features

Individual		Duration (A)			Duration (B)			Short interval			Long interval		
		Mean	SE	CV	Mean	SE	CV	Mean	SE	CV	Mean	SE	CV
Male	1	98	6	22.0	198	3	5.2	347	4	3.0	580	45	15.7
	2	65	3	14.3	238	6	2.4	357	3	2.3	640	8	2.6
	3	105	7	20.9	237	2	3.3	423	8	4.6	565	19	6.7
	4	47	6	43.4	217	3	5.3	337	3	2.4	625	61	19.6
	5	75	6	23.6	217	3	5.3	343	3	2.4	850	86	20.2
	6	62	6	28.2	207	3	4.8	303	6	5.0	523	13	6.1
	7	73	6	28.2	202	2	2.9	367	7	4.5	670	47	13.9
	8	64	7	33.9	205	3	4.4	357	6	4.2	620	36	11.5
	11	x			245	6	7.9	367	4	4.2	x		
Female	1	xx			177	7	13.5	383	10	6.1	596	21	8.0
	2	xx			193	3	5.1	448	8	4.0	1000	102	22.7
	3	xx			212	3	4.9	373	18	12.1	532	39	16.5
	4	69	8	39.6	235	6	8.2	420	12	6.7	780	47	12.0
	5	71	8	38.6	223	2	3.5	353	4	2.9	625	30	9.6
	6	xx			208	6	9.6	370	4	3.0	596	23	8.7
Juvenile	1	50	10	28.3	180	10	17.8	392	15	8.5	980	53	9.3
	2	40	6	25.0	200	5	6.3	467	18	6.5	850	10	1.7

A-2. 'K.hoo' (the primary call): frequency features

		Maximum (A)			Minimum (A)			Maximum (B)			Minimum (B)		
Individual		Mean	SE	S	Mean	SE	S	Mean	SE	S	Mean	SE	S
Male	1	319	8	29	248	5	16	712	4	13	505	4	12
	2	456	5	45	334	9	30	742	6	22	493	12	40
	3	384	12	34	294	5	15	649	8	26	498	3	10
	4	396	12	33	333	19	62	693	6	22	550	3	10
	5	503	3	8	450	11	32	772	5	18	618	8	28
	6	327	3	8	292	4	14	695	6	19	458	13	44
	7	400	8	20	387	20	66	714	9	29	542	13	45
	8	500	0	0	476	9	29	745	3	9	638	10	34
	11	x			x			633	8	29	507	3	10
Female	1	xx			xx			743	6	21	633	11	37
	2	xx			xx			733	12	41	646	12	43
	3	xx			xx			837	10	34	673	5	17
	4	564	8	26	458	20	65	777	7	25	606	9	33
	5	520	0	0	439	18	58	755	7	15	591	12	41
	6	xx			xx			663	11	40	552	5	18
Juvenile	1	x			x			816	16	49	689	17	53
	2	630	15	26	587	7	12	1063	15	37	720	17	41

A-3. 'K.hoo' (the primary call): harmonic patterns of part B, 'hoo'

Individual		Harmonics				
		2H	3H	4H	5H	6H
Male	1	0.5	3.8***	0.2	2.8*	0
	2	2.2	5.0***	1.1	3.5**	0
	3	0	2.5*	0	0	0
	4	0	4.9***	0	2.6*	0
	5	0.4	4.8***	0.7	1.8	0
	6	0	5.0***	0	3.0***	0
	7	0	2.8**	0	0	0
	8	1.7	4.4**	0.1	2.2	0
	11	1.8	0.2	0	0	0
Female	1	0	0	0	0	0
	2	0.3	0.3	0.3	0.3	0
	3	1.1	2.8	0	0	0
	4	1.3	4.3**	0	3.1*	0
	5	3.5***	1.5	0.8	0	0
	6	0	0	0	0	0

Note: Binomial test (*, $p < 0.025$; **, $p < 0.01$; ***, $p < 0.001$), $n = 12$.

A-4. 'K.hoo' (the primary call): types of frequency modulation

		Types of part A					Types of part B					
Individual		A	F	D	DA	FDA	F	A & AF	AFD & AD			DF & D
									R	C	L	
Male	1	2	6	0	3	1	0	0	7	5	0	0
	2	1	0	0	10***	0	0	0	8*	3	1	0
	3	3	1	0	6	1	0	0	9**	3	0	0
	4	0	4	0	7	0	0	0	12****	0	0	0
	5	1	1	1	5	0	0	0	0	12***	0	0
	6	2	6	1	0	0	0	0	0	12***	0	0
	7	2	7*	0	1	0	0	0	3	9	0	0
	8	6	2	0	3	0	0	3	2	0	7****	0
	11	x	x	x	x	x	0	1	5	6	0	0
Female	1	x	x	x	x	x	1	5***	2	1	2	1
	2	x	x	x	x	x	0	9****	2	1	0	0
	3	x	x	x	x	x	0	0	1	8	3	0
	4	0	2	0	9*	0	0	0	4	8	0	0
	5	7***	4	0	0	0	0	2	7	3	0	0
	6	x	x	x	x	x	0	1	0	7	4**	0

Note: The number of occurrences in a sample ($n = 12$) is shown. Binominal test (*, $p < 0.05$; **, $p < 0.025$; ***, $p < 0.01$; ****, $p < 0.001$).

A-5. 'K.hoo' (the primary call): number of elements in a bout

Individual		Md	Range	sk	n
Male	1	6	2 - 60	1.04	88
	2	8	2 - 24	0.88	163
	9	8	1 - 22	0.40	54
	10	8	2 - 24	0.82	42

Note: Skewness (sk) was obtained using the following formula:-

$$sk = \frac{3\ (M - Md)}{S}$$

where M = mean, Md = median, and S = standard deviation (Mills 1965).

A-6. 'Hoh': temporal features

		Duration (A)			Duration (B)			Interval		
Individual		Mean	SE	CV	Mean	SE	CV	Mean	SE	CV
Male	1	x			198	2	0.1	408	7	7.5
	8	27	7	43.3	252	7	12.2	447	8	7.1
	9	127	26	50.6	246	17	20.9	509	57	31.9
	10	x			147	15	25.4	403	6	3.7
	11	x			220	9	10.0	456	10	4.8
	12	x			87	13	26.6	540	101	32.3
	13	157	27	41.5	190	12	24.3	501	13	9.7
Female	1	134	10	28.3	211	7	12.4	409	8	6.8
	3	x			160	13	17.7	440	18	8.3
	4	x			178	17	27.2	480	38	20.8
	5	x			200	12	10.0	560	140	35.4
	6	x			130	17	26.6	440	20	6.4

A-7. 'Hoh': frequency features

Individual		Maximum (A)			Minimum (A)			Maximum (B)			Minimum (B)		
		Mean	SE	S	Mean	SE	S	Mean	SE	S	Mean	SE	S
Male	1	x			x			634	7	31	530	7	31
	8	415	6	25	335	45	64	509	3	14	415	6	25
	9	420	40	99	293	28	69	549	8	27	388	25	76
	10	x			x			477	10	23	450	7	17
	11	x			x			480	9	22	443	6	15
	12	x			x			467	7	12	427	27	46
	13	307	11	27	283	13	33	486	3	12	449	7	29
Female	1	329	3	12	259	4	15	519	5	19	451	6	24
	3	x			x			552	12	27	544	15	33
	4	x			x			584	13	37	523	15	42
	5	x			x			553	7	12	487	7	12
	6	x			x			530	17	35	490	19	38

A-8. 'Hoh': types of frequency modulation of part B

	Types								
Individual	A	F	AF	AFD & AD			FD	D	O
				R	C	L			
Male 1	0	0	2	7	7	3	1	0	0
8	0	0	1	0	6	12	1	0	0
9	1	0	1	2	2	3	0	0	0
10	1	0	2	0	0	2	0	0	0
11	0	0	1	0	1	1	2	1	0
12	0	0	2	0	1	0	0	0	0
13	0	5	1	0	1	7	0	2	0
Female 1	0	0	5	0	4	5	1	0	0
3	0	0	-	0	1	0	0	3	1
4	0	0	-	0	6	2	0	0	0
5	0	0	-	0	0	1	1	1	0
6	1	0	2	0	0	0	0	1	0

A-9. 'Guf': temporal features

Individual		Duration (A)			Duration (B)			Interval		
		Mean	SE	CV	Mean	SE	CV	Mean	SE	CV
Male	1	x			173	8	21.0	453	10	2.8
	10	x			187	6	14.8	412	9	6.0
	11	x			248	12	22.1	427	15	5.2
Female	1	145	5	12.8	229	14	22.7	445	15	7.0

A-10. 'Guf': frequency features

Individual		Maximum (A)			Minimum (A)			Maximum (B)			Minimum (B)		
		Mean	SE	S	Mean	SE	S	Mean	SE	S	Mean	SE	S
Male	1	x			x			503	6	25	409	6	25
	10	x			x			448	3	15	392	3	12
	11	x			x			482	8	37	416	6	29
Female	1	318	13	54	225	11	38	568	9	32	347	8	30

A-11. 'Guf': types of frequency modulation of part B

Individual		A	F	AF	AFD & AD			FD	D	O
					R	C	L			
Male	1	0	1	0	0	0	14	5	0	0
	10	0	3	4	0	2	7	0	2	2
	11	1	1	4	0	2	4	4	4	0
Female	1	0	0	0	1	5	5	0	0	2

A-12. 'Oo.coo': temporal features

Individual		Duration (A)			Duration (B)			Interval		
		Mean	SE	CV	Mean	SE	CV	Mean	SE	CV
Male	1	198	12	18.5	179	4	10.6	469	10	8.7
	3	276	13	10.9	287	11	9.5	532	12	5.0
	8	180	5	10.8	245	2	4.5	402	3	3.4
	9	158	13	27.0	194	5	12.6	507	23	19.0
	10	118	9	29.1	189	9	21.8	328	9	11.6
	12	160	20	47.2	185	7	16.8	446	8	8.1
	14	154	11	22.1	241	6	11.6	369	7	8.7
Female	1	107	11	34.7	185	7	17.8	507	25	20.5
	3	x			229	16	21.5	250	15	16.6

A-13. 'Oo.coo': frequency features

Individual		Maximum (A)			Minimum (A)			Maximum (B)			Minimum (B)		
		Mean	SE	S	Mean	SE	S	Mean	SE	S	Mean	SE	S
Male	1	254	4	13	181	16	49	507	4	18	415	12	53
	3	286	4	9	234	4	9	496	4	9	410	7	17
	8	407	5	22	259	10	42	502	4	16	402	5	21
	9	428	8	21	316	32	96	529	9	40	480	7	32
	10	369	14	54	332	14	56	481	6	28	437	8	34
	12	288	8	33	265	4	15	509	4	19	452	5	23
	14	238	5	17	224	5	17	348	5	22	324	4	18
Female	1	327	11	35	261	5	15	498	7	30	451	5	22
	3	x			x			593	3	10	556	9	28

A-14. 'Oo.coo': types of frequency modulation

Individual		Types of part A						Types of part B								
		A	F	D	AFD & AD	DFA & DA	0	A	F	AF	AFD & AD			FD	D	0
											R	C	L			
Male	1	0	4	0	0	0	0	0	1	0	0	0	8	4	7	0
	3	0	0	5	0	0	0	0	0	0	0	0	6	0	0	0
	8	0	0	18	0	0	0	0	0	0	0	5	15	0	0	0
	9	0	2	4	0	1	2	0	1	1	0	14	3	1	0	0
	10	0	4	10	3	0	0	1	0	4	1	8	6	0	0	0
	12	2	3	6	1	1	1	0	1	1	0	10	5	2	1	0
	14	0	6	3	2	0	0	1	0	0	3	0	12	1	2	1
Female	1	0	2	6	2	0	0	0	2	1	1	5	6	0	4	0
	3	x	x	x	x	x	x	8	1	0	0	0	0	0	0	0

A-15. 'Poo': temporal features

Individual		Duration			Interval		
		Mean	SE	CV	Mean	SE	CV
Female	2	194	7	16.8	456	28	26.0
	7	204	7	14.4	344	17	21.6

A-16. 'Poo': frequency features

Individual		Maximum			Minimum		
		Mean	SE	S	Mean	SE	S
Female	2	566	4	9	512	4	20
	7	517	4	18	503	2	10

A-17. 'Poo': types of frequency modulation

Individual		Types								
		A	F	AF	AFD & AD			FD	D	O
					R	C	L			
Female	2	8	0	9	1	2	0	0	0	0
	7	1	19	0	0	0	0	0	0	0

A-18. 'Hyu': temporal features

		Duration			Short interval			Long interval		
Individual		Mean	SE	CV	Mean	SE	CV	Mean	SE	CV
Male	1	174	13	25.0	387	12	7.8	580	64	19.2
	8	177	5	11.2	423	26	14.8	630	24	7.6
	11	204	18	20.1	390	30	10.9	560	-	-
	12	170	8	16.3	327	11	8.4	733	53	12.6
	13	154	7	20.3	422	16	11.2	818	92	33.7
	15	108	9	46.6	345	19	9.4	657	192	41.3
Female	2	108	9	17.6	210	20	13.5	340	-	-
	5	178	9	18.2	417	10	5.6	740	36	9.6
	7	133	6	12.1	418	9	3.7	815	196	41.7

Note: There was only one sample of the long interval for male 11 and female 2 each.

A-19. 'Hyu': frequency features

Individual		Maximum			Minimum		
		Mean	SE	S	Mean	SE	S
Male	1	525	10	36	464	9	28
	8	580	14	50	517	11	38
	11	528	5	11	476	4	9
	12	661	15	53	584	15	52
	13	576	9	40	533	11	49
	15	563	6	15	523	3	8
Female	2	700	20	41	588	13	25
	5	633	13	45	548	11	37
	7	xxx			xxx		

Note: xxx, absence of the fundamental frequency

A-20. 'Hyu': harmonic patterns

Individual		Harmonics				
		2H	3H	4H	5H	6H
Male	1	0.4	1.3	0.8	0.3	0.1
	8	0.5	2.9	1.9	0	0
	11	0.2	4.0	2.4	0	0
	12	2.5	2.1	0	0	0
	13	0.7	3.3	3.6	0	0
	15	0	0	0.3	0.5	0
Female	2	1.0	1.5	3.3	0	0
	5	2.5	4.7	3.2	0.8	0.3
	7	0.9	3.4	3.3	0	0

A-21. 'Hyu': types of frequency modulation

Individual		Types								
		A	F	AF	AFD & AD			FD	D	O
					R	C	L			
Male	1	0	0	4	0	3	2	1	0	0
	8	0	0	6	2	4	0	1	0	0
	11	0	0	2	1	2	0	0	0	0
	12	0	0	1	1	9	0	0	0	0
	13	0	2	8	3	7	0	0	0	0
	15	0	2	3	1	0	0	0	0	0
Female	2	1	0	2	0	1	0	0	0	0
	5	0	0	2	5	5	0	0	0	0
	7	0	0	0	1	0	6	0	0	0

A-22. 'Krrr': duration and frequency

		Duration			Frequency					
					Maximum			Minimum		
Individual		Mean	SE	CV	Mean	SE	S	Mean	SE	S
Male	1	995	65	9.2	580	20	28	570	20	28
Female	1	1456	104	21.6	542	8	23	467	7	20
	4	1040	40	5.4	600	0	0	540	40	57
	8	986	98	19.8	594	4	8	540	8	15
	9	1047	124	20.4	560	12	20	560	12	20
Unidentified sex		937	100	28.3	587	11	32	530	14	42
		1160	74	21.2	509	15	49	418	23	75

PART B. Behavioural Contexts of Vocalizations of the Japanese Brown Hawk Owl

Percentages of occurrences of observed behaviour are listed for the three phases of vocal occasions: PR, preceding phase; SI, simultaneous phase; FO, following phase. The result is shown for total individuals (T), males (M) and females (F). Occurrences between zero and one percentage are indicated by "0". Those with a probability level of less than 0.05 (binominal test) are underlined. Sample numbers are as follows:-

for 'k.hoo'

	Sexes		
Phase	T	M	F
PR	446	258	8
SI	612	313	13
FO	522	285	10

for 'hoh'

	Sexes		
Phase	T	M	F
PR	140	65	23
SI	206	73	28
FO	157	64	25

for 'hyu'

	Sexes (1976-1978)		
Phase	T	M	F
PR	33	9	11
SI	47	9	10
FO	40	9	10

	Sexes (1979-1981)		
Phase	T	M	F
PR	41	35	6
SI	41	35	6
FO	41	35	6

for 'krrr'

	Sexes		
Phase	T	M	F
PR	346	103	139
SI	381	106	144
FO	374	103	149

Behaviour codes used for the analysis of the context of vocalizations are listed below:-

CO	Confront rivals
AT	Attack rivals
RET	Retreat from rivals
O(v)	Neighbouring territorial males or rivals produced vocalization, v
A0	Perch within 20 m from the mate
A1	Perch within 1 m from the mate
A2	Feed the mate
A3a	Mount
A3b	Copulate
A4	Preen the mate
A5	Approach the stationary mate
A6	Approach the flying mate
A7	Fly with the mate
A8	Fly away from the mate
AE	Chase the mate with physical contacts
M(v)	The mate produced vocalization, v
N1	Fly to/around the nest
N2	Enter the nest
N3	Stay in the nest
N4	Stay near the nest
N5	Leave the nest
m	A postfixed symbol for N1-N5 to indicate that the mate is in the nest

FLY	Fly to a fledgling
SY	Stay with a fledgling
DY	Fly away from a fledgling
FY	Feed a fledgling

FP	Fly to the parent
HM	Juveniles bobbed their heads
YFD	Juveniles were near or on the ground and were approached by a potential enemy
J(v)	Juveniles produced vocalization, v

H	Hunt
HF	Hold food
PF	Prepare food
E	Eat
PRE	Preen
R	Rest with the eyes closed
P	Perch with the eyes open
L	Look around
AL	Alert
F	Fly and jump
-	A prefixed symbol for the behaviour codes listed above to indicate non-caller's behaviour

B-1. Behavioural contexts of 'k.hoo'

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
CO	1	2	0	1	3	0	0	0	0
AT	0	0	0	0	0	0	1	2	0
RET	0	1	0	0	0	0	0	0	0
O(k.hoo)	9	13	0	18	26	8	6	10	0
A0	13	10	38	17	13	46	9	8	20
A1	6	7	13	6	8	8	5	6	10
A2	0	0	0	0	0	0	0	0	0
A5	3	5	13	1	1	0	3	4	10
-A5	1	0	0	0	0	0	4	3	0
A6	0	0	0	0	0	0	0	0	0
-A6	0	0	0	0	0	0	0	0	0
A7	1	0	0	0	0	0	2	1	0
A8	1	1	0	0	0	0	2	2	10
AE	0	0	0	0	0	0	0	0	0
M(k.hoo)	4	0	13	15	4	77	3	1	0
N1	4	3	0	2	1	0	3	3	10
N2	0	0	0	0	0	0	1	0	0
N3	0	0	0	1	1	0	0	0	0
N4	12	7	13	21	13	23	11	8	20
N5	1	0	0	0	0	0	1	1	0
N1m	2	3	0	0	0	0	1	1	0
N2m	0	0	0	0	0	0	0	0	0
N3m	0	0	0	0	0	0	0	0	0
N4m	5	5	0	4	7	0	4	5	0
N5m	0	0	0	0	0	0	0	0	0

B-1 (continued)

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
FLY	0	0	0	0	0	0	0	0	0
SY	0	0	0	1	0	0	1	0	0
DY	0	0	0	0	0	0	0	0	0
FY	0	0	0	0	0	0	0	0	0
FP	0	0	0	0	0	0	1	0	0
HM	0	0	0	0	0	0	0	0	0
J(leee & gililili)	0	0	0	2	0	0	5	0	0
H	3	2	13	0	0	0	2	3	0
HF	0	0	0	1	1	0	1	0	0
PF	0	0	0	0	0	0	0	0	0
E	1	1	13	0	0	0	1	1	0
PRE	1	1	0	0	0	0	0	0	0
P	24	31	0	33	39	23	11	8	30
L	5	6	0	4	5	0	5	6	0
F	21	19	13	2	0	0	24	22	10

B-2. Behavioural contexts of 'hoh'

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
A0	15	20	17	33	33	36	21	22	28
A1	6	6	4	21	8	39	15	8	12
A2	0	0	0	1	1	4	4	9	0
A3a	0	0	0	0	0	0	3	5	8
A5	22	31	13	2	5	0	5	9	4
-A5	9	3	30	0	0	0	3	3	4
A6	0	0	0	0	0	0	1	2	0
-A6	1	0	4	0	0	0	1	0	0
A7	3	2	4	0	0	0	3	2	4
A8	2	2	4	2	4	0	11	11	20
AE	3	0	5	0	0	0	1	0	0
M(k.hoo)	4	3	4	33	27	61	3	2	0
N1	22	25	13	0	0	0	2	5	0
N2	1	0	0	6	7	0	4	3	8
N3	1	2	0	2	3	0	3	6	0
N4	20	32	0	44	49	14	20	27	4
N5	4	3	0	1	3	0	8	8	0
N1m	7	14	0	0	0	0	0	0	0
N2m	1	0	0	1	4	0	3	5	0
N3m	1	2	0	1	3	0	2	5	0
N4m	6	12	0	7	14	0	6	13	0
N5m	1	2	0	1	3	0	3	6	0
SY	1	0	4	1	0	4	0	0	0
FP	1	0	0	0	0	0	1	0	0
J(lee & gilililili)	0	0	0	0	0	0	1	0	0

B-2 (continued)

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
H	2	3	0	0	1	0	1	2	0
HF	5	6	0	5	8	0	3	3	4
-HF	1	0	0	0	0	0	0	0	0
PF	1	3	0	0	0	0	0	0	0
E	1	2	0	0	0	0	2	3	0
PRE	0	0	0	0	1	0	0	0	0
R	0	0	0	0	0	0	1	2	0
P	2	0	4	3	1	4	4	3	4
L	0	0	0	0	0	0	1	2	0
F	6	3	0	0	1	0	8	9	4

B-3. Behavioural contexts of 'hyu' (a) Observations during 1976–1978

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
RET	3	11	0	0	0	0	0	0	0
O(k.hoo)	0	0	0	6	11	0	3	11	0
A0	6	11	0	15	33	0	13	33	0
A1	3	0	0	4	0	10	3	0	0
A5	12	22	9	0	0	0	0	0	0
-A5	0	0	0	0	0	0	3	11	0
A6	0	0	0	0	0	0	3	0	0
A7	0	0	0	0	0	0	5	0	10
M(k.hoo)	3	0	10	13	0	10	3	0	0
N1	30	78	9	0	0	0	3	0	10
N2	0	0	0	2	0	0	3	0	0
N3	3	0	0	2	0	0	0	0	0
N4	21	11	18	45	89	30	25	56	10
N5	3	0	9	0	0	0	13	33	0
N1m	6	22	0	0	0	0	0	0	0
N4m	3	11	0	6	33	0	8	33	0
FLY	6	0	18	6	0	10	0	0	0
SY	6	0	18	13	0	40	8	0	30
DY	3	0	0	0	0	0	0	0	0
FY	0	0	0	0	0	0	10	0	20
J(leee & gililili)	0	0	0	4	0	0	13	0	10
H	3	0	9	0	0	0	0	0	0
HF	6	0	9	9	0	10	8	11	0
PF	3	0	0	0	0	0	0	0	0
P	0	0	0	9	0	0	3	0	0
F	15	0	9	2	0	10	10	0	0

B-3 (continued) (b). Obsrvations during 1979-1981

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
A0	0	0	0	2	0	0	0	0	0
A1	2	3	0	2	0	0	2	3	0
A2	0	0	0	0	0	0	20	23	0
A5	0	0	0	20	0	0	2	3	0
-A5	0	0	0	0	0	0	7	6	17
A8	2	0	17	0	0	0	0	0	0
M(k.hoo)	2	0	17	2	0	0	2	0	17
M(krrr)	0	0	0	0	0	0	2	3	0
N1	5	3	17	0	0	0	2	3	0
N2	0	0	0	0	0	0	2	0	17
N4	0	0	0	5	0	0	7	9	0
N2m	0	0	0	5	0	0	17	20	0
N3m	0	0	0	0	0	0	5	3	17
N4m	22	26	0	29	0	0	7	9	0
FLY	2	3	0	0	0	0	5	3	17
SY	2	0	17	5	0	0	2	3	0
FY	0	0	0	0	0	0	5	0	33
FP	0	0	0	0	0	0	2	3	0
J(leee & gililili)	2	0	17	0	0	0	2	3	0
H	41	43	33	0	0	0	2	3	0
HF	12	11	17	56	0	0	27	29	17
PF	7	9	0	2	0	0	0	0	0
E	0	0	0	0	0	0	2	3	0
P	20	20	17	20	0	0	12	11	17
L	0	0	0	2	0	0	0	0	0

Note: The binominal test was not applied to these results.

B-4. Behavioural contexts of 'krrr'

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
O(k.hoo)	0	0	1	0	0	1	0	0	1
A0	27	43	28	34	56	36	30	53	31
A1	3	4	4	8	10	3	5	8	5
A2	0	0	0	1	0	2	1	0	2
A4	1	1	1	1	2	2	0	0	1
A5	9	12	9	4	5	8	3	3	2
-A5	4	4	6	2	2	3	3	2	3
A6	0	0	0	0	0	0	0	0	0
-A6	0	0	0	0	0	0	0	0	0
A7	0	0	0	0	0	0	1	1	1
A8	3	4	4	1	1	3	4	4	3
AE	0	0	0	1	1	1	0	1	0
M(k.hoo)	1	0	4	8	12	10	1	1	2
N1	11	12	11	5	6	5	3	3	3
N2	1	0	1	2	1	2	8	2	12
N3	1	0	2	1	0	2	1	0	2
N4	42	62	42	59	75	60	43	70	46
N5	3	2	3	1	1	1	2	2	2
N1m	1	3	0	1	2	0	0	0	0
N2m	0	0	0	1	0	0	0	0	0
N3m	0	0	0	0	0	0	0	0	0
N4m	3	10	1	4	12	1	4	13	1
N5m	0	0	0	0	1	0	1	0	0
FLY	3	0	1	0	0	0	2	1	1
SY	1	0	0	4	1	3	1	1	1
DY	1	1	1	0	0	0	1	0	0
FY	0	0	0	0	0	0	3	1	1

B-4 (continued)

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
FP	0	0	0	0	0	0	0	0	1
HM	0	0	0	0	0	0	0	0	0
J(leee & gilililі)	0	0	0	0	0	0	3	0	2
H	5	7	4	0	0	0	3	2	5
HF	7	2	6	10	5	11	7	1	12
-HF	2	0	4	2	1	1	0	0	0
PF	3	5	0	2	1	1	0	0	0
E	1	0	2	0	0	0	2	0	4
PRE	3	7	5	2	6	0	3	8	1
R	0	0	0	0	0	0	0	1	0
P	4	0	3	7	3	6	5	0	3
L	1	0	1	0	0	0	1	1	1
F	7	7	8	2	2	0	7	4	5

B-5. Behavioural contexts of 'mew' and 'meeew'

	Mew			Meeew		
Behaviour	PR	SI	FO	PR	SI	FO
CO	0	0	0	0	1	0
AT	0	0	0	1	0	0
O(k.hoo)	0	0	0	2	0	1
O(buf)	1	0	1	0	0	0
A5	0	0	0	0	0	2
M(k.hoo)	0	0	0	1	0	0
M(krrr)	1	0	0	0	0	0
RM1	0	1	1	2	5	2
RM2	1	0	0	7	7	8
RM3	1	1	0	2	2	2
RM(k.hoo)	0	0	0	7	4	4
RM(hoh)	0	0	0	1	0	1
RM(oo.coo)	0	0	0	2	2	2
N1	0	0	0	5	1	0
N2	0	0	0	0	0	1
N4	0	2	2	4	7	5
N5	3	0	0	2	0	2
N4m	0	0	0	2	0	1
YFD	4	4	4	0	0	0
OS1	0	0	0	6	6	7
OS2	0	0	0	3	3	3
OS3	0	0	0	1	1	1
OS4	2	2	2	0	0	0

Note: Number of occurrences is shown. RM1, A widowed female (caller) was chased by a replacing male; RM2, A replacing male stayed

B-5 (continued)

near the nest of a widowed female (caller); RM3, A replacing male was near a widowed female (caller); RM(v), A replacing male produced vocalization, v; OS1, the presence of Strix uralensis; OS2, the presence of Milvus migrans; OS3, the presence of Nycticorax nycticorax; OS4, wailing noises from an unidentified bird.

B-6. Behavioural contexts of 'hooh'

Behaviour	PR	SI	FO
A1	5	11	11
A5	5	5	0
-A6	0	0	5
N1	16	16	5
N2	0	5	11
N3	0	0	5
N4	11	5	16
SY	5	5	0
FY	0	0	42
J(leee & gilililí)	5	5	5
H	53	0	0
HF	0	53	0

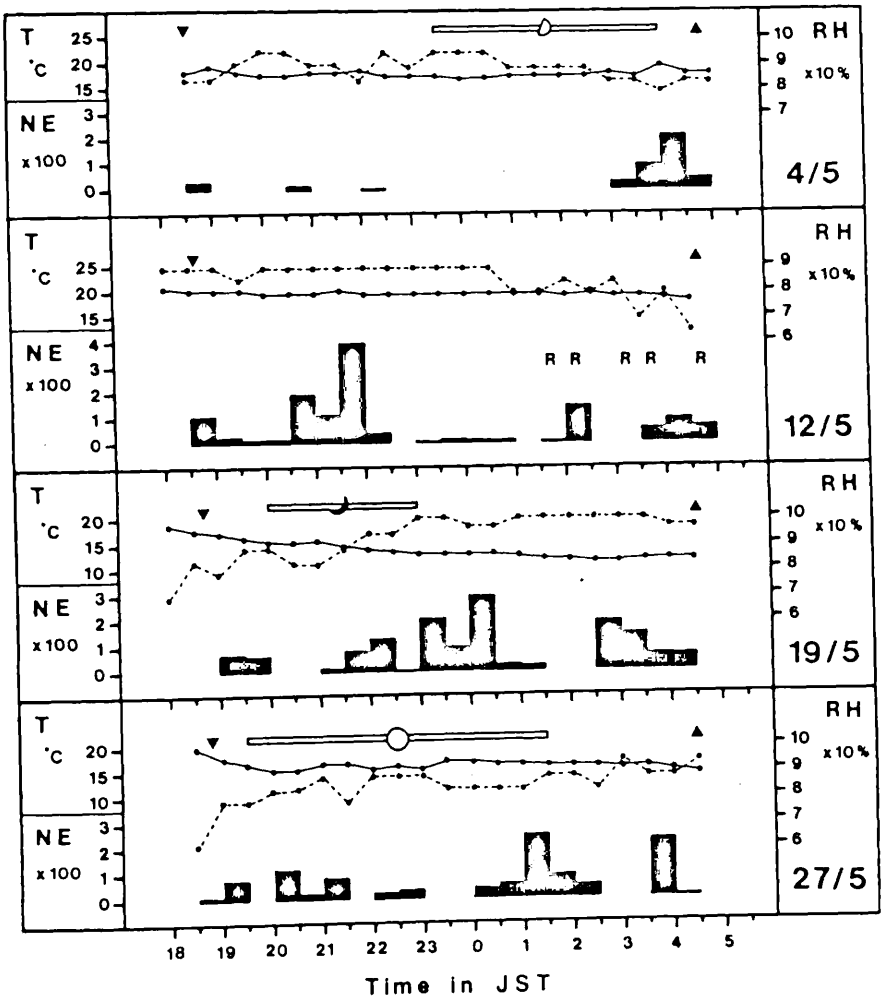
Note: Samples are taken from observations during 1979-1981. Sample number was 19. The binominal test was not applied.

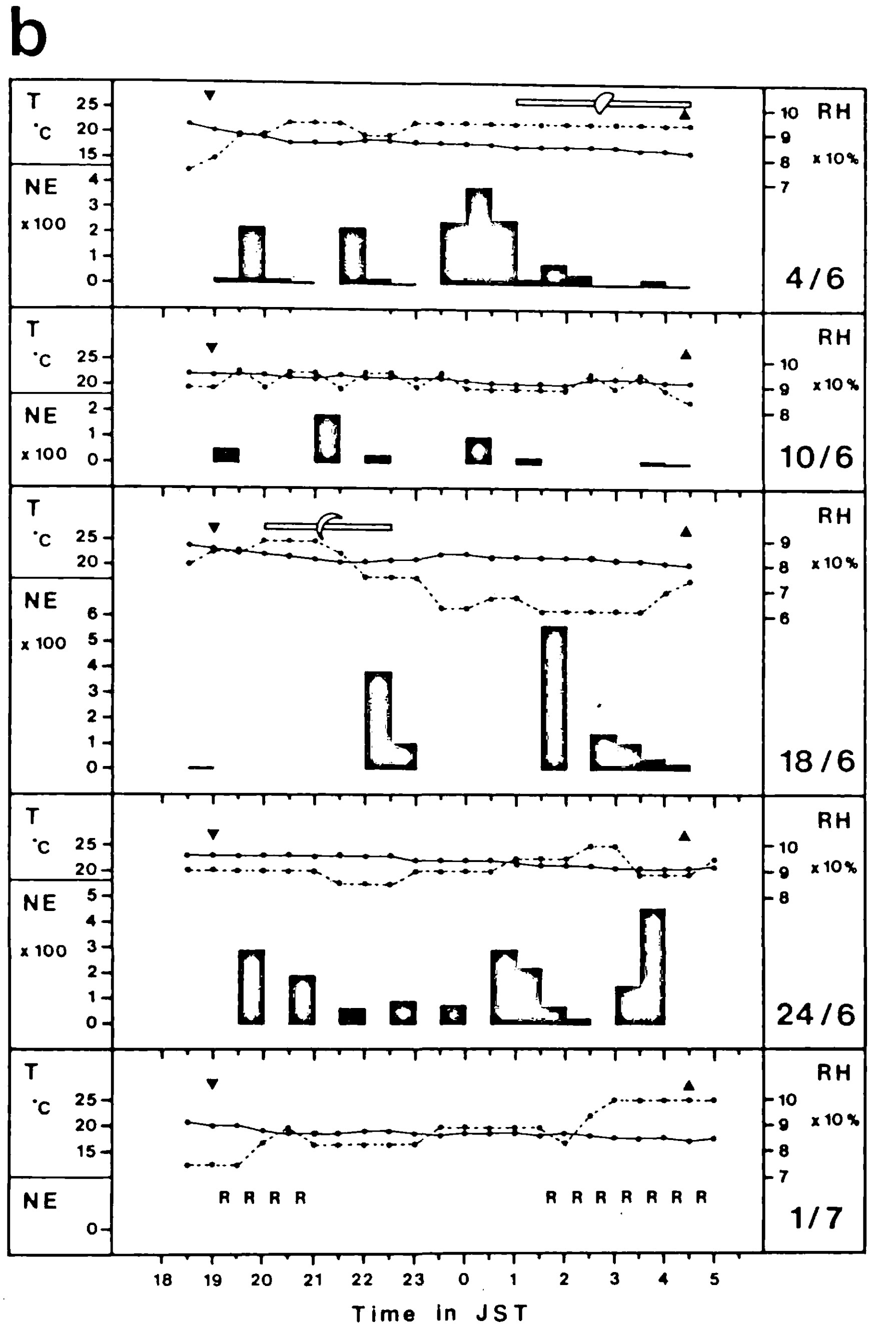
PART C. Primary Call Production of the Japanese Brown Hawk Owl

C-1. Nocturnal patterns of primary call production of the original and replacing males at Zushi in 1980

Number of primary call elements (NE) produced from 18:00 to 5:30 Japanese Standard Time (JST) is shown in histograms. Also included in the figures are the environmental conditions such as time of sunset (▼) and sunrise (▲), the age and appearance of the moon (e.g. ═○═ , full moon), rainfall (R), ambient temperature (T, solid line), and relative humidity (RH, broken line). On July 31, temperature could not be measured due to the heavy rain. Subjects and breeding stages in respective figures are as follows: (a) the original male during the pre-incubation stage; (b) the original male from the incubation to early nestling stage; (c) the replacing male during the nestling stage; (d) the replacing male from the fledgling stage (July 31 - September 1) to post-breeding stage.

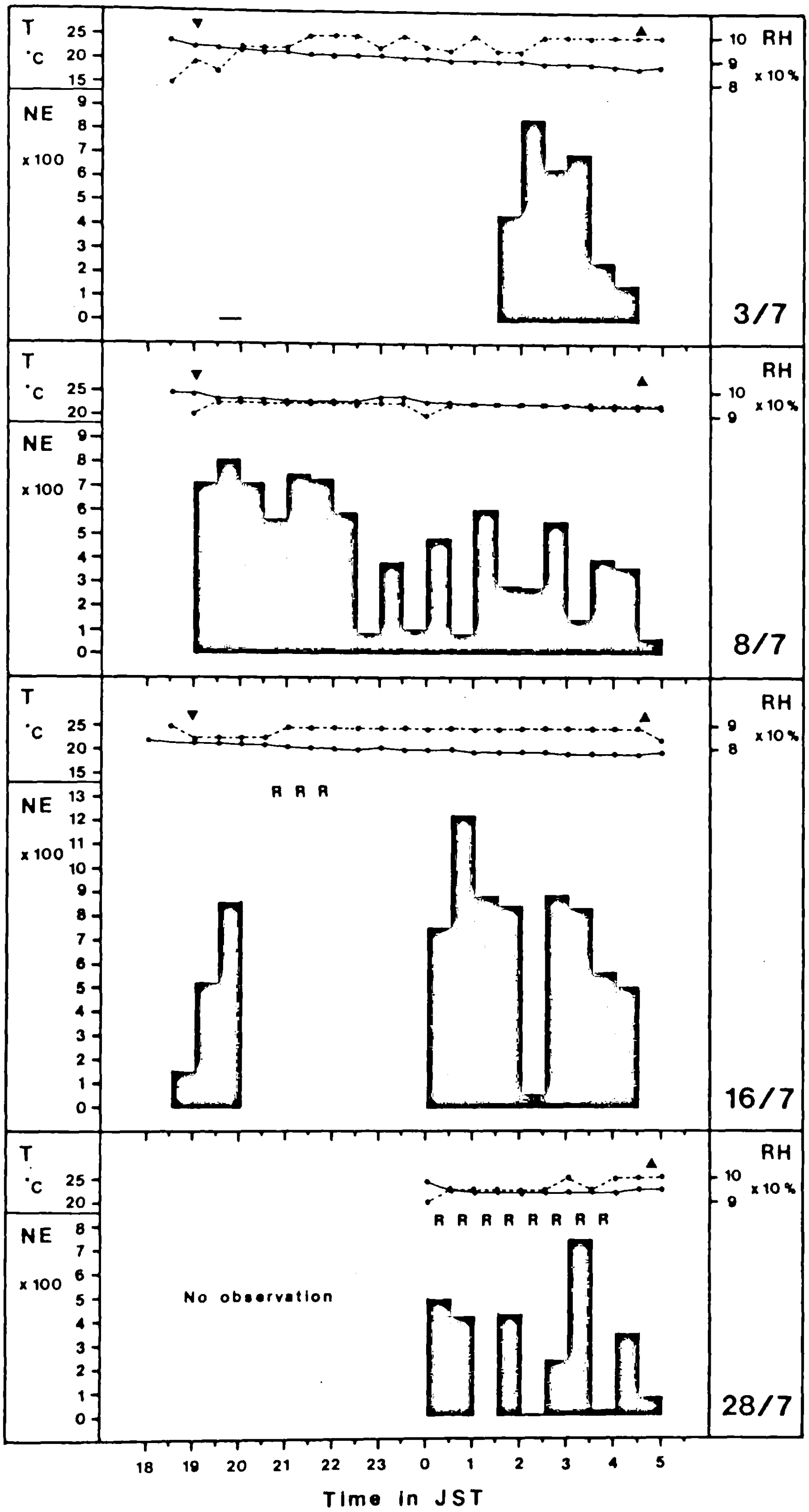
a



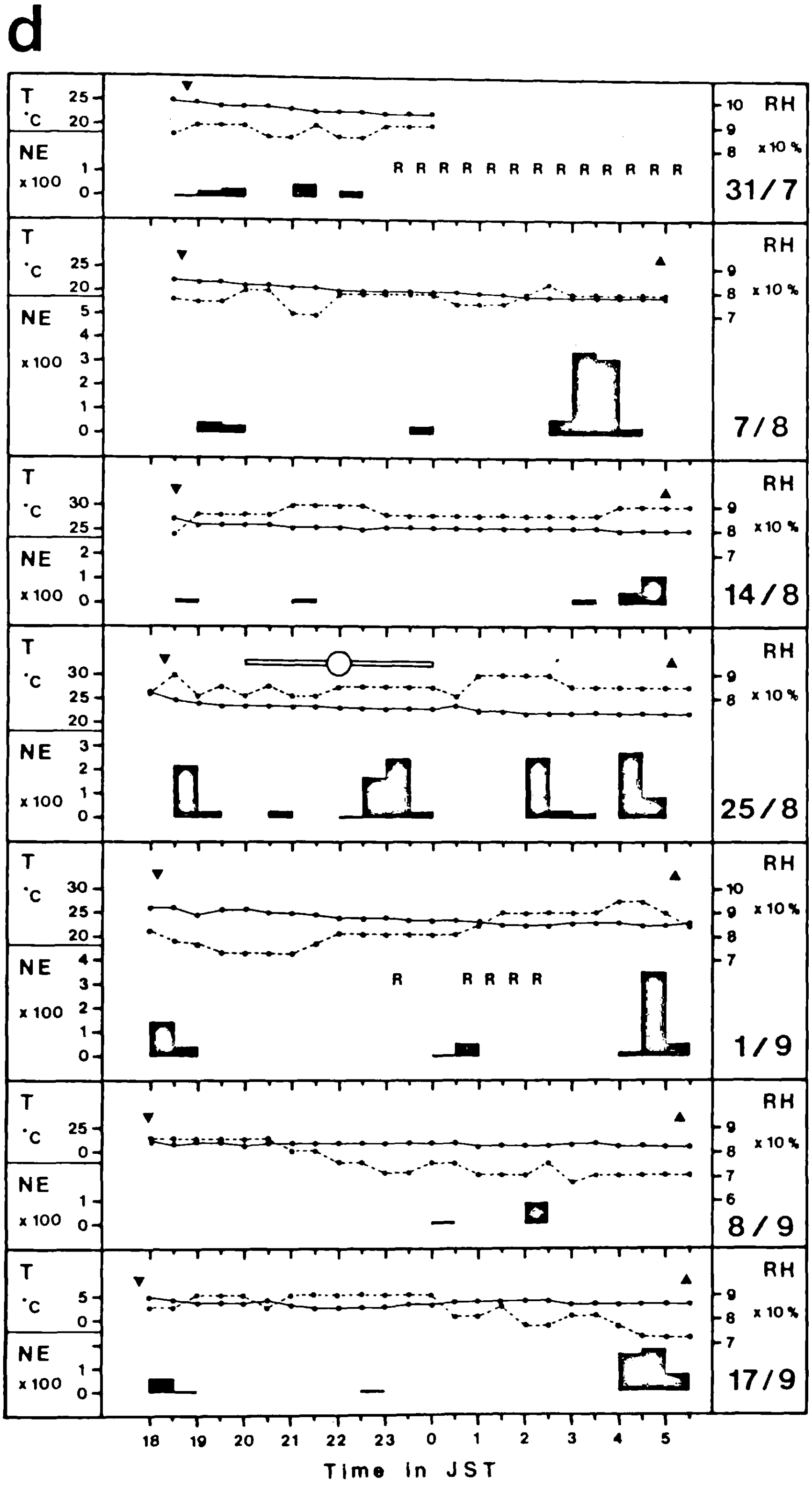


C-1 (continued)

C



C-1 (continued)



C-1 (continued)

C-2. Conspecific environment of primary call production

Number of primary call elements produced in the ten-minute period is given for the following conspecific environment:-

▭ , No other conspecifics produced primary calls.
▣ , The mate of the original male produced primary calls.
░ , Conspecifics produced primary calls.
▦ , Conspecifics invaded the territory.
$\boxed{m}$, The mate of the original male produced 'meeew'.
▭ , The mate of the original male was within 20 m.

Subjects and breeding stages in respective figures are as follows:-

(1) The original male during the pre-incubation stage.
(2) The original male during the incubation stage.
(3) The replacing male during the vocal accentuation.
(4) The replacing male after the vocal accentuation.

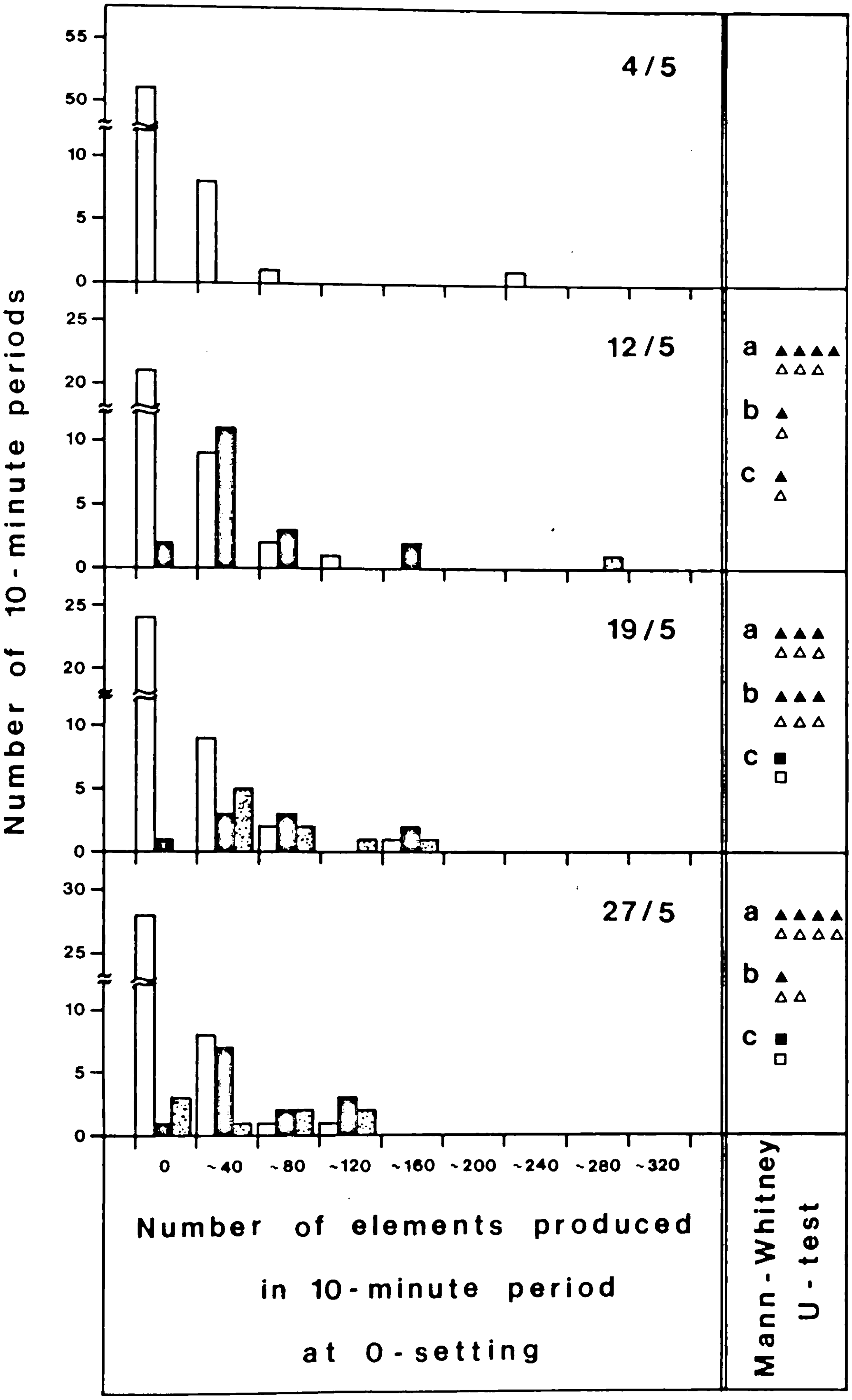
Mann-Whitney U-test was carried out to examine whether the subject produced more primary calls in the following conditions:-

(a) When the mate of the original male produced primary calls than when no other conspecifics did.
(b) When conspecifics produced primary calls than when no other conspecifics did.
(c) When conspecifics produced primary calls than when the mate of the original male did.
(d) When conspecifics invaded the territory than when they neither invaded it nor emitted primary calls.
(e) When the mate of the original male was within 20 m than when other conspecifics were neither within 20 m nor emitted primary calls.
(f) When the mate of the original male called 'meeew' than when other conspecifics called neither 'meeew' nor primary calls.

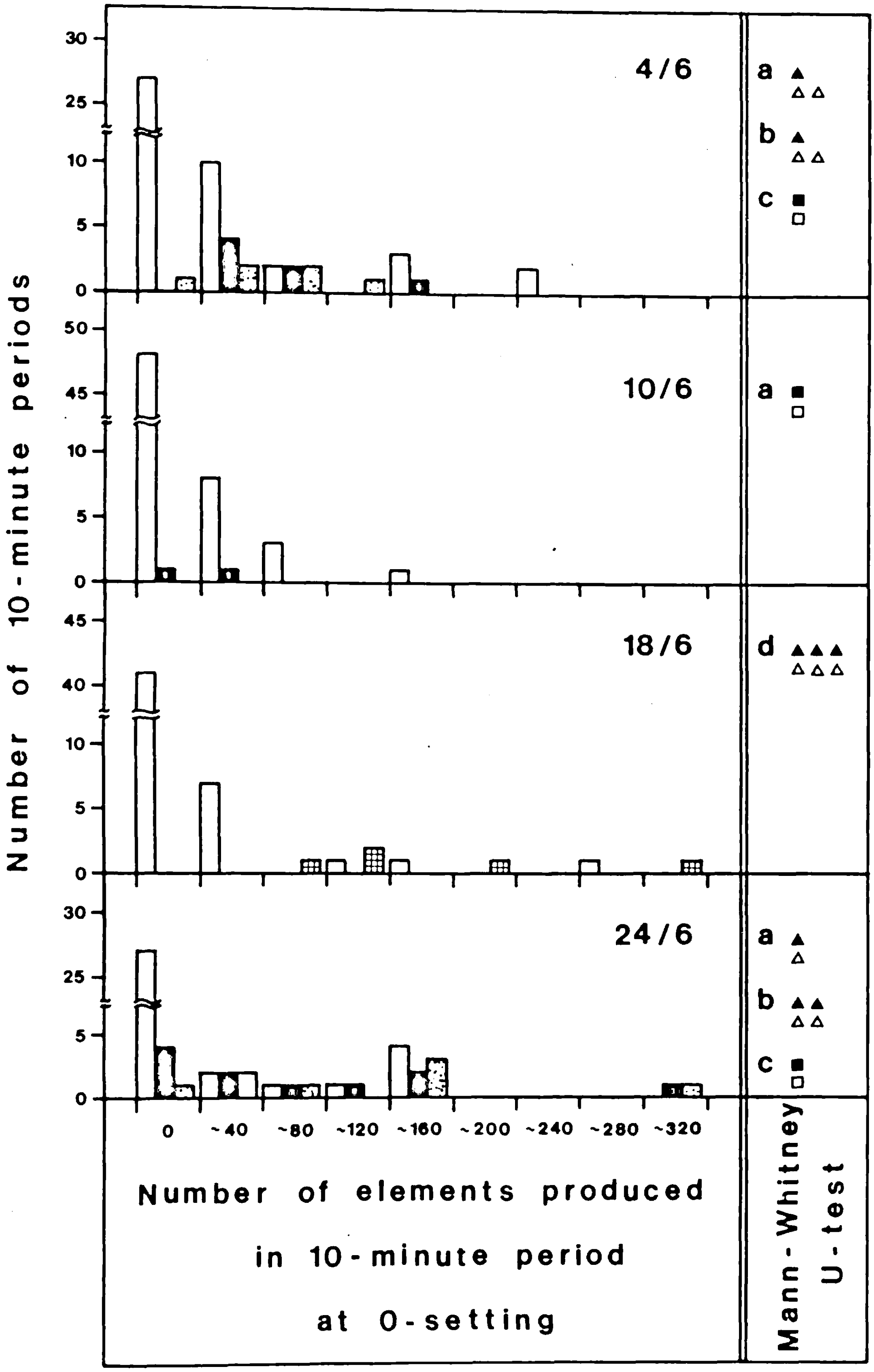
Significance levels are indicated by black symbols for 0-setting and white symbols for 5-setting as follows:

$p < 0.0001$ by four triangles
$p < 0.001$ by three triangles
$p < 0.01$ by two triangles
$p < 0.05$ by one triangle
$p \geq 0.05$ (not significant) by a square

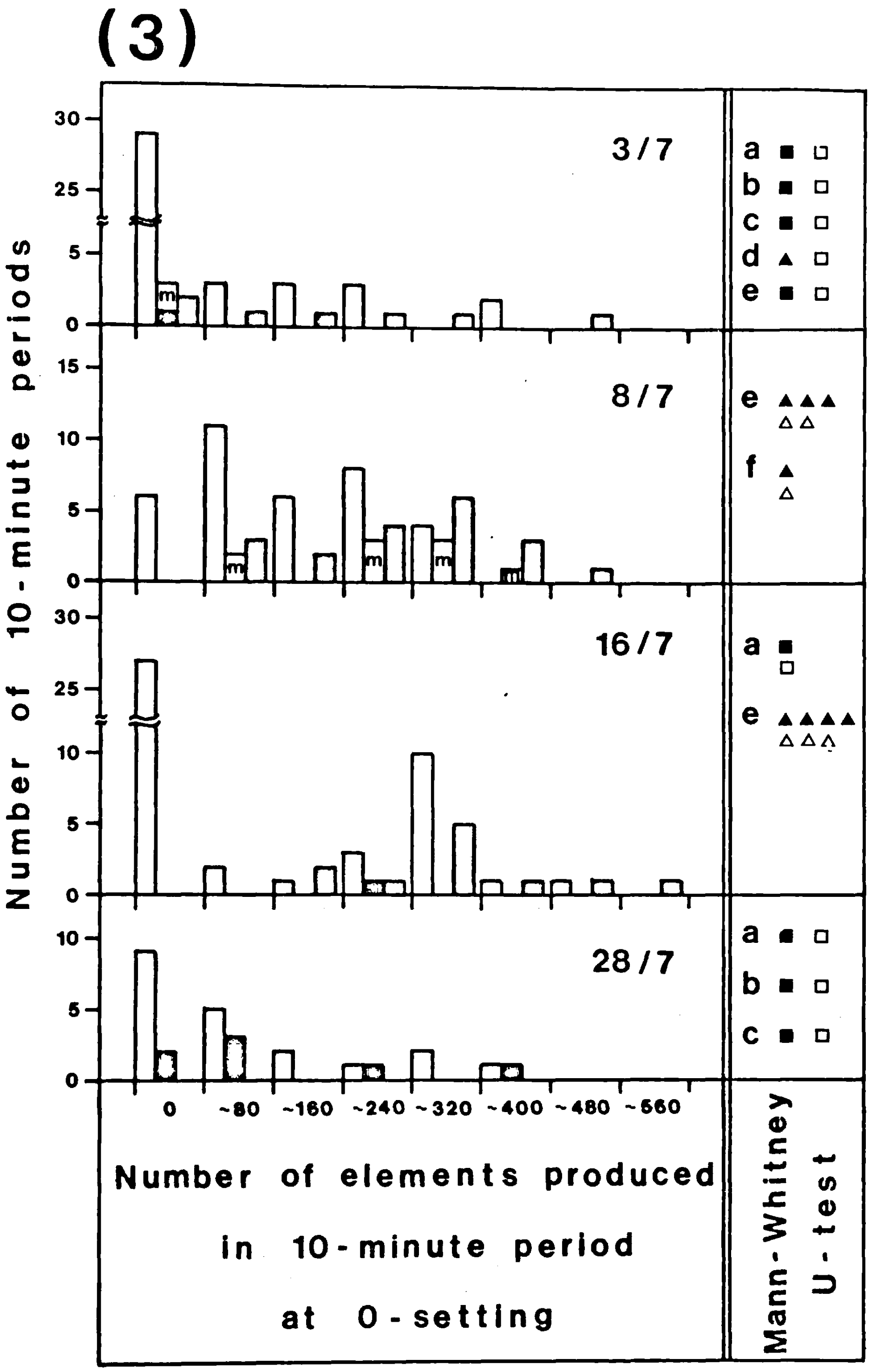
(1)


4/5
12/5
19/5
27/5
Number of 10-minute periods
55
50
10
5
0
25
20
30
0
~40
~80
~120
~160
~200
~240
~280
~320
Number of elements produced in 10-minute period at 0-setting
a ▲▲▲▲ △△△
b ▲ △
c ▲ △
a ▲▲▲ △△△
b ▲▲▲ △△△
c ■ □
a ▲▲▲▲ △△△△
b ▲ △△
c ■ □
Mann-Whitney U-test

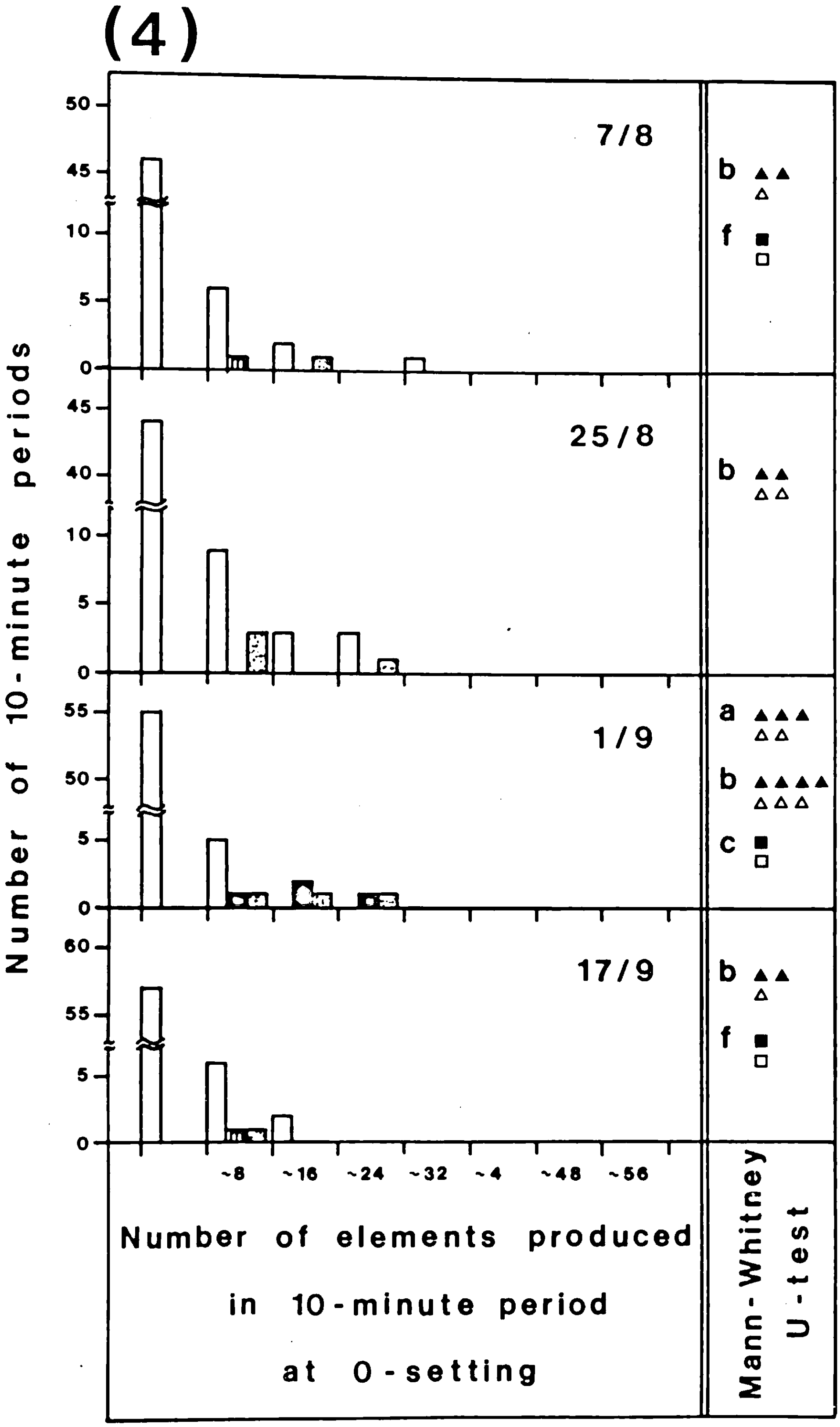
(2)



C-2 (continued)



C-2 (continued)



C-2 (continued)

PART D. Effects of Speaker's Location in the Territory and Breeding Stage (Two-way ANOVA Tables)

Symbols: df, degrees of freedom; SS, sums of squares; MS, mean squares; F_s, sample statistics of F-distribution.

Probability: ***, $p < 0.01$; **, $p < 0.025$; *, $p < 0.05$; ns, $p \geq 0.05$ (not significant)

D-1. Latency of response and speaker's location in the territory

a. Pre-incubation stage

Source of variation	df	SS	MS	F_s
Individuals	4	1446.9	361.7	0.797^{ns}
Locations	2	688.9	344.5	0.759^{ns}
Error	8	3633.1	454.1	
Total	14	5768.9		

b. Fledgling stage

Source of variation	df	SS	MS	F_s
Individuals	4	592.9	148.2	0.259^{ns}
Locations	1	1338.4	1338.4	2.338^{ns}
Error	4	2289.6	572.4	
Total	9	4220.9		

D-2. Latency of response and breeding stage

a. Central location

Source of variation	df	SS	MS	F_s
Individuals	4	4261.3	1065.3	0.849^{ns}
Breeding stages	2	1161.7	580.9	0.463^{ns}
Error	8	10042.3	1255.3	
Total	14	15465.3		

b. Middle location

Source of variation	df	SS	MS	F_s
Individuals	4	3422.6	855.7	9.137*
Breeding stages	1	230.4	230.4	2.460^{ns}
Error	4	374.6	93.7	
Total	9	4027.6		

D-3. Number of flights and speaker's location in the territory

a. Pre-incubation stage: the first playback period

Source of variation	df	SS	MS	F_s
Individuals	4	46.9	11.7	9.142***
Locations	2	24.4	12.2	9.506***
Error	8	10.3	1.3	
Total	14	81.6		

b. Pre-incubation stage: the second playback period

Source of variation	df	SS	MS	F_s
Individuals	4	20.9	5.2	1.570^{ns}
Locations	2	10.0	5.0	1.570^{ns}
Error	8	26.7	3.3	
Total	14	57.6		

c. Fledgling stage: the playback period

Source of variation	df	SS	MS	F_s
Individuals	4	4.6	1.2	0.237^{ns}
Locations	1	0.1	0.1	0.021^{ns}
Error	4	19.4	4.9	
Total	9	24.1		

D-4. Number of flights and breeding stage

a. Central location: the first playback period

Source of variation	df	SS	MS	F_s
Individuals	4	11.0	2.8	0.337^{ns}
Breeding stages	1	14.4	14.4	1.767^{ns}
Error	4	32.6	8.2	
Total	9	58.0		

b. Middle location: the first playback period

Source of variation	df	SS	MS	F_s
Individuals	4	12.3	3.1	2.244***
Locations	2	5.7	2.9	2.098^{ns}
Error	8	10.9	1.4	
Total	14	28.9		

D-5. Nearest distance from speaker and the speaker's location in the territory

a. Pre-incubation stage: the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	14	29062.6	2075.8	7.663***
Individuals (A)	4	8238.5	2059.6	7.602***
Individuals (B)	2	7215.0	3007.5	11.100***
Interaction (A x B)	8	13609.1	1701.1	6.279***
Within subgroups	45	12192.4	270.9	
Total	59	41255.0		

b. Pre-incubation stage: the second playback period

Source of variation	df	SS	MS	F_s
Individuals	4	1306.3	326.6	1.457^{ns}
Locations	2	140.8	70.4	0.314^{ns}
Error	8	1792.5	224.1	
Total	14	3239.6		

c. Fledgling stage: the playback period

Source of variation	df	SS	MS	F_s
Subgroups	9	9142.9	1015.9	30.599***
Individuals (A)	4	1425.4	356.4	10.723***
Locations (B)	1	3132.9	3132.9	94.270***
Interaction (A x B)	4	4584.6	1146.2	34.388***
Within subgroups	30	997.0	33.2	
Total	39	10139.9		

D-6. Nearest distance from speaker and breeding stage

a. Central location: the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	9	2251.3	250.1	8.346***
Individuals (A)	4	728.8	182.2	6.078***
Breeding stages (C)	1	522.0	522.0	17.416***
Interaction (A x C)	4	1000.5	250.1	8.345***
Within subgroups	30	899.2	30.0	
Total	39	3150.5		

b. Middle location: the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	14	20493.1	1463.8	8.360***
Individuals (A)	4	9536.8	2384.2	13.620***
Breeding stages (C)	2	4645.2	2322.6	13.268***
Interaction (A x C)	8	6311.1	788.9	4.507***
Within subgroups	45	7877.5	175.1	
Total	59	28370.6		

D-7. Number of primary and graded call elements and speaker's location in the territory

a. Pre-incubation stage: the first playback and its post-play period

Source of variation	df	SS	MS	F_s
Subgroups	14	13973.3	998.1	3.672*
Individuals (A)	4	3694.9	923.7	3.398**
Locations (B)	2	6453.3	3226.7	11.872***
Interaction (A x B)	8	3825.1	478.1	1.759^{ns}
Within subgroups	105	28540.6	271.8	
Total	119	42513.9		

b. Pre-incubation stage: the second playback and its post-play period

Source of variation	df	SS	MS	F_s
Subgroups	14	7174.3	512.5	2.716**
Individuals (A)	4	493.5	123.4	0.654^{ns}
Locations (B)	2	3279.3	1639.6	8.688***
Interaction (A x B)	8	3401.5	425.2	2.253^{ns}
Within subgroups	28	5284.0	188.7	
Total	42	12458.3		

c. Fledgling stage: the playback period

Source of variation	df	SS	MS	F_s
Subgroups	9	6308.0	700.9	3.407***
Individuals (A)	4	1936.9	484.2	2.354^{ns}
Locations (B)	1	680.6	680.6	3.308^{ns}
Interaction (A x B)	4	3690.5	922.6	4.485***
Within subgroups	30	6171.8	205.7	
Total	39	12479.8		

D-8. Number of primary and graded call elements and breeding stage

a. Central location: the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	9	6445.0	716.1	3.177***
Individuals (A)	4	4346.4	1086.6	4.821***
Breeding stages (C)	1	765.6	765.6	3.397^{ns}
Interactions (A x C)	4	1333.0	333.3	1.479^{ns}
Within subgroups	30	6761.8	225.4	
Total	39	13206.8		

b. Central location: the first post-play period

Source of variation	df	SS	MS	F_s
Subgroups	9	12064.9	1340.5	13.233***
Individuals (A)	4	4956.8	1239.2	178.986***
Breeding stages (C)	1	6916.9	6916.9	68.315***
Interactions (A x C)	4	191.2	47.8	0.472^{ns}
Within subgroups	30	3037.5	101.3	
Total	39	15102.4		

c. Middle location: the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	14	11173.2	798.1	4.890***
Individuals (A)	4	3585.6	896.4	5.491***
Breeding stages (C)	2	472.4	236.2	1.447^{ns}
Interactions (A x C)	8	7115.2	889.4	5.449***
Within subgroups	45	7345.5	163.2	
Total	59	18518.7		

D-8 (continued)

Source of variation	df	SS	MS	F_s
Subgroups	14	12913.9	922.4	12.584***
Individuals (A)	4	2948.4	737.1	10.061***
Breeding stages (C)	2	1013.0	506.5	6.913***
Interactions (A x C)	8	8952.5	1119.1	15.274***
Within subgroups	45	3297.0	73.3	
Total	59	16210.9		

D-9. Speaker's location in the territory and difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls

a. Pre-incubation stage: the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	11	546249.5	49659.0	6.388***
Individuals (A)	3	41426.6	13808.9	1.776^{ns}
Locations (B)	2	300243.5	150121.7	19.310***
Interaction (A x B)	6	204579.4	34096.6	4.386***
Within subgroups	81	629727.0	7774.4	
Total	92	1175976.5		

b. Pre-incubation stage: the first two minutes of the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	11	281211.4	25564.7	2.393**
Individuals (A)	3	15641.7	5213.9	0.488^{ns}
Locations (B)	2	202680.5	101340.3	9.488***
Interaction (A x B)	6	62889.2	10481.5	0.981^{ns}
Within subgroups	34	363149.1	10680.9	
Total	45	644360.5		

c. Pre-incubation stage: the first post-play period

Source of variation	df	SS	MS	F_s
Subgroups	11	445133.5	40466.7	11.412***
Individuals (A)	3	407844.3	135948.1	38.338***
Locations (B)	2	13989.2	6994.6	1.972^{ns}
Interaction (A x B)	6	23300.0	3883.3	1.095^{ns}
Within subgroups	84	297870.7	3546.1	
Total	95	743004.2		

D-9 (continued)

d. Pre-incubation stage: the second playback period and the following one minute

Source of variation	df	SS	MS	F_s
Subgroups	8	156161.3	19520.2	3.715***
Individuals (A)	2	68405.1	34202.5	6.510***
Locations (B)	2	74297.8	37148.9	7.071***
Interaction (A x B)	4	13458.4	3364.6	0.640^{ns}
Within subgroups	27	141854.8	5253.9	
Total	35	298016.1		

e. Fledgling stage: the playback period

Source of variation	df	SS	MS	F_s
Subgroups	9	841425.0	93491.7	9.346***
Individuals (A)	4	696014.7	174003.7	18.325***
Locations (B)	1	47852.1	47852.1	5.040**
Interaction (A x B)	4	97558.2	24389.5	2.569*
Within subgroups	68	645683.3	9495.3	
Total	77	1487108.3		

f. Fledgling stage: the post-play period

Source of variation	df	SS	MS	F_s
Subgroups	9	586091.5	65121.3	52.666***
Individuals (A)	4	504548.2	126137.1	102.011***
Locations (B)	1	13536.0	13536.0	10.947***
Interaction (A x B)	4	68007.3	17001.8	13.750***
Within subgroups	70	86551.8	1236.5	
Total	79	672643.3		

D-10. Breeding stage and difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls

a. Central location: the initial two minutes of the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	9	212003.8	23556.0	2.939**
Individuals (A)	4	96537.8	24134.5	3.011*
Breeding stages (C)	1	1367.6	1367.6	0.170^{ns}
Interactions (A x C)	4	114098.4	28524.6	3.559*
Within subgroups	28	224396.7	8014.2	
Total	37	436400.5		

b: Central location: the last two minutes of the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	9	148947.0	13216.3	3.399***
Individuals (A)	4	69132.4	17283.1	4.444***
Breeding stages (C)	1	42211.0	42211.0	10.855***
Interaction (A x C)	4	37603.6	9400.9	2.417^{ns}
Within subgroups	30	116660.9	3888.7	
Total	39	265607.9		

c. Central location: the initial two minutes of the first post-play period

Source of variation	df	SS	MS	F_s
Subgroups	9	198203.0	22022.6	10.095***
Individuals (A)	4	109211.5	27302.9	12.515***
Breeding stages (C)	1	57912.1	57912.1	26.546***
Interaction (A x C)	4	31079.4	7769.9	3.562**
Within subgroups	30	65446.6	2181.6	
Total	39	263649.6		

d. Central location: the last two minutes of the first post-play period

Source of variation	df	SS	MS	F_s
Subgroups	9	115953.2	12883.7	9.246***
Individuals (A)	4	83266.1	20816.5	14.960***
Breeding stages (C)	1	4068.3	4068.3	2.919^{ns}
Interaction (A x C)	4	28618.8	7154.7	5.134***
Within subgroups	30	41805.1	1393.5	
Total	39	157758.3		

e. Middle location: the initial two minutes of the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	11	451014.9	41001.4	2.718***
Individuals (A)	3	123096.2	41032.1	2.720^{ns}
Breeding stages (C)	2	17966.4	8983.2	0.596^{ns}
Interaction (A x C)	6	309952.3	51658.7	3.425*
Within subgroups	36	543008.4	15083.6	
Total	47	994023.3		

D-10 (continued)

f. Middle location: the last two minutes of the first playback period

Source of variation	df	SS	MS	F_s
Subgroups	11	484534.2	44048.6	16.713***
Individuals (A)	3	113221.0	37740.3	14.319***
Breeding stages (C)	2	7891.0	3945.5	1.497^{ns}
Interaction (A x C)	6	363422.2	60570.4	22.982***
Within subgroups	36	94881.7	2635.6	
Total	47	579415.9		

g. Middle location: the first post-play period

Source of variation	df	SS	MS	F_s
Subgroups	11	737412.1	67037.5	26.269***
Individuals (A)	3	240070.9	80023.6	31.357***
Breeding stages (C)	2	80510.3	40255.2	15.774***
Interaction (A x C)	6	416830.9	69471.8	27.222***
Within subgroups	79	201608.4	2552.0	
Total	90	939020.5		

PART E. Inter-individual differences in primary calls

E-1. One-way ANOVA tables for inter-individual differences of physical features of primary calls

Symbols: df, degrees of freedom; SS, sum of squares; MS, mean squares; F_s, sample statistics of F-distribution; [ ], sample.

Probability: ***, $p < 0.01$.

a. Duration of part A

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	29295.8	4185.1	11.126***
Within groups	77	28963.0	376.1	
Total	84	58258.8		

[8 males and 3 females]

Source of variation	df	SS	MS	F_s
Among groups	10	46413.1	4641.3	15.704***
Within groups	98	28963.0	295.5	
Total	108	75376.1		

E-1 (continued)

b. Maximum frequency of part A

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	82247.5	11749.6	19.972***
Within groups	52	30592.5	588.3	
Total	59	112840.0		

[8 males and 2 females]

Source of variation	df	SS	MS	F_s
Among groups	9	326633.3	36292.6	68.077***
Within groups	63	36832.5	584.6	
Total	72	363465.8		

c. Minimum frequency of part A

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	351818.3	50259.8	53.472***
Within groups	100	93991.9	939.9	
Total	107	445810.2		

[8 males and 2 females]

Source of variation	df	SS	MS	F_s
Among groups	9	655282.0	72809.1	37.400***
Within groups	98	190784.7	1946.8	
Total	107	846066.7		

E-1 (continued)

d. Duration of part B

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	98799.4	14114.2	95.159***
Within groups	152	22545.0	148.3	
Total	159	121344.4		

[9 males and 6 females]

Source of variation	df	SS	MS	F_s
Among groups	14	59990.4	4285.0	24.213***
Within groups	165	29200.7	177.0	
Total	179	89191.1		

e. Maximum frequency of part B

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	248819.1	35545.6	130.653***
Within groups	150	40809.2	272.1	
Total	157	289628.3		

[9 males and 6 females]

Source of variation	df	SS	MS	F_s
Among groups	14	352607.5	25186.2	17.977***
Within groups	164	229765.7	1401.0	
Total	178	582373.2		

E-1 (continued)

f. Minimum frequency of part B

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	314366.4	44909.5	137.911***
Within groups	152	49497.6	325.6	
Total	159	363864.0		

[9 males and 6 females]

Source of variation	df	SS	MS	F_s
Among groups	14	745107.4	53222.0	55.003***
Within groups	165	159658.7	967.6	
Total	179	904766.1		

g. Short interval between the elements of a unit

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	105355.0	15050.7	90.004***
Within groups	72	12040.0	167.2	
Total	79	117395.0		

[9 males and 6 females]

Source of variation	df	SS	MS	F_s
Among groups	14	108359.6	7740.0	21.342***
Within groups	80	29013.0	362.7	
Total	94	137372.6		

E-1 (continued)

h. Long interval between units

[8 males]

Source of variation	df	SS	MS	F_s
Among groups	7	1101879.8	157411.4	12.747***
Within groups	69	852102.0	12349.3	
Total	76	1953981.8		

[8 males and 6 females]

Source of variation	df	SS	MS	F_s
Among groups	13	1092982.2	84075.6	8.008***
Within groups	48	503953.3	10499.0	
Total	61	1596935.5		

E-2. Comparison of physical features of part B between the first and second elements

				Frequency			
		Duration		Maximum		Minimum	
Male	Element	ms	t	Hz	t	Hz	t
1	First	167 ± 2		714 ± 4		607 ± 4	-2.429 *
	Second	166 ± 2		719 ± 3		617 ± 3	
2	First	207 ± 3	-2.425 *	726 ± 3	3.255 **	594 ± 4	
	Second	217 ± 2		712 ± 3		594 ± 9	
3	First	209 ± 2	-3.867 **	632 ± 9		528 ± 6	
	Second	222 ± 2		637 ± 8		531 ± 6	
4	First	184 ± 8		651 ± 10		560 ± 5	
	Second	193 ± 5		664 ± 7		566 ± 5	
5	First	199 ± 2	1.715 *	768 ± 3	3.075 **	658 ± 3	-6.565 ***
	Second	190 ± 3		757 ± 3		683 ± 2	

E-2 (continued)

		Duration		Frequency			
				Maximum		Minimum	
Male	Element	ms	t	HZ	t	Hz	t
6	First	183 ± 3		686 ± 2		573 ± 11	
	Second	180 ± 3		684 ± 2		579 ± 7	
7	First	132 ± 5		690 ± 4		629 ± 6	
	Second	133 ± 7		685 ± 3		629 ± 5	
8	First	178 ± 2		742 ± 3	2.222 *	653 ± 2	
	Second	173 ± 2		733 ± 3		656 ± 0	

Note: Significant results of _t_-test are given with significant levels: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. Degrees of freedom (df) is 18, except for the maximum frequency of male 6 where df is 16.

PART F. Individual recognition by male primary calls: response to playback (two-way ANOVA tables including planned comparisons between strange and neighbouring territorial males' primary calls and also between the normal and opposite locations of the speaker by *a priori* test)

Symbols: df, degrees of freedom; SS, sums of squares; MS, mean squares; F_s, sample statistics of F-distribution; S, strange males' primary calls; NN, neighbours' primary calls at the normal location; NO, neighbours' primary calls at the opposite location.

Probability: ***, $p < 0.01$; **, $p < 0.025$; *, $p < 0.05$; ns, $p \geq 0.05$.

F-1. Latency of response

a. Experiment I

Source of variation	df	SS	MS	F_s
Playback conditions	2	62452.1	31226.1	15.650***
S vs. NN	1	42120.1	42120.1	21.110***
NN vs. NO	1	51122.5	51122.5	25.622***
S vs. NO	1	435.6	435.6	0.218^{ns}
Test males	4	9584.9	2387.2	1.197^{ns}
Error	8	15961.9	1995.2	
Total	14	87998.9		

F-1 (continued)

b. Experiment II

Source of variation	df	SS	MS	F_s
Playback conditions	2	6630.2	3315.1	8.344**
S vs. N	1	3570.1	3570.1	8.986**
NN vs. NO	1	6050.0	6050.0	15.228***
S vs. NO	1	325.1	325.1	0.818^{ns}
Tested males	3	3870.9	1290.3	3.248^{ns}
Error	6	2383.8	397.3	
Total	11	12884.9		

F-2. Number of flights during playback

a. Experiment I

Source of variation	df	SS	MS	F_s
Playback conditions	2	6.5	3.3	6.323**
S vs. N	1	6.4	6.4	12.387***
NN vs. NO	1	0.9	0.9	1.742^{ns}
S vs. NO	1	2.5	2.5	4.839^{ns}
Tested males	4	2.3	0.6	1.097^{ns}
Error	8	4.1	0.5	
Total	14	12.9		

F-2 (continued)

b. Experiment II

Source of variation	df	SS	MS	F_s
Playback conditions	2	0.7	0.3	0.300^{ns}
Test males	3	29.3	9.8	8.800**
Error	6	6.7	1.1	
Total	11	36.7		

F-3. Nearest distance from speaker during playback

a. Experiment I

Source of variation	df	SS	MS	F_s
Subgroups	14	64870.4	4633.6	5.271***
Playback conditions (P)	2	16892.6	8446.3	9.608***
Test males (M)	4	4144.8	1036.2	1.179^{ns}
Interaction (P x M)	8	43833.0	5479.1	6.233***
Within subgroups (Error)	45	39558.5	879.1	
Total	59	104428.9		

b. Experiment II

Source of variation	df	SS	MS	F_s
Subgroups	11	39010.6	3546.4	10.827***
Playback conditions (P)	2	6694.6	3347.3	10.219***
Test males (M)	3	13181.1	4393.7	13.414***
Interaction (P x M)	6	19134.9	3189.1	9.736***
Within subgroups (Error)	36	11791.7	327.5	
Total	47	50802.3		

F-4. Number of graded and primary call elements

a. Experiment I: during playback

Source of variation	df	SS	MS	F_s
Subgroups	14	8106.7	579.1	3.657***
Playback conditions (P)	2	3654.2	1827.1	11.538***
Test males (M)	4	1191.7	297.9	1.881^{ns}
Interaction (P x M)	8	3260.8	407.6	2.574**
Within subgroups (Error)	45	7126.3	158.4	
Total	59	15233.0		

b. Experiment I: after playback

Source of variation	df	SS	MS	F_s
Subgroups	14	13291.2	949.4	8.725***
Playback conditions (P)	2	2711.4	1355.7	12.459***
Test males (M)	4	3295.1	823.8	7.571***
Interaction (P x M)	8	7284.7	910.6	8.369***
Within subgroups (Error)	45	4896.5	108.8	
Total	59	18187.7		

c. Experiment II: during playback

Source of variation	df	SS	MS	F_s
Subgroups	7	4644.2	663.5	2.261^{ns}
S vs. NN	1	552.8	552.8	1.884^{ns}
Test males	3	3129.3	1043.1	3.555*
Interaction	3	962.1	320.7	1.092^{ns}
Within subgroups	24	7041.3	293.4	
Total	31	11685.5		

F-5. Difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls in Experiment I

a. Comparison between neighbour's and stranger's calls during the last three minutes of playback

Source of variation	df	SS	MS	F_s
Subgroups	7	81097.7	11585.4	1.318^{ns}
S vs. NN	1	1674.6	1674.6	0.190^{ns}
Test males	3	65885.0	21961.7	2.498^{ns}
Interaction	3	13538.1	4512.7	0.513^{ns}
Within subgroups	39	342857.8	8791.2	
Total	46	423955.5		

b. Comparison between neighbour's and stranger's calls during the first minute after playback

Source of variation	df	SS	MS	F_s
Subgroups	7	51160.4	7308.6	2.640^{ns}
S vs. NN	1	1596.0	1596.0	0.576^{ns}
Test males	3	44921.4	14973.8	5.408*
Interaction	3	4643.0	1547.7	0.559^{ns}
Within subgroups	8	22151.9	2769.0	
Total	15	73312.3		

F-5 (continued)

c. Comparison between the normal and opposite locations during the last three minutes of playback

Source of variation	df	SS	MS	F_s
Subgroups	9	217501.4	24166.8	5.470***
NN vs. NO	1	632.2	632.2	0.143^{ns}
Test males	4	196308.2	49077.1	11.108***
Interaction	4	20560.9	5140.2	1.163^{ns}
Within subgroups	47	207663.7	4418.4	
Total	56	425165.1		

d. Comparison between the normal and opposite locations during the first minute after playback

Source of variation	df	SS	MS	F_s
Subgroups	9	29058.8	3228.8	2.298^{ns}
NN vs. NO	1	2832.2	2832.2	2.016^{ns}
Test males	4	10959.2	2739.8	1.950^{ns}
Interaction	4	15267.4	3816.8	2.717^{ns}
Within subgroups	10	14047.3	1404.7	
Total	19	43106.1		

PART G. **Individual Recognition by Female Primary Calls:** response to playback (two-way ANOVA tables including planned comparisons between sexes and also between different female calls by *a priori* test)

Symbols: df, degrees of freedom; SS, sums of squares; MS, mean squares; F_s, sample statistics of F-distribution; SM, strange male's primary calls (control); SF, strange female's primary calls; NF, neighbouring female's primary calls; MF, mate's primary calls; M, male's primary calls; F, female's primary calls.

Probability: ***, $p < 0.01$; **, $p < 0.025$; *, $p < 0.05$; ns, $p \geq 0.05$.

G-1. Number of flights during playback

Source of variation	df	SS	MS	F_s
Playback conditions	3	3.0	1.0	0.645^{ns}
Tested males	4	15.3	3.8	2.508^{ns}
Error	12	18.3	1.5	
Total	19	36.6		

G-2. Nearest distance from speaker during the first two one-minute periods of playback

Source of variation	df	SS	MS	F_s
Subgroups	19	6142.9	323.3	5.897***
Playback conditions (P)	3	479.7	159.9	2.916^{ns}
Tested males (M)	4	2471.0	617.8	11.268***
Interaction (P x M)	12	3192.2	266.0	4.852***
Within subgroups (Error)	20	1096.5	54.8	
Total	39	7239.4		

G-3. Number of primary and graded call elements

a. During playback: four one-minute periods

Source of variation	df	SS	MS	F_s
Subgroups	19	13241.6	696.9	2.897***
Playback conditions (P)	3	5167.6	1722.5	7.159***
SM vs. SF	1	38.0	38.0	0.158^{ns}
SM vs. NF	1	6.4	6.4	0.027^{ns}
SM vs. MF	1	3534.4	3534.4	14.690***
SF vs. NF	1	75.6	75.6	0.314^{ns}
SF vs. MF	1	2839.2	2839.2	11.800***
NF vs. MF	1	3841.6	3841.6	15.966***
Tested males (M)	4	3451.3	862.8	3.586**
Interaction (P x M)	12	4622.7	385.2	1.601^{ns}
Within subgroups	60	14436.8	240.6	
Total	79	27678.4		

b. After playback: four one-minute periods

Source of variation	df	SS	MS	F_s
Subgroups	19	26884.8	1415.0	15.174***
Playback conditions (P)	3	17407.9	5802.6	62.227***
Tested males (M)	4	3590.7	897.7	9.627***
Interaction (P x M)	12	5886.2	490.5	5.260***
Within subgroups	60	5595.0	93.3	
Total	79	32479.8		

G-3 (continued)

c. After playback: one four-minute period

Source of variation	df	SS	MS	F_s
Playback conditions	3	69631.6	23210.5	11.830***
SM vs. SF	1	12460.9	12460.9	6.351*
SM vs. NF	1	1768.9	1768.9	0.902^{ns}
SM vs. MF	1	20611.6	20611.6	10.505***
SF vs. NF	1	4840.0	4840.0	2.467^{ns}
SF vs. MF	1	65124.9	65124.9	33.192***
NF vs. MF	1	34456.9	34456.9	17.561***
Tested males	4	14362.7	3590.7	1.830^{ns}
Error	12	23544.9	1962.1	
Total	19	107539.2		

G-4. Difference between the observed maximum frequency of primary and graded calls and individual standard maximum frequency of primary calls

a. During the first two minutes of playback

Source of variation	df	SS	MS	F_s
Subgroups	19	274045.6	14423.5	1.776*
Playback conditions (P)	3	144684.7	48228.2	5.939***
SM vs. SF	1	94851.3	94851.3	11.680***
SM vs. NF	1	34190.4	34190.4	4.210*
SM vs. MF	1	118032.0	118032.0	14.535***
SF vs. NF	1	13482.0	13482.6	1.660^{ns}
SF vs. MF	1	2345.1	2345.1	0.300^{ns}
NF vs. MF	1	25396.5	25396.5	3.127^{ns}
M vs. F	1	117594.7	117594.7	14.481***
Tested males (M)	4	42061.4	10515.4	1.295^{ns}
Interaction (P x M)	12	87299.4	7275.0	0.896^{ns}
Within subgroups (Error)	50	406027.5	8120.6	
Total	69	680073.1		

G–4 (continued)

b. During the last two minutes of playback

Source of variation	df	SS	MS	F_s
Subgroups	19	270010.0	14211.1	5.892***
Playback conditions (P)	3	43910.2	14636.7	6.068***
SM vs. SF	1	1860.8	1860.8	0.771^{ns}
SM vs. NF	1	11764.9	11764.9	4.878*
SM vs. MF	1	38893.9	38893.9	16.126***
SF vs. NF	1	4087.0	4087.0	1.659^{ns}
SF vs. MF	1	22962.4	22962.4	9.520***
NF vs. MF	1	7876.4	7876.4	3.266^{ns}
M vs. F	1	20690.2	20690.2	8.578***
Tested males (M)	4	94216.6	23554.2	9.766***
Interaction (P x M)	12	131883.2	10990.3	4.557***
Within subgroups (Error)	59	142304.8	2411.9	
Total	78	412314.8		

PART H. Differences Between Races of the Brown Hawk Owl

The differences between races have been described in terms of size and plumage colour. In H-1, a summary of published measurements from different races is given. In general, northern races are larger and paler than southern races.

There are distinct intraspecific differences in the primary call (see H-2):

Type A, 'k.hoo-k.hoo, k.hoo-k.hoo..... k.hoo-k.hoo'

Type B, 'hoo-oip, hoo-oip..... hoo-oip'

Type C, 'hoop, hoop..... hoop'

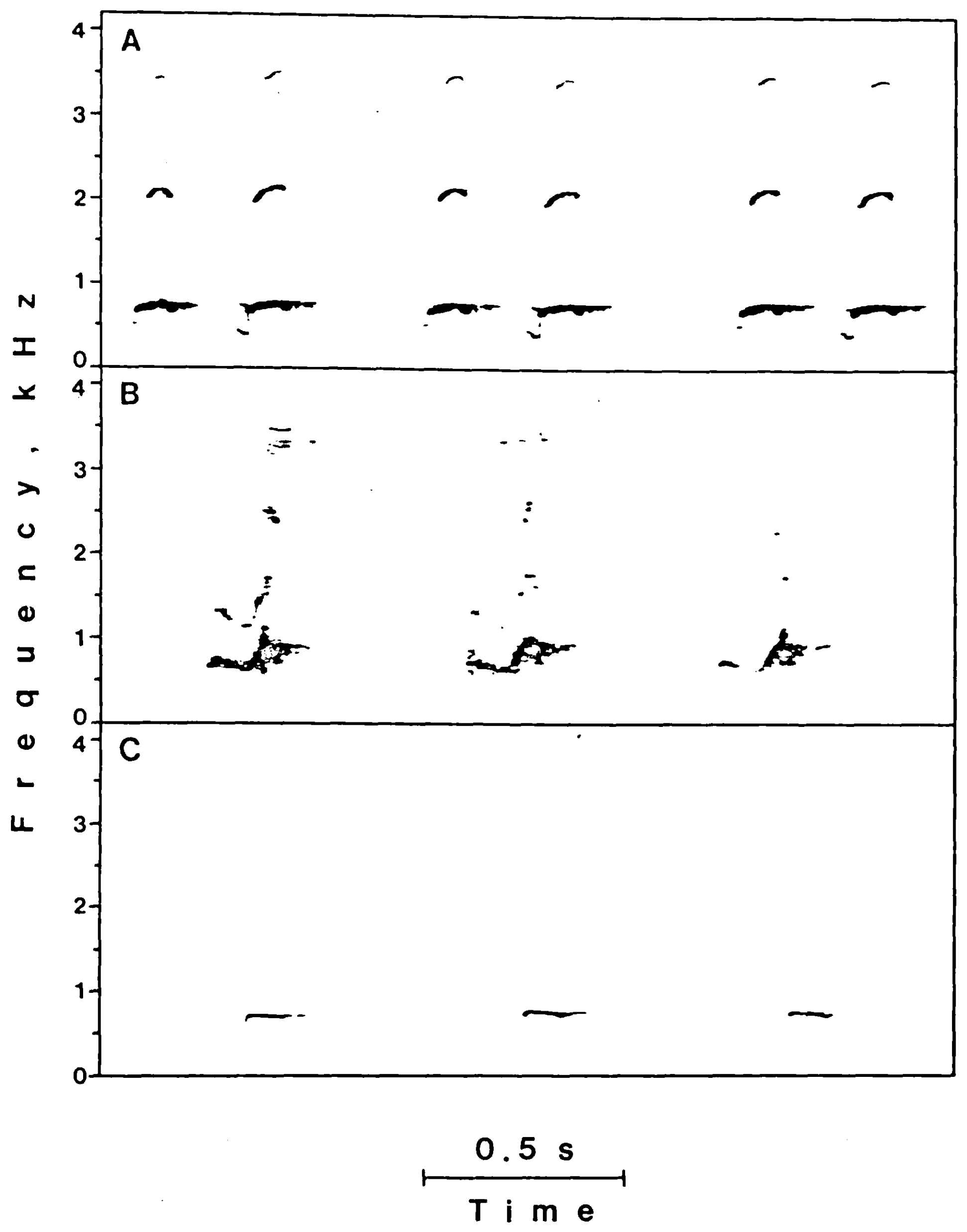
Type A is found in the northern races, *japonica* and *ussuriensis*. Although Yuri and Aragaki (1975) described the call of *totogo* as 'k.hoo-k.hoo-k.hoo', trisyllabic calls are considered to be a casual variation from Type A (Yonashiro pers. comm.). Type B belongs to southern races, *lugubris*, *hirsuta*, *obscura*, *burmanica* and *scutulata*, and possibly *bornensis* and *javanensis*. Unlike other authors, Henry (1971) described the first element 'hoo' as higher pitched than the second 'oip' in the call of Sri Lankan birds. Type C is suggested to belong to *randi* (see H-3 for geographical references).

Vaurie (1960) proposed synonymizing *japonica* and *ussuriensis* in his argument based upon the comparison of wing-lengths. Dement'ev (1966) also questioned the difference between them. The discreteness observed between the different types of primary calls and its correspondence to the geographical isolation of breeding populations of races suggest the need for a study of the subspecific status of these two races, and possibly *totogo*.

H-1. A summary of the published measurements of body parts of different races of *Ninox scutulata* (unit: mm)

Race	Wing	Tail	Tarsus	Beak
ussuriensis	221-245	117-128	--	--
japonica	202-229	107-128	25-30	20-25
totogo	201-214	112-122	-	-
lugubris	204-228	124-135	24	21-22
burmanica	206-222	128-134	24-25	21-22
hirsuta	190-212	112-122	24-28	22-24
obscura	197-220	120-126	28	22-23
randi	218-242	135	28	26-28
scutulata	180-202	119-127	25-28	-
bornensis	175-193	-	-	-
javanensis	175	-	-	-

References: Buturlin 1910; Stevens 1924; Robinson 1927; Stresemann 1928; Mishima 1956; Ripley & Rabor 1958; Kiyosu 1965; Vaurie 1965; Dement'ev 1966; Sálim & Ripley 1969; Du Pont 1971; Kobayashi 1976.



H-2. Different types of primary calls of the Brown Hawk Owl: A, separate disyllabic type 'k.hoo-k.hoo' recorded from a Japanese bird by the author in 1980; B, continuous disyllabic type 'hoo-oip' recorded from an Indian bird by Marshall in 1974; C, monosyllabic type 'hoop' recorded from a bird of Mindanao Island in the Philippines by Marshall in 1971.

H-3. Geographical distribution of primary call types

Location	Type	References
Japan	A	Hayashi 1902; Kuroda 1914, 1922b, 1931, 1934; Kawaguchi 1918; Momiyama & Nomura 1919; Kawaguchi & Ikemura 1920; Saito 1924; Ishizawa 1934; Yamashina 1961; Kiyosu 1965; Abe _et al_. 1979; Ito _et al_. 1979.
Korea	A	Gore & Won 1971.
China	A	La Touche 1931-1934; Etchécopar & Hüe 1978.
Ussuriland	A	Dement'ev 1966; Panov 1973; Zubakin _et al_. 1979*.
Okinawa	A	Yonashiro pers. comm.
Nepal	B	Proud 1949; Fleming _et al_. 1979.
North India and Bangladesh	B	Inglis _et al_. 1920; Hoogerwerf 1949; Sálim 1954, 1977; Wright 1957; Sálim & Ripley 1969.
South India	B	Davidson 1898; Fergusson & Bourdillon 1904; Sálim 1943, 1969; Sálim & Ripley 1969.
Sri Lanka	B	Butler 1896; Wait 1931; Sálim & Ripley 1969.
Andaman and Nicobar Islands	B	Butler 1899a; Abdulali 1964, 1978; Sálim & Ripley 1969; Marshall pers. comm.
Burma	B	Stanford & Ticehurst 1939; Smythies 1953; Sálim & Ripley 1969.
Thailand	B	Lokagul & Cronin 1974; Holmes 1974*; Marshall pers. comm.*
Malay Peninsula	B	Medway & Wells 1976; Kersley 1972*; Marshall pers. comm.*
Sumatra	B	Marshall pers. comm.*

H-3 (continued)

Location	Type	References
Borneo	(B)	Hose 1893; Smythies 1968.
Java	(B)	Bartels 1928; Hoogerwerf 1949.
Mindanao	C	Marshall pers. comm.*

Note: *, disc or tape recordings; (), a possible type.

PART I. List of the Scientific Names of Avian Species, Genera and Families Referred to in the Thesis

Acrocephalus
Aegolius funereus
Asio
A. flammeus
A. otus
Athene
A. brama
A. (Speotyto) cunicularia
A. noctua
Bonasa umbellus
Bubo
B. bubo
B. capensis
B. virginianus
Cardinalinae
Cardinalis cardinalis
Carduelinae
Colinus virginianus
Cracticidae
Dendrogapus obscurus
Emberiza citrinella
E. schoeniclus
Emberizinae
Estrildidae
Fringillidae
Gallus domesticus
Gavia immer
Geothlypis trichas
Glaucidium
G. passerinum
Gymnorhinus cyanocephalus
Haematopus ater
Hydrobatidae
Icteridae
Ketupa blakistoni
Laridae
Luscinia luscinia
Melopsittacus undulatus
Micrathene whitneyi
Milvus migrans
Muscicapidae
Ninox
N. connivens
N. novaeseelandiae
N. rufa
N. scutulata
N. strenua
Numida meleagris
Nyctea scandiaca
Nycticorax nycticorax
Otus
O. asio
O. flammeolus
O. trichopsis
Paridae
Parulidae
Parus major
Petroica australis
Phasianidae
Picidae
Procellariidae
Psittacidae
Puffinus puffinus
Pulsatrix
Rallidae
Recurvirostra avosetta

Sceloglaux albifacies
Scolopacidae
Scotopelia peli
Seiurus aurocapillus
Setophaga rusticilla
Spheniscidae
Spizella pusilla
Strigidae
Strix
S. aluco
S. nebulosa
S. occidentalis
S. uralensis
Sturnidae
Sturnus vulgaris
Surnia ulula
Thryothorus ludovicianus
Troglodytidae
Turdus ericetorum
T. merula
Tyrannus tyrannus
Tyto alba
T. capensis
Vermivora Chrysoptera
Zonotrichia albicollis

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PART B. Recordings

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