Vocal Repertoire of the Japanese Brown Hawk Owl *Ninox scutulata japonica* with Notes on its Natural History

by

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ERRATA

Please correct the following three misprints in the previous issue of Natural History Research, Special Issue, No.2: 1-64, March 1996.

1) Please replace the journal title on the top left of page 1.

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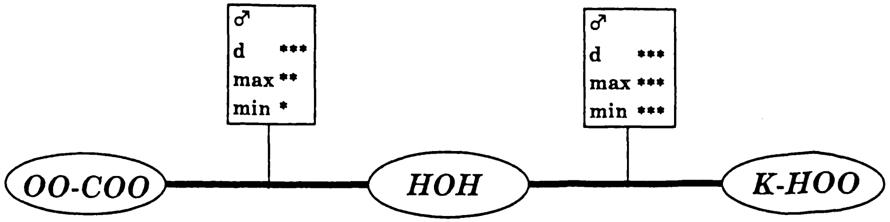
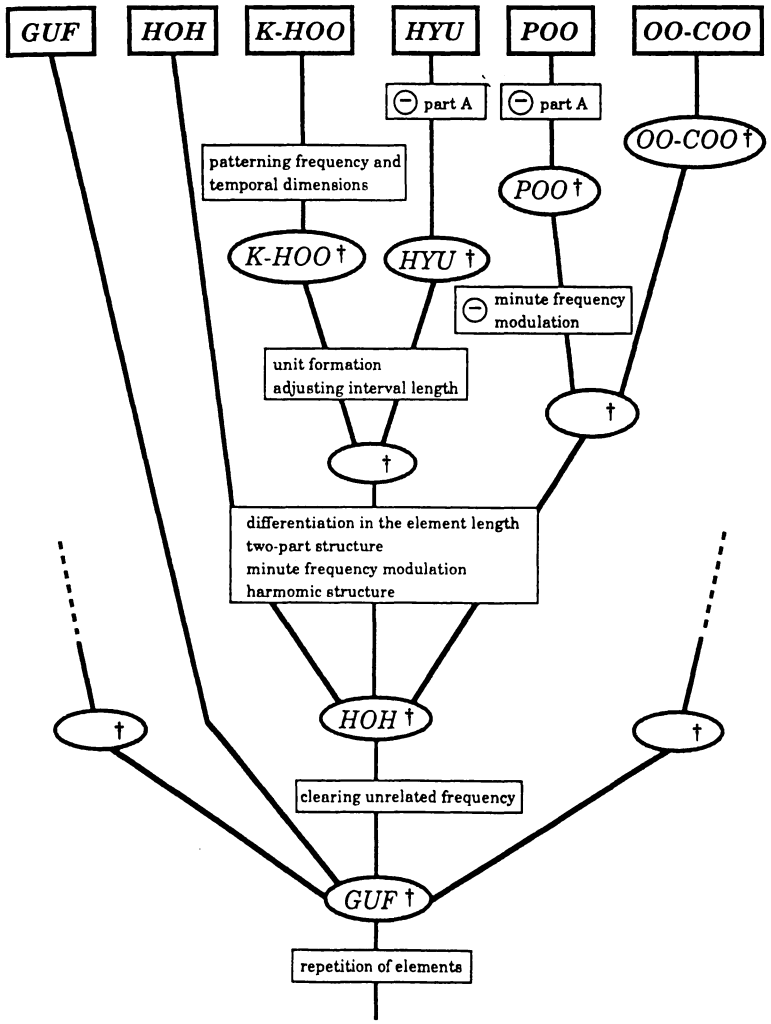
2) Please replace Fig.13 A of page 34 with the below.



3) Please replace Fig.15 of page 36 with the below.



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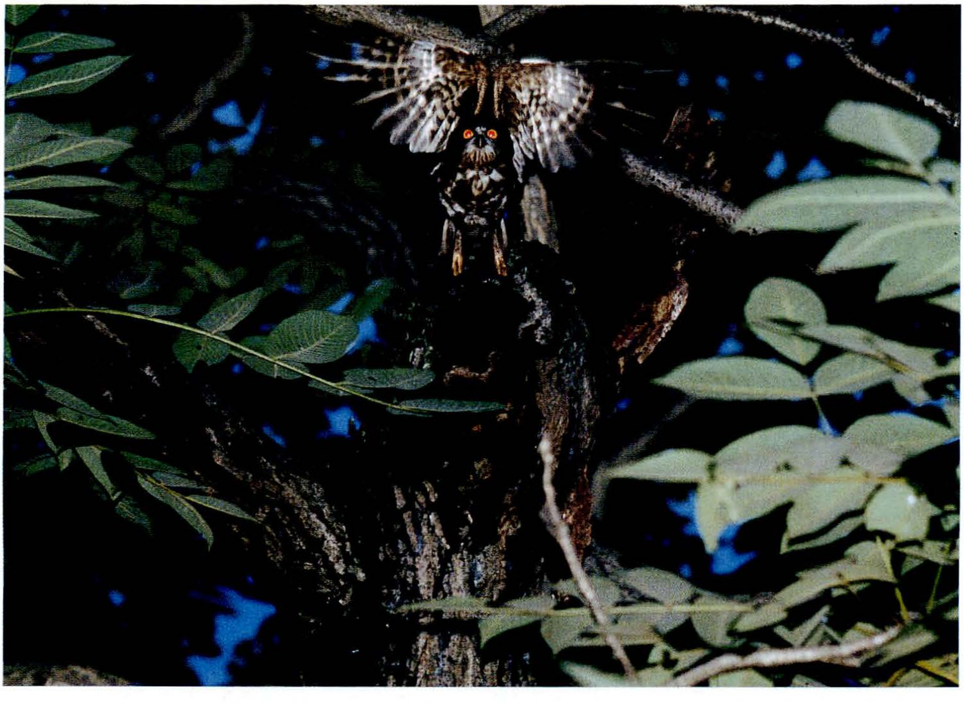

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Abstract The vocal repertoire of the Japanese Brown Hawk Owl *Ninox scutulata japonica* was studied based upon the detailed observation of behaviour and sound recordings of wild birds with additional data of captive birds. In adult birds, there were at least thirteen types of vocalisations, *K-HOO* (the song), *HOH*, *GUF*, *OO-COO*, *POO*, *HYU*, *KRRR*, *CHEEE*, *MEW*, *MEEEW*, *HOOH*, *QUAY* and *BUF*, with a possible addition of *BYAHBYAH*. Also, there were three non-vocal sounds: wing clapping, wing rustling and bill snapping *PACK*. The development of vocal repertoire was studied during the first year of life. Nestlings had 4 vocal sounds of *LEEE*, *GILILILI*, *CHILILILI* and *KYRRKYRR*, and a non-vocal *PACK*. Fledglings increased the number to the following 8 vocal sounds: *LEEE*, *GILILILI*, *CHEWLEE*, *BYAHBYAH*, *PUH*, *SOO*, *POOH* and *O-GUF*. Juveniles further added *PY-O*, *BEH*, *SCHEEE* and *PUR*. The subsong *O-GUF O-GUF* appeared after 10 weeks, and some of juvenile calls transformed to adult versions afterwards.

The physical structure of sounds was analysed by sonagraph. Their behavioural contexts were surveyed for both sender and receivers before, during and after sound production. Based upon the results, messages and meanings of sounds were interpreted for further discussion of functions after Smith (1977a). In particular, *K-HOO* was discussed for its relevance as the song.

In the adult repertoire, *K-HOO*, *HOH*, *GUF*, *OO-COO*, *POO* and *HYU* were graded in the physical structure. Their relationships were closely examined for both physical and behavioural aspects, which showed a good correspondence. The development of vocal repertoire and underlying motivational mechanism were further examined. Motivation-structural model by Morton (1977) well fits in the graded vocalisations.

Comparison was made between Japanese birds and other races or congeneric species to draw the minimal design of *Ninox* vocal repertoire: the song, shrieking, screaming, a cat-like mewing and trilling. Further, 87 species from 21 genera of the Strigiformes were reviewed. Twenty-seven species out of them had more than 5 types of vocalisations, and the maximum number of adult repertoire was 14 vocal sounds and 3 non-vocal noises. Juveniles had 1–4 vocalisations and 1 non vocal sound. Japanese birds reached the largest repertoire.

General accounts of the species are compiled to cover the description, classification, distribution, habitat, general behaviour, feeding, hunting, breeding, the pair-bond, nest and territory, based upon the original observation in 1974–1981 and the past literature including those published in Japanese.

Key words: vocal repertoire, non-vocal sound, development, physical structure, context, interpretation, message, meaning, function, grading, *Ninox scutulata*, owl, general behaviour and ecology

Introduction

Humans have always been attracted to bird sounds, asking the same fundamental question: why do they sing and make different calls? The beauty and complexity of bird songs has naturally been the attention of naturalists and aestheticians, whilst eerie sounds of night birds have rather been detested as omen in many parts of the world. The Japanese Brown Hawk Owl *Ninox scutulata japonica*, a common summer visitor to Japan, is a mainly nocturnal species living in the neighbourhood of human habitation (Plates I and II). Their plaintive songs often frighten young children in bed, as they are often associated with grave yards and deserted shrines. However, the main vocalisation is so striking and familiar that local people tend to give them nicknames like 'Pompom-dori' ('dori' for bird), 'Hawhaw-dori', 'Hoho-dori', 'Tekuppo', and even a popular girls' name 'Yoshiko' (Kiyosu, 1965; Momiyama & Nomura, 1919). Since their arrival at the breeding ground overlaps the time of fresh plant growth in spring, they are commonly named as 'Aoba-zuku': 'aoba' for fresh green leaved and 'zuku' for owls. Local farmers also nicknamed them in relation to cultivation. 'Imo-oyaji' means the Old Man Taro who tells them to plant taros, and 'Mugitsuki' is a barley keeper to tell them to harvest barley (Kawaguchi, 1972).

In general, crepuscular and nocturnal owls are believed to rely more upon acoustic than visual communication, and their vocalisations have intrigued many naturalists into their life history. However, the difficulty in visual observation during the night has prevented researchers from constructing complete vocal repertoires in most cases. So far there were four studies on the nocturnal Spotted Owls *Strix occidentals* (Forsman *et al.*, 1984), diurnal Burrowing Owl *Athene cunicularia* (Martin, 1973) and captive Snowy Owl *Nyctea scandiaca* (Scherzinger, 1974) and captive Ural Owl *Strix uralensis* and Tawny Owl *Strix alco* (Scherzinger, 1980). The Brown Hawk Owl is relatively easy to observe at night, and scattered accounts appeared to suggest that they should have a rich vocal repertoire as means of communication (Hayashi, 1902; Kuroda, 1914; Kawaguchi & Ikemura, 1920; Kawaguchi, 1937; Ito *et al.*, 1979; Tomita, 1990).

The background to the present research is many studies of avian acoustic communication through calls and songs. Calls are the arbitrary category of vocal utterance by any members of bird families in diverse contexts. Songs are the prominent sound produced generally by territorial males during the breeding season. They are adopted as important acoustic character to specify a particular systematic group of birds, songbirds or oscines. Hitherto distinction between songs and calls, however, is rather inadequate to non-oscine birds such as owls. The past studies of stirigidine vocalisations made clear that there is at least one prominent sound which specifies each species and plays an equivalent role to oscine songs (Van der Weyden, 1973, 1975; Van der Weyden & Ginn, 1973). The present paper supports the view.

What is the significance to study the vocal repertoire? Most studies in avian vocal communication have largely been carried out on oscine songs. Detailed mechanisms have considerably been made clear in the last two decades (Catchpole & Slater, 1995). Non-oscine calls have also attracted many studies to examine encoded information (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). However, the total picture of avian acoustic communication cannot be drawn without the vocal repertoire. Its range, size and mechanisms are the base for comparative studies of acoustic communication.

In the present paper, it is aimed to reveal and assess the vocal repertoire of the Japanese Brown Hawk Owl as the basic mode of acoustic communication. The adult repertoire and its development are studied in the following three aspects.

a) Detailed observation of behaviour, sound-recording of vocalisations and other noises in the wild state and captivity, and supplemental information on the owls' development.
b) Sonagraphic analysis of sounds recorded in the field and captivity to compile the physical structure.
c) Investigation of behavioural contexts before, during and after an acoustic event. The context cover both behavioural features of senders and receivers, and other non-behavioural factors in the surrounding environment.

Then, respective vocalisations are interpreted for messages, meanings and functions of sounds. Messages are the kind of information encoded in a signal and shared among birds engaged in the communication. Information is defined as entity which permits choices to be made. Meanings are specific to the receiver of signal, and are interpreted from the receiver's response to the signal. Functions are both 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 sender and receiver, and also among different classes of receivers (Smith, 1965, 1966, 1977a, b).

Firstly, the relevance between the physical structure and information encoded in an acoustic signal has been an important subject (Marler, 1957, 1967; Morton, 1977, 1982). The modality of physical structure can be characterised as conformity and variability, and different kinds of information can be encoded in the same one piece of sound. Stable features are likely to relate to the identity of signaller to encode information of dif ferent hierarchies such as species, sex, individual and so on. Variable features may reflect the changing state of signaller to carry information concerning the probability, intensity, relative stability and direction of behaviour (Smith, 1977a). Secondly, behavioural contexts provide important sources to interpret encoded information content such as behavioural selections.

Graded vocalisations are closely investigated, for they may provide some clues to the evolution of vocal repertoire. They are studied for the physical dimensions and behavioural aspects. The physical mechanisms in development of vocal repertoire is discussed. Since graded features of signals are suggested to contain motivational information in primates (Marler, 1965; Green, 1975) and birds (Huxley & Wilkinson, 1977), motivational mechanism is tested under the motivation-structural rule (Morton, 1977).

Finally, the vocal repertoire of the Japanese Brown Hawk Owl is reviewed with those of other subspecies, *Ninox* species and those in the Strigiformes. The prediction that nocturnal owls have larger repertoire than diurnal birds is examined.

I. General

This section is compiled from the original observation of Japanese birds in Zushi in 1974–1981 and literature on the species published in 1822–1990.

A. Description and distribution

1. English common names

Ninox scutulata was first described by Raffles in 1822. The English common name Brown Hawk Owl was used in many checklists (Vaurie, 1965; the Ornithological Society of Japan, 1974a, b; Gruson, 1976; Howard & Moore, 1980) and has extensively been 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 paper, the first English common name, Brown Hawk Owl is used, as it is the original common name and more closely describes its appearance than the other names.

2. Classification and distribution

The Brown Hawk Owl is widely distributed through Asia (Peters, 1940; Vaurie, 1965; Howard & Moore, 1980). This vast range is considered to be inhabited by eleven subspecies (Fig. 1). In Japan, *N. s. japonica* is one of the six breeding strigidine species. It is a common summer visitor throughout the country. It breeds in the main islands, Izu Islands (all islands except Shikine-jima and Aoga-shima), and other coastal islands such as Sado, Oki, Tsushima and Iki. The winter range is roughly shown as a shaded area, where another migratory subspecies *N. s. ussuriensis* also stays in winter (Seebohm, 1892; Kuroda, 1922a; Takatsukasa & Ikeda, 1936; Peters, 1940; Kiyosu, 1965; Vaurie, 1965; Higuchi, 1973; the Ornithological Society of Japan, 1974ab; Howard & Moore, 1980).

3. Description

The Brown Hawk Owl is a medium-sized brown bird, normally 254–320 mm in length. The migratory subspecies breeding in the

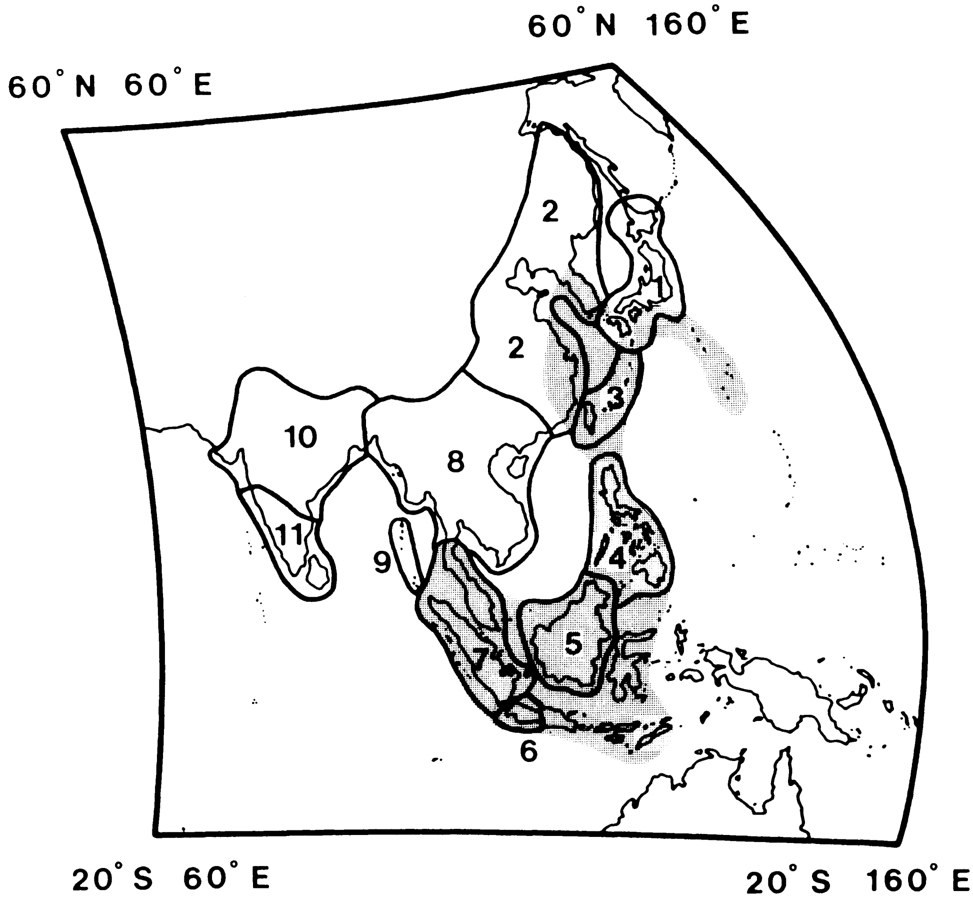


Fig. 1. Distribution of the Brown Hawk Owl. Eleven subspecies of *Ninox scutulata*: 1) *japonica*, 2) *ussuriensis* (or *macropterata*), 3) *totogo*, 4) *randi*, 5) *bornensis*, 6) *javanensis*, 7) *scutulata* (or *malaccensis*), 8) *burmanica*, 9) *obscura*, 10) *lugubris*, 11) *hirsuta*. Nominate *scutulata* 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 subspecies 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, 1974a, b; Zheng, 1976; Etchécopar & Hüe, 1978; Howard & Moore, 1980). Winter ranges of *N. s. japonica* and *N. s. ussuriensis* are shown as a shadowed area.

northern range of distribution tend to be paler in colour and larger in length than sedentary subspecies in the south (e.g. wing length by Mishima, 1956: *N. s. scutulata* 207–223 mm, *N. s. ussuriensis* 221–239 mm, *N. s. bornensis* 175–193 mm, *N. s. scutulata* 180–202 mm). 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, however males tend to be bigger than females (Ripley, 1953; Mishima, 1956; Ripley & Rabor, 1958; Dement'ev, 1966).

4. Habitat

In Japan, they have been reported from many different parts of country from lowlands to hills and mountains up to 1000 m above sea level. They inhabit in woodlands of broad-leaved deciduous and broad-leaved evergreen trees mixed with needle-leaved plantation, and tend to frequent on forest edges. They associate with human habitation and even breed in the urban area, as far as Shinto shrines, Buddhism temples, parks and gardens provide well-wooded areas for day-time retreat, hunting, nesting and a safe ground for young birds (Yamashina, 1961; Kiyosu, 1965; Kobayashi, 1976; the Wild Bird Society of Japan, Shizuoka Chapter, 1982).

B. Behaviour and ecology

1. General behaviour

Brown Hawk Owls usually perch in the upright posture with the head up and plumages relaxed. They face in the direction of attention. As they rest, they keep an upright posture with nictating membranes closed. To sleep they slightly lower their heads buried into the fluffed plumages and close eyes. When the wind blows strong, they take the horizontal posture by lowering the body in parallel with the perch. The same posture is taken to walk and ready for jump and flight. Fledglings rest in the horizontal posture with the wings half open on the sides. On the alert, they stand up with plumages pressed tight against the body and watch the enemy. In imminent danger and threat, they crouch with the head and body forward, wings spread half to full and plumages fluffed out to exaggerate the size. They repeatedly bow as they stare at the enemy with eyes of bright yellow irises wide open and snap the bills occasionally.

The flight is characteristically hawk-like beating the wings rapidly and quietly. They glide, make sharp ascent and decent, and turn abruptly. To alight, they first glide slightly downward and then rise up to the perch.

To walk on the branch and ground, they step forward by alternating left and right legs. On the narrow branch or telephone cable, they step sideways without crossing the legs. They take balance with the wings spread or fluttered.

They clean themselves by preening, scratching, stretching, fluffing and shaking in a sequence. Mutual preening about the face and head is occasionally seen between the mates. After eating, both sides of the beak and the underside of toes are repeatedly rubbed against the perch. Bathing was not observed. Captive birds indulged in sunbathing, taking a horizontal posture with the wings wide spread in the sun.

2. Feeding

The Brown Hawk Owl is known to be mainly insectivorous. Food items have been studied from the stomach contents (Ishizawa, 1934; Ikeda & Ishizawa, 1949), prey items brought to the nest, inedible parts discarded by parent birds and pellets (Abe *et al.*, 1979). In Zushi, they take a variety of insects including cicadas, Noctuidine and Sphingidine moths and Coleoptera beetles. Taniguchi (1983) identified 123 species over 40 families of insects showing seasonal changes. They also hunt frogs, lizards, small snakes, small birds, mice, small bats, and even 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). There was no apparent difference of food items between adults and nestlings.

3. Hunting

They hunt on forest edges, isolated trees in open fields, and also river banks. In urban area, wooded gardens and patches of cultivated fields are the favourite sites. Hunting grounds generally consist of a perch with a good view and open space of 10–20 m from the perch. Individual birds have several favourite perches including television aerials and telephone cables. They scan for a prey by turning their head around continuously. They often hunt in the vicinity of street and garden lamps which attract moths and beetles. Since they have fairy symmetrical ears with small round openings (Dement'ev, 1966; Kuroda, 1967), they may not depend upon hearing so much as other nocturnal owls but use their sight to locate preys. Four different methods of hunting are listed below in the order of frequency:

- Flycatching: From a perch they flutter up or dive down toward the air-borne prey, and thrust the legs out to grasp it firmly by a foot or both feet.
- Skimming: They fly out from a perch to skim over bushes, foliage, branches, trunks

and the ground for a landed prey. Even aquatic insects are taken in this way from the surface of water (Kelham, 1881).

- Hawking: They search for an air-borne prey on the wing like a nightjar, alternating fluttering and gliding above the forest canopy and roof-tops. Rapid and jerky flight of bats does not deter them, although flying bats are not easy to catch (McCann, 1933; Henry, 1971).
- Stalking: For a prey hiding in the grass or under fallen leaves, they locate it from a slightly elevated point on the ground or feel for it with foot. They jump on to catch it and quickly flutter up to a higher perch. In south-east Asia they stalk crabs on foot on the shore (Everett, 1977).

Sharp claws and bristles of the toes facilitate to hold slippery prey (Robinson, 1927; Dement'ev, 1966). The use of bills in catching (Abe *et al.*, 1979; Ito *et al.*, 1979) cannot be denied, however a small-sized prey is usually passed quickly from the feet to bills before returning to perch. Sometimes, the bird bring back the relatively large prey in one foot to free the other foot to alight. Small-sized preys are normally swallowed straight away. Large ones need to be processed by tearing off indigestible parts and crushing skulls and bones.

4. Breeding

In Japan, they return to the same breeding site every year (Masuda, 1974). Due to their migratory habit, Japanese birds have a shorter breeding season than southern sedentary subspecies and are regarded as single-brooded (Kiyosu, 1965; Sálim, 1979). They arrive in Japan from early April to early May and stay in the breeding area until late September–early October. There are five stages at the breeding ground.

1) Pre-incubation stage (arrival–late May)

Their arrival is usually detected by hearing their song at night. The exact date may be tested by playback of conspecific songs at potential nest sites. In many cases, both members of a pair jointly makes the first response. Where a single male arrives first, it is joined by a female within a week or so.

Males are quite vocal at this stage. They are engaged in spontaneous singing, counter-singing with neighbouring males, and general choruses with local birds. They sing perched at different songposts and even on the wing moving about the territory. On invasion of rival males, a series of aggressive behaviour such as an intense vocal interaction and physical combat break out. Usually, resident males successfully keep the intruders away from the territory without fighting. However, fighting can be fatal (Iwaya, 1936). Two birds grapple with each other in the air, fall to the ground and tumble about the ground beating the wings. On occasions, females join their mates in a territorial dispute. By mid-May territory boundaries are established.

Initially, mutual chasing frequently occurs between the mates. As pre-incubation period progresses, they associate more and spend longer time together. The male engages in nest invitation. He inspects tree holes and flies back and forth between the prospective nest hole and his mate. The two birds interact vocally until the female enters the hole. Now, the male guards the female quite tight. They move about together and perch side by side day and night. Mutual preening, intimate vocal interaction and courtship feeding increased. Copulation takes place as early as soon after settling down until egg-laying. They copulate as hour at many locations in the territory at any time of the night. The male perches next to the female and start to interact with her in duetting performances. The male jumps on to the female's back and holds her nape with the beak. The male copulates as he flaps the wings vigorously and leaves her with a sharp call. The next copulation may occur within half an hour.

2) Incubation stage (end of May–late June)

The female roosts in the nest hole during the daytime, and lays a clutch of 2–5 eggs within 5–7 days from the end of May to early June. Eggs are white and almost spherical. Incubation starts after the third egg (Masuda, 1974). Eggs are incubated solely by the female through day and night.

Territorial interaction declines, and the male spends more time in guarding the nest. They perch at the habitual branch within 10 m of the nest. When the nest site is seriously trespassed by a conspecific rival or predator, the male is engaged in threat and attack. Otherwise, it is mildly alerted or leaves the nest site to hide.

The male starts the nocturnal activity at 1–10 minutes after sunset, by stretching, preening and scratching for approximately 5–15 minutes. The first song of the male is responded by the female inside the nest. The male visits the nest, and he tends to hunt on the way. The female eventually comes out from the nest to feed at the hunting ground for 5–30 minutes. Courtship feeding supplies 25–75% of her food items there and continues at the nest. At dawn she comes out of the nest again and courtship feeding similarly takes place before retiring for the day after sunrise. Since the temperature inside the nest is higher than the outside by 2–3℃, eggs are rarely cooled down below 30℃ (Masuda, 1974).

3) Nestling stage (end of June–late July)

Hatching takes place from the end of June to the beginning of July. Although Masuda (1974) suggested synchronous hatching within two days, there are conspicuous differences in size among the brood. Feeding occurs for approximately one hour each at dusk and dawn. Both parents are equally involved in feeding, however the male reduces the number of feeding visits as nestlings grow despite increasing demand. He spares more time in guarding the nest site. Occasionally he chases after the female or engages in countersinging with neighbours. The female broods nestlings during day and night for the first week, and afterwards she stays at a favourite branch near the nest. As the fledging day draws near, nestlings clime up to the nest entrance and the male tends to sing around the nest site.

4) Fledgling stage (end of July–late August)

Fledglings emerge from the nest 24–27 days after hatching. During the first week, they stay near the nest, walking about branches and on the ground, climbing up trees and jumping from branch to branch. As the flight skill improves, the family group leaves the nest site for cover in woodlands. Parents occasionally divide a large brood of more than 4 chicks between them. With a smaller brood, the female raises chicks by herself. Young birds begin to hunt in the second week, and parents gradually decrease feeding. Adult birds seem to be in moult and are generally quiet, except for casual nest invitation behaviour. Young birds leave the parents' territory by mid-September. A recovery record suggests that they disperse quickly over 10 km from the original nest site.

5) Post-breeding stage (September – departure)

They are often seen hunting alone, although they are generally inconspicuous. Associative behaviour, duetting and persistent vocal interaction between the mates resume to some extent.

5. The pair-bond

The Brown Hawk Owl is considered to be monogamous. They maintain the pair-bond for years, unless one of the pair dies or disappears. Sedentary subspecies appear to keep the pair-bond all year round (Proud, 1949), and so do the migratory subspecies, since the identical pair returns to the same breeding site every year (Masuda, 1974).

6. Nest

In Japan, they use natural holes of old trees such as *Zelkova serrata* and *Castanea crenata.* The hole is 30–80 cm deep with the diameter of 20–30 cm at the height of 5–20 m above the ground (Plate III). Although nest building behaviour is not obvious, a layer of dead leaves and wood chips is found at the bottom. The inside is damp and smells of faeces and leftover food. The same nest hole is used for consecutive years over 20 years by several pairs. They sometimes nest on the ground between garden rocks and piled timbers, and also in nest boxes (Kiyosu, 1965).

7. Territory

There are local differences in the territory size: 7–13 ha for a less crowded population in Zushi and 3–4 ha for a dense population in Miyake-jima Island (see p. 9). The territory is divided into two zones. The central zone is an area within approximately 100 m of the nest, where basic needs for individual maintenance and breeding activity are fulfilled. The outer zone extends outward further 100 m or so, where males spend more time in regular patrolling, countersinging, an intense

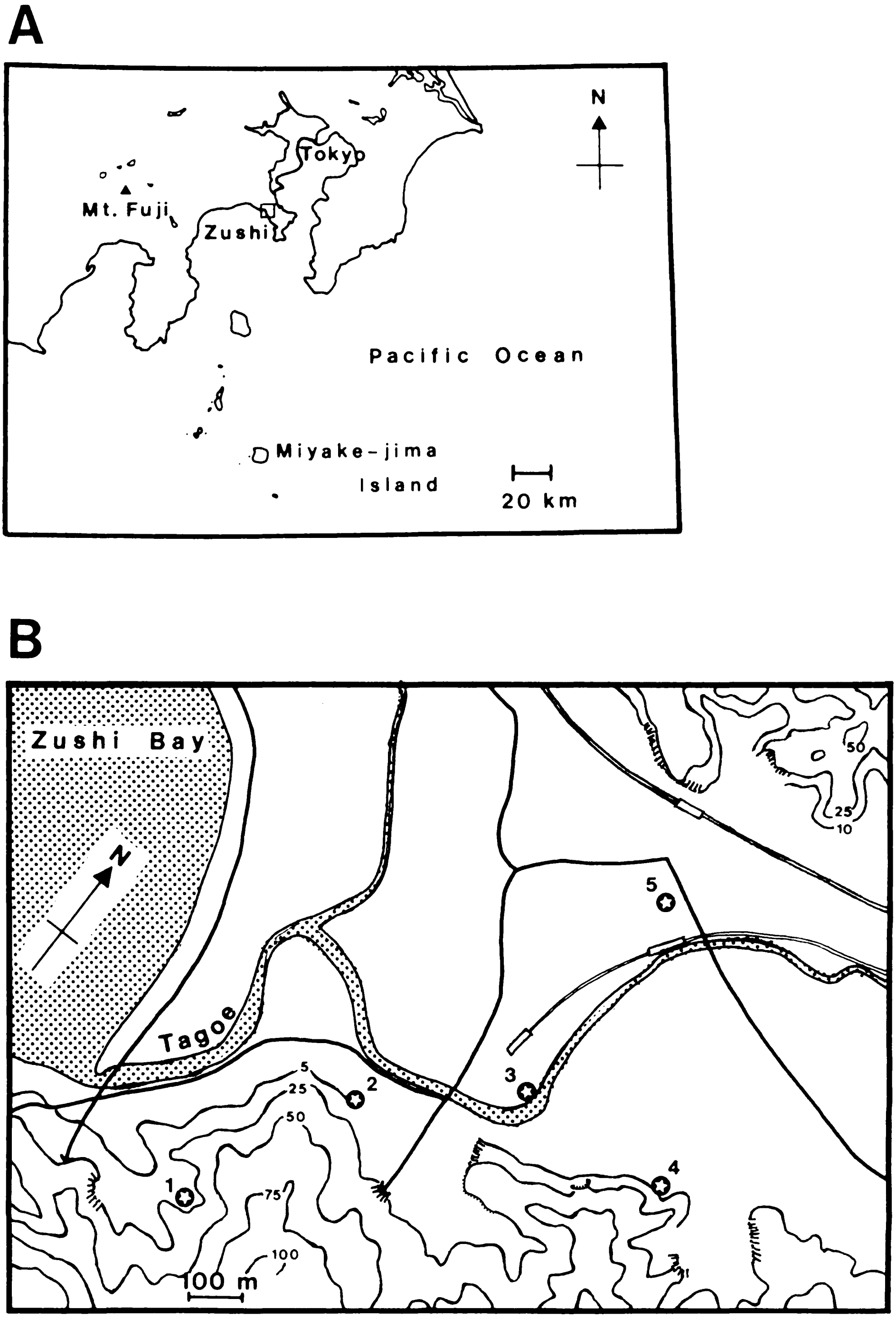


Fig. 2. Study areas. A, location of Zushi and Miyake-jima Island in Japan. B, study area in Zushi. Nest sites studied in 1981 (stars): 1) Fuboku, 2) Rokudai, 3) Sotaiji, 4) Kongoji, 5) Kamegaoka. Main roads (bold line), railways (double lines) and stations (rectangle) are also shown.

territorial disputes or physical combat in pre-incubation stage. However, males sing more frequently in the central zone than the outer zone (Oba, 1981).

II. Methods for the Vocal Repertoire

A. The study areas

Field work was mainly carried out at Zushi during 1974–1981. Also, Miyake-jima Island was visited for shorter periods in April and June during 1980–1981.

1. Zushi

Zushi is situated in the neck of the Miura Peninsula, 35° 18′N, 139° 35′E (Fig. 2A). The study area was a narrow piece of land along the River Tagoe, facing Sagami Bay to the west (Fig. 2B). To the south of the study area, low hills up to 50–100 m above sea level extended east and west with complicated systems of narrow valleys. To the north of the study area, a narrow plain spread to another row of low hills up to 50 m high. The plain was almost completely residential, and towards the seashore and hills there were quieter quarters with gardens (Plate IV). 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*, and *Zanthoxylum ailanthoides*, mixed with a dwarf bamboo *Arundinaria chino*, evergreen broad-leaved trees such as *Castanopsis cuspidata* var. *sieboldii*, *Quercus salicina*, *Q. acuta*, *Ilex integra*, *Machilus thunbergii*, *Camellia japonica*, and a shrub *Aucuba japonica*. Such forests were often mixed with coniferous plantation consisting of *Cryptomeria japonica* and *Chamaecyparis obtusa*. The undergrowth of *Neolitsea sericea*, *Cinnamomum japonicum* and *Liriope platyphyla was* also seen (Miyawaki *et al*., 1971).

2. Miyake-jima Island

The Miyake-jima Island is one of the Izu Seven Islands and is situated at approximately 150 km south of Zushi in the Pacific Ocean (Fig. 2A). 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 flanked by thick vegetation of evergreen broad-leaved trees (e.g. *Castanopsis cuspidata* var. *sieboldii*, *Machilus thunbergii*, *Camellia japonica*, *Neolitsea sericea*), deciduous broad-leaved trees (e.g. *Alnus sieboldiana*, *Mallotus japonicus*, *Styrax japonica*, *Ligustrum ovalifolium* var. *pacificum*, *Morus australis*, *Celtis sinensis* var. *japonica*, *Hydrangea involucrata*, *H. macrophylla*, *Stachyurus praecox*, *Weigela coraeensis*) and needle-leaved plantation (e.g. *Cryptomeria japonica*) with patches of cultivated field and residential quarters.

B. Methods

1. Birds

In 1976–1979, observation was made at one of the nest sites which was occupied by two or three different breeding pairs. During 1980–1981, observations were extended to the surrounding area, where five neighbouring nest sites were regularly visited (Fig. 2B). Vocalisations were recorded from a total of twenty-six adult birds (sixteen males and ten females) and three broods.

In captivity, 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×3 m×3 m, where the bird had an opportunity to see and hear wild non-parent birds. Two other juveniles were also available in 1978.

2. Identification of individuals and sexes

As owls are strongly territorial, individuals could be recognised by their presence at particular nest sites. Individuals and sexes could also be identified from their behavioural context, their songs, and in some cases by their breast plumage patterns. In 1980, catching and marking owls was attempted. Duonset Balchatris traps with baits (Berger & Hamerstrom, 1962) and mistnets coupled with playback of recorded songs were tried, but proved unsuccessful. Juveniles were ringed with a registered number ring and reflective colour rings (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. Colours were strongly reflected in light from an electric torch during night-time, and they were effective as well during daytime. Reflective colour rings were durable for more than 10 years in outdoor conditions.

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 provided sufficient light in addition to the moonlight. Residential areas were generally open enough to follow the birds visually. The owls were observed with 10× 50 Topcon and 7×30 Nikon binoculars at a distance of up to 100 m. In 1980, a NEC Noctovision NVD2001 (an infra-red telescope 4.2×75) with an infra-red torch IRW2001 and a battery NVC2001 was used near the nest. A hide was used near the nest in the rainy season. Otherwise observers either made use of natural hides or simply kept stationary.

4. Recording sounds

Vocalisations for sonagraphic analysis 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' vocalisations. 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.

5. Analysis of recorded sounds

The Nagra 4.2 tape recorder was coupled with a Kay Sonagraph 6061B 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.

6. Physical structure of vocalisations

An element of vocalisation refers to a piece of continuously produced sound. It may be composed of parts which are visually recognisable as separate blocks. For each type of vocalisation, 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 (%):

$$CV = 100 \times (\text{standard deviation})/(\text{mean})$$

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 variation in temporal structure, while standard deviation was applied to compare those in frequency structure.

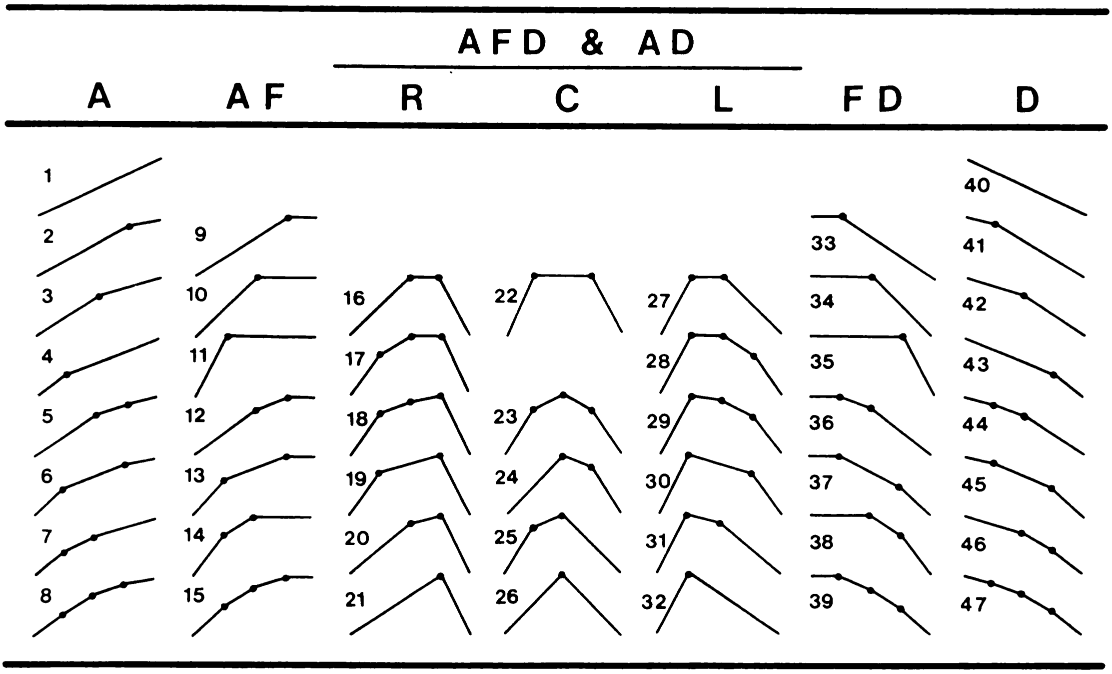
In addition, harmonic structure was classified into the following six categories which indicate relative strengths of harmonic:

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 vocalisations. Categories were devised in terms of relative locations of inflection points, as shown in Table 1.

Sexual differences in vocalisations were tested by applying to respective physical dimensions one-way analysis of variance (ANOVA) with *a priori* test. Mutually graded vocalisations 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 differ-

Table 1. Categories of frequency modulation of graded vocalisations.



Note: There are additional two types: F, flat form; DA & DFA, upside down form of AFD & AD; A, ascending frequency; F, flat frequency; D, descending frequency; R, inflected towards the right; C, inflected near the centre; L, inflected towards the left.

ent types (Sokal & Rohlf, 1973).

7. Behavioural contexts of vocalisations

Behavioural contexts of adult vocalisations 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 sound element or audibly identical elements emitted in a bout. The context of the vocal display was examined for the following three phases:

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

For each phase, behaviour of both sender and receivers (Appendix B), 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 sender of a particular sex should perform appropriately. However, the sender may not necessarily go through the appropriate actions as circumstances change. Thus, an attempt was made to sort out the most probable behaviour patterns by the binomial test (Siegel, 1956; Poole, 1974). When behaviour u, B(u), and vocalisation 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:

$$E(B(u),\ V(v)) = O(B(u)) \times O(V(v))/N$$

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

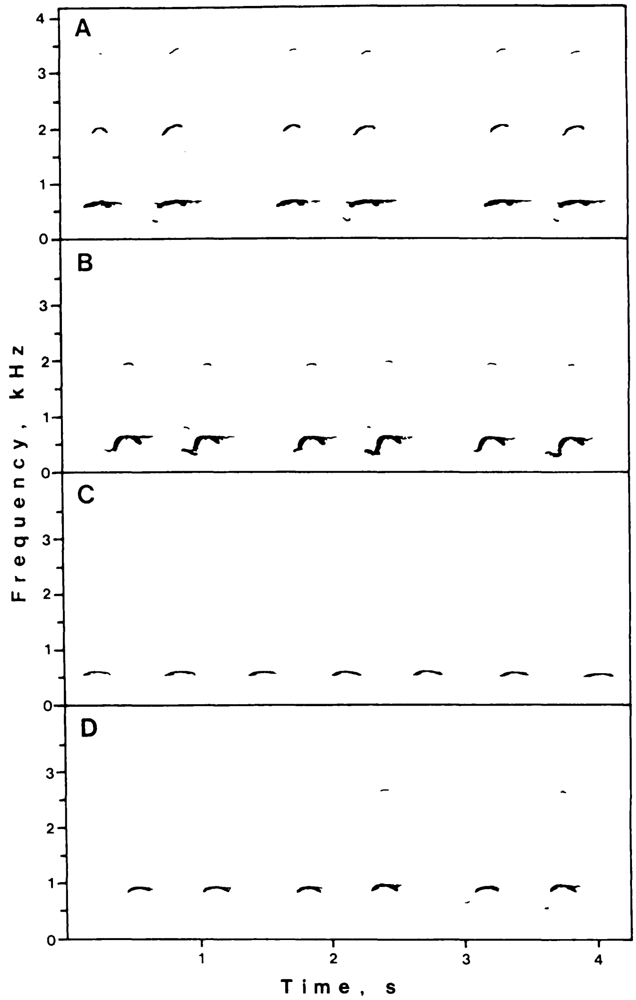


Fig. 3. Sonagrams of adult sound 1: *K-HOO* (the song). A, B, and C, male calls. Unit structure is missing from C. D, female calls. (narrow-band, 40–4000 Hz)

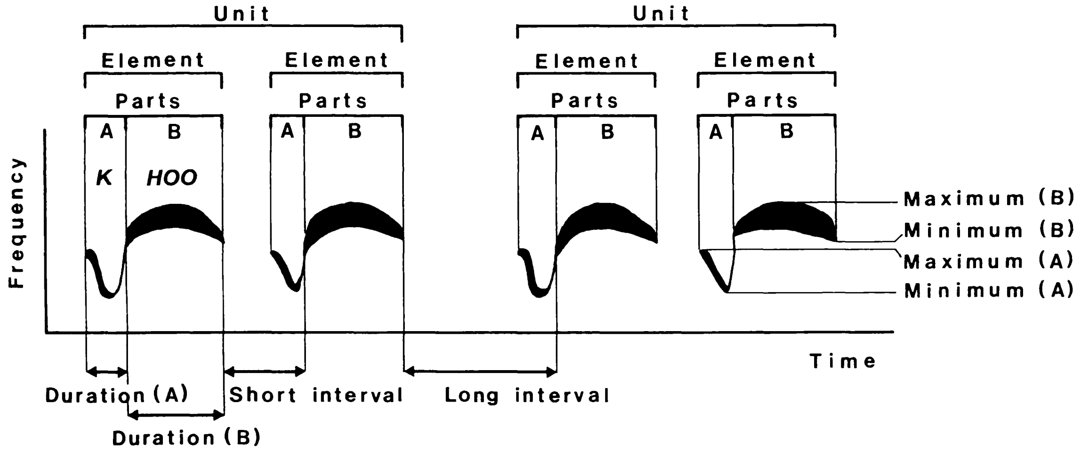


Fig. 4. The physical structure of *K-HOO*.

four, the test was not applied. The result was further checked and supplemented by observations during 1979–1981.

III. The Vocal Repertoire of Adult Birds

Adult Japanese Brown Hawk Owls were observed to have 13 types of vocalisations: *K-HOO* (the song), *HOH*, *GUF*, *OO-COO*, *POO*, *HYU*, *KRRR*, *CHEEE*, *MEW*, *MEEEW*, *HOOH*, *QUAY*, *BUF*. Eleven of these were common between the sexes, while *POO* was specific to female and *CHEEE* was heard only from males. There is another possibility of a vocal sound *BYAHBYAH*. While it was only heard from juveniles in the present study, adults are also likely to call. As for non-vocal sounds, the owls made two types of wing noises in addition to the sound *PACK* by snapping bills. In the present section, the physical structure and behavioural contexts of the adult sounds are given.

A. *K-HOO* (the Song)

K-HOO was the most characteristic vocalisation regarded as the song of the Japanese Brown Hawk Owl. It was produced by both male and female (Fig. 3). There are significant differences in the physical structure among individual birds and also between sexes, while the birds of Zushi population did not clearly differ from those of Miyake-jima Island (Oba, 1987).

1. Physical structure

1) Male songs

Male songs were constructed of the four hierarchical structure: parts, elements, units and bouts. As shown in Fig. 4, an element *K-HOO* was composed of two parts. Part A, *K*, was a low, short sound of a hoarse quality, while part B, *HOO*, was noted for its full, clear sound of a pure tone.

From the study of nine males, part A occupied the first 18–33% of element, lasting less than 100 ms with considerable inter-individual variation (Appendix A-1). The individual mean maximum frequency was between 319 and 503 Hz, and the individual mean minimum frequency was between 248 and 476 Hz (Appendix A-2). It was produced at a low amplitude, and tended to diminish quickly as it propagated through the air. Part A is missing from some of the elements.

As for part B, the individual mean duration was between 198 and 245 ms (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 633–772 Hz, and the individual mean minimum frequency was 458–638 Hz (Appendix A-2). Part B was loud enough to reach up to 300 m from the singer 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 (Appendix A-3). The third and fifth harmonics tended to be emphasised. The third harmonic added brilliance and gave a hollow, throaty and nasal quality, while the fifth was responsible for 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 (Appendix A-4).

Two elements tended to form a unit as described *K-HOO K-HOO* (Fig. 4). 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 (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. 3C). The number of elements in a bout exhibited a skew distribution toward lower numbers ($sk>0$, Appendix A-5). From the study of four males, one bout most typically contained 6–8 elements and uncommonly over 20 elements. Frequency fluctuation in a bout provided the intonation. Gradually ascending frequency in a bout yielded a rising intonation, accompanying gradual increase in amplitude.

Table 2. Sexual differences in the primary call *K-HOO* (one-way ANOVA with *a priori* test).

Physical feature	*Fs*	*df*	*p*
Part A			
-duration	1.074	[1, 98]	ns
-maximum frequency	410.367	[1, 63]	*
-minimum frequency	92.786	[1, 98]	*
Part B			
-duration	25.785	[1, 165]	*
-maximum frequency	63.340	[1, 164]	*
-minimum frequency	302.504	[1, 165]	*
Short interval	66.569	[1, 80]	*
Long interval	5.177	[1, 48]	ns

Note: *Fs*, 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; *, p < 0.01; ns, p > 0.05.

2) Female songs

Female songs also exhibited the hierarchical structure similar to that of male's. Details of the physical features of female song are listed in Appendices A-1 and A-2. Here is a summary of six females:

for part A	
duration	69 - 71 ms
maximum frequency	520 - 564 Hz
minimum frequency	439 - 458 Hz
for part B	
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

There were significant differences between sexes (Table 2). The duration of part B was significantly shorter in female than male songs, while those of both intervals were significantly longer in females than males'. Also, female songs were significantly higher in pitch than male songs. Patterns of harmonics were not clear in female songs (Appendix A-3). As for the frequency modulation, A and AF types were specific to females (binomial test: $z = 2.862$, $p < 0.01$; Appendix A-4).

2. Behavioural contexts

The details of behaviour observed before, during and after *K-HOO* are listed in Appendix B-1.

1) Spontaneous singing

K-HOO was most frequently produced spontaneously by solitary territorial males. They occasionally sang on the wing but mainly at conspicuous perches in the territory. They changed perches as they sang from the outer zone of territory. Males also sang near the nest site. Persistent singing was observed from males visiting the nest hole 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 sang vigorously and powerfully. Unless invaders retreated, intense vocal interactions developed and sometimes the vocalisation switched to *GUF.* Territorial males were likely to attack and chase intruders away from the territory. When a neighbouring male sang from its territory, resident males orientated and emitted *K-HOO* in the direction of the singing 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 produced *K-HOO.*

3) Interactions between mates

Brief exchanges or prolonged antiphonal singing was recorded from a pair perched close together. The male initiated *K-HOO* near the nest hole. His mate gradually approached the hole, emitting *K-HOO* also. When a female sang from a perch or from inside the nest, her mate tended to attend or feed her during the pre-incubation and incubation stages.

4) Interaction between parents and offspring

During the nesting stage, parents often produced *K-HOO* while being perched near or approaching the nest. The song was immediately followed by nestlings' *LEEE* or *GILI-*

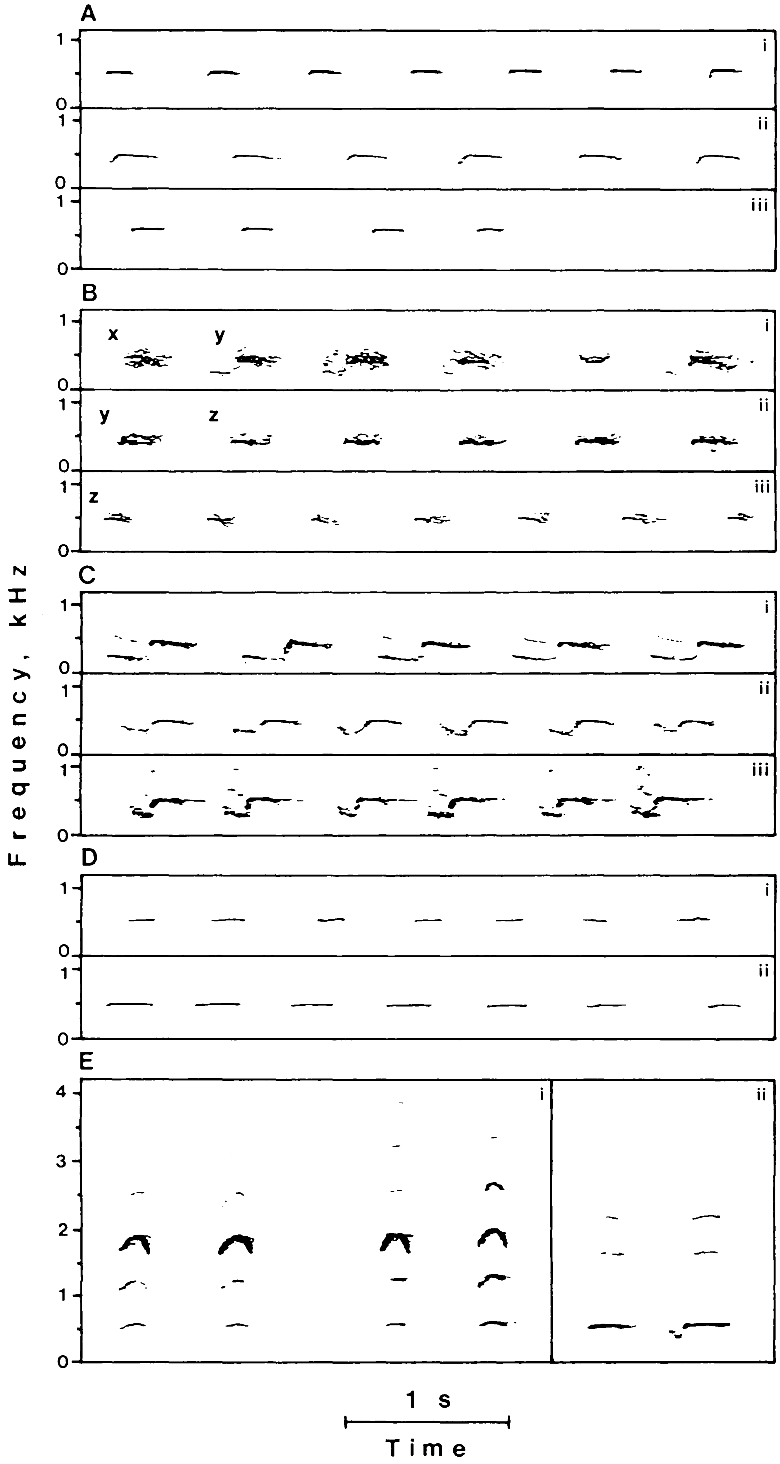


Fig. 5. Sonagrams of adult sound 2: graded calls *HOH*, *GUF*, *OO-COO*, *POO* and *HYU*. A, *HOH*: i and ii, males; iii, female. B, *GUF*: i, female; ii and iii, males; x, y and z, different types of frequency structure. C, *OO-COO*: i and iii, males; ii, female. D, *POO*: i and ii, females. E, *HYU* : i, female; ii, male. (narrow-band, 40–4000 Hz: the whole range is shown as long as harmonics are noticeable.)

LILI (see p. 22). The female parent uttered *K-HOO* as she flew back and forth between fledglings and the site where she attempted to take her young.

Males tended to produce a bout of *K-HOO* starting with *HOH* 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*.

B. *HOH*

1. Physical structure

HOH was a low gentle sound with a hollow quality. It did not reach over 100 m. Both males and females produced *HOH* (Fig. 5A).

The male *HOH* was constructed from two parts, A and B. Part A was too faint a noise. From the study of seven males, the duration was variable with the individual mean between 27 and 157 ms (Appendix A-6). The individual mean maximum frequency was from 307 to 420 Hz and the individual mean minimum frequency from 283 to 335 Hz (Appendix A-7). Part B also had a variable duration with the individual mean between 87 and 252 ms (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 (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 (Appendix A-8).

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 (Appendix A-6). It was sometimes constant enough to characterise 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. From the study of five females, the individual mean interval was from 409 to 560 ms (Appendix A-6) and did not exhibit a significant difference from that of male *HOH* ($Fs=0.492$, $df=[1, 88]$, $p>0.05$). However, the duration of part B of female calls, having a range of individual means over 130–211 ms (Appendix A-6), was significantly shorter than that of male calls ($Fs=11.657$, $df=[1, 103]$, $p<0.001$). The minimum frequency of part B of female calls, having a range of individual means over 451–544 Hz (Appendix A-7), was significantly higher than that of male calls ($Fs=25.174$, $df=[1, 103]$, $p<0.001$). 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 ($Fs=3.276$, $df=[1, 103]$, $p>0.05$). However, female calls lacked frequencies below 500 Hz (Appendix A-7).

2. Behavioural contexts

HOH was mainly produced in intra-pair interactions and breeding behaviour (Appendix B-2).

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* before receiving food. The vocal interaction was sometimes prolonged. Males also produced *HOH* on feeding incubation 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 changes to *OO-COO* as copulation was about to take place.

4) Nest calling

Early in the pre-incubation stage, males sang in a prospective nest tree and repeatedly visited a prospective nest hole. On entering the hole, males' voice shifted to long bouts of *HOH*. The calling lasted continuously for 15–20 minutes and intermittently through the night. As soon as their mates had entered the hole, males ceased to call.

Afterwards the pair was often heard duetting *HOH* inside the nest.

C. *GUF*

1. Physical structure

GUF was a low-pitched, powerful grunt. It was unlikely to travel farther than 30 m. Both sexes emitted the call, however males were heard more than females (Fig. 5B).

GUF appeared to have two parts: part A, *O*, and part B, *GUF*. Part A, however, was less regular and too faint to hear. In the calls of three males, part B showed a widely variable duration between and within individuals, having the individual mean over 173–248 ms (Appendix A-9). 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 (Appendix A-10). The frequency structure exhibited different stages of formation: a cloud over a wide range of frequency (x), double or triple fundamental frequencies in the cloud (y) and one dominant fundamental frequency with a partial cloud (z). As the structure advanced from (x) to (z), raucousness reduced. Most common types of frequency modulations of the main fundamental frequency were AFD & AD with the inflection located from the centre to left half (Appendix A-11). 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 (Appendix A-9). Possibly due to a higher maximum frequency of 568±9 Hz, female calls sounded lighter than male calls.

2. Behavioural Contexts

When an intense territorial confrontation developed, territorial males switched their vocalisations from *K-HOO* to *GUF*. They were perched close and seldom moved their positions. They firmly faced their opponent, showing the white patches below the carpals. They persistently called *GUF* and were likely to attack the opponent at any moment. Otherwise, they switched back to *K-HOO*, and became silent or withdrew.

Females also called during confrontation. Firstly, they were together with their mates during the aggressive encounter with invaders. Secondly, a widowed female resisted against the insistent disturbance of an invading male at the nest site. In both cases, females did not engage in actual attacks but simply watched or avoided the encounter.

D. *OO-COO*

1. Physical structure

OO-COO was a dulcet, cooing sound. It was not loud enough to reach beyond 30–40 m. Both male and female birds produced it (Fig. 5C).

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. From the study of seven males, the individual mean duration was from 118 to 276 ms, showing a high variation within an individual (Appendix A-12). The individual mean maximum frequency was from 238 to 428 Hz and the individual mean minimum frequency was from 181 to 332 Hz (Appendix A-13). Harmonics were often present at the second. Most common types of frequency modulation were D and F (Appendix A-14).

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 (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 (Appendix A-13). Harmonics were observed at the second and third. The types of frequency modulation were mostly AFD & AD with the inflection located from the centre to left (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 (Appendix A-12). Sexual differences were not apparent in both temporal and frequency features (Appendices A-12, A-13 and A-14). However, females called part B in the slightly higher frequency than males (maximum, $Fs=26.620$, $df=[1, 175]$, $p<0.001$; minimum, $Fs=63.407$, $df=[1, 177]$, $p<0.001$).

2. Behavioural contexts

1) Pre-copulatory calling

The pair, which initially called *HOH* to-

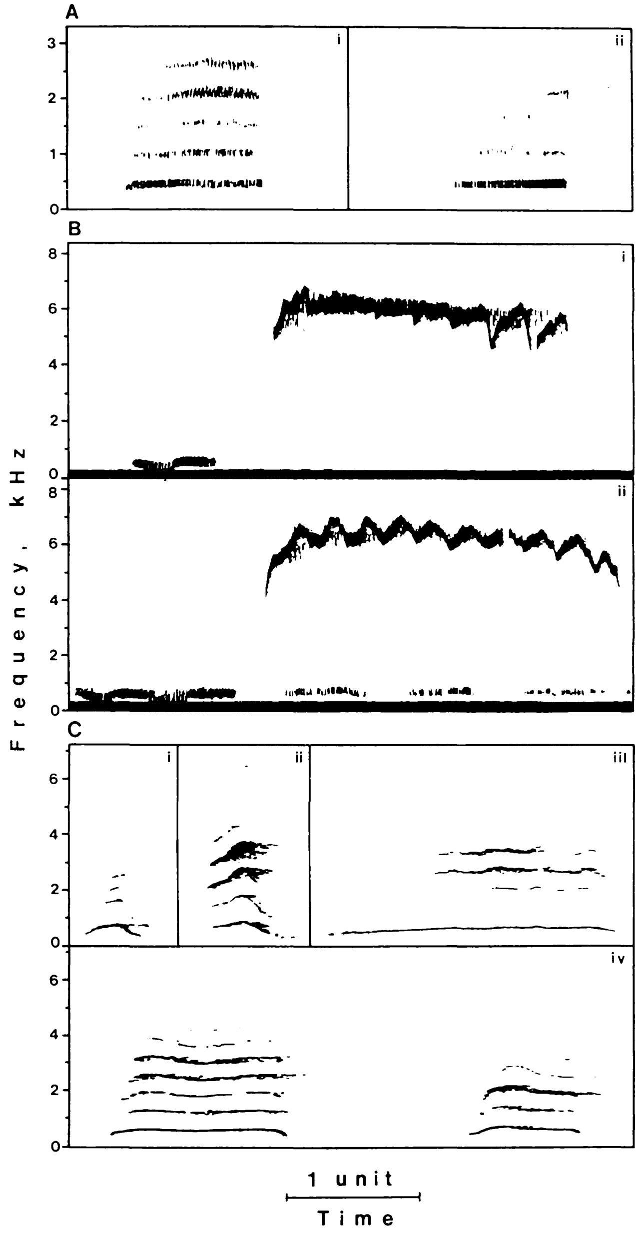


Fig. 6. Sonagrams of adult sound 3: *KRRR*, *CHEEE*, *MEW* and *MEEEW*. A, *KRRR*: i, female; ii, male (wide-band, 40–4000 Hz, unit time of one second). B, *CHEEE* was produced during copulation preceded by bouts of *OO-COO*: i, only a male called; ii, the female also called *OO-COO* in a duet with the mate and kept calling during copulation (narrow-band, 80–8000 Hz, unit time of 0.5 second). C, i and ii, *MEW*; iii and iv, *MEEEW*. (narrow-band setting, 80–8000 Hz, unit time of 0.5 second).

gether, turned their vocalisations to *OO-COO* while mounting. Males kept calling *OO-COO* until copulation and then replaced it with *CHEEE*. Females sometimes called even 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.

E. *POO*

1. Physical structure

POO was a faint, short-range peep produced by females (Fig. 5D). 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 (Appendices A-15, A-16 and A-17).

2. 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.

F. *HYU*

1. 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 males and females produced it (Fig. 5E). Male calls tended to sound softer than female ones. From the study of six males, the individual mean duration was ranged between 108 and 204 ms and showed a large variation within an individual (Appendix A-18). The individual mean maximum frequency was from 525 to 661 Hz and the individual mean minimum frequency was from 464 to 584 Hz (Appendix A-19). Harmonics were generally observed from the second to the fourth (Appendix A-20). Emphasised 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 with the inflection located from the centre to right (Appendix A-21). 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 (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 (Appendix A-18). However, they were higher pitched than male calls. The individual mean maximum frequency was from 633 to 700 Hz ($Fs=27.196$, $df=[1, 87]$, $p<0.001$). The individual mean minimum frequency was from 548 to 588 Hz ($Fs=70.290$, $df=[1, 85]$, $p<0.001$).

2. Behavioural contexts

Kawaguchi (1937) has defined the use of *HYU* from parents to their young. Indeed in the study during 1976–1978, *HYU* was significantly associated with parental behaviour in attending nestlings and fledglings (Appendix B-3a). However, in later observations during 1979–1981, *HYU* was repeatedly produced by birds with food in the bills, perching alone out of sight of the recipient (Appendix B-3b). The sender was likely to be approached by another bird, or sometimes the sender itself made an approach to the other. Then the food was transferred either from a male to a female or from parents to offspring.

G. *KRRR*

1. Physical structure

KRRR was a quiet, rolling, protracted noise, resembling cats' purring (Fig. 6A). 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 sender. Females called it more often than males. Calls were similar between the sexes. For female calls (Appendix A-22), 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.

2. Behavioural contexts

KRRR was most frequently heard from females during the pre-incubation and incubation stages. Females emitted the call when they were likely to be fed by their mates, who were staying nearby, hunting,

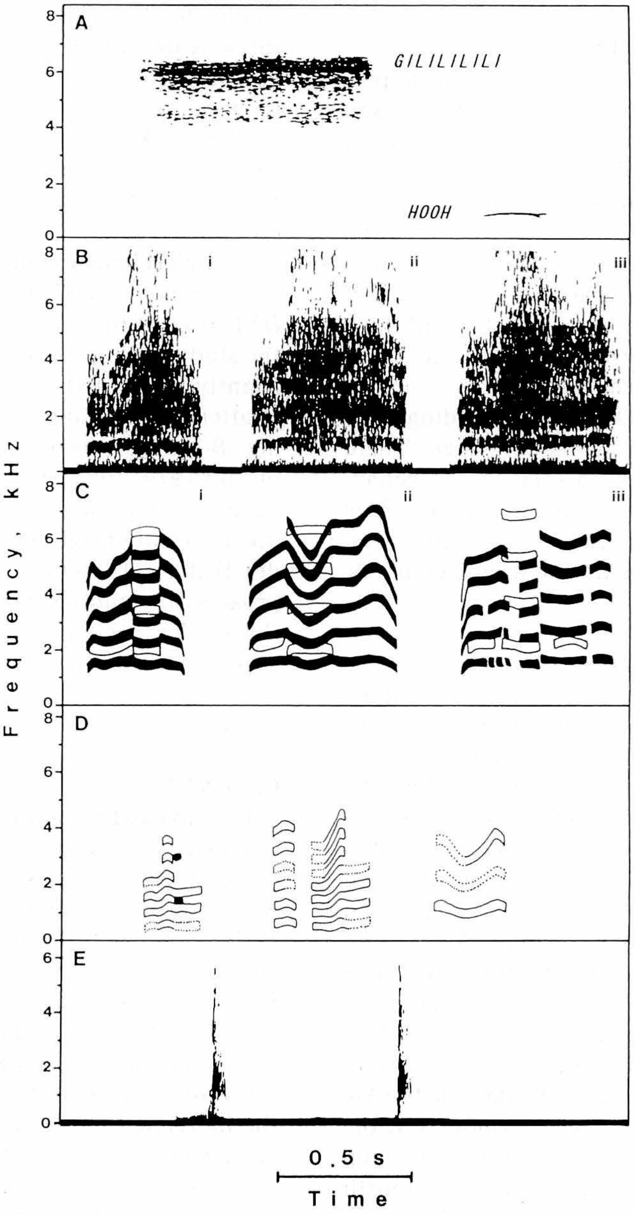


Fig. 7. Sonagrams of adult sound 4: *HOOH, QUAY, BUF,* and *PACK.* A, *HOOH* produced after a nestling's *GILILILI* (narrow-band, 80–8000 Hz). B, three calls of *QUAY* (wide-band, 80–8000 Hz). C, *QUAY* (main frequencies and their harmonics for B). D, *BUF* (main frequencies and their harmonics obtained for three calls). An unrelated short sound (black) is found in the first call. Dotted line indicates weakly presented parts. E, *PACK* recorded from a young male (wide-band, 80–8000 Hz).

holding a prey, preparing food and calling *HYU.* On hearing *KRRR,* the male approached the mate or *vice versa.* Food was quickly passed to the female. Parent birds also called *KRRR* when they fed offspring. Further, birds called *KRRR* when they were separated from their mates by the distance of 1–20 m. The distance was often shortened after the vocalisation. *KRRR* was also significantly associated with preening, in particular mutual preening (Appendix B-4).

H. *CHEEE*

1. Physical structure

CHEEE was a long, piercing squeal. It was heard from a distance of up to approximately 100 m. Only males produced the call (Fig. 6 B). The physical features for three birds were as follows:

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

2. Behavioural contexts

CHEEE was produced as males copulated. Males immediately left females after the call, while females stayed at the site of copulation.

I. *MEW* and *MEEEW*

1. Physical structure

As Kiyosu (1965) reported, local people in Japan call the Japanese Brown Hawk Owl with nick names: Neko-dori (Cat-birds) and Miyah-tsuku (Meow-owls). Certainly, both males and females had cat-like vocalisations. They varied between soft *MEW* and quite weird caterwauling *MEEEW* (Fig. 6C).

From the study of eight calls of one individual, *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. The frequency ascended slowly and descended quickly, and its range widened towards the end. The third and fourth harmonics were emphasised. The bird called *MEW* as quietly as to reach only the vicinity of the sender or sometimes as powerfully as to be heard from up to 100 m away.

MEEEW was a longer, lower-pitched call than *MEW*. The individual mean duration (CV, number of sample calls) 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 (number of sample calls) 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.

2. Behavioural contexts

MEW was heard from parents, when their young fledglings were perched near the ground, or were wandering about the ground. There was potential danger from ground-living animals including humans (Appendix B-5). 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. They called as larger bird species, such as the Ural Owl *Strix uralensis*, the Black Kite *Milvus migrans* and the Night Heron *Nycticorax nycticorax* came nearby. Unlike *MEW*, the vocalisation is accompanied by dashing flights towards the enemy. The enemy usually retreated from the attack. In some cases, people were assaulted with *MEEEW*. It was also used against conspecific birds. Territorial males called in the persistent territorial dispute. The rivals eventually fled away from the callers or were chased away. Secondly, a widowed female called it whenever the replacing male disturbed her to attend her offspring.

J. *HOOH*

1. Physical structure

HOOH was a hollow sound stressed at the onset. It was always emitted singly (Fig. 7A). Both sexes called, and the physical features were as follows:

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

2. Behavioural contexts

HOOH was most frequently produced 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 (Appendix B-6).

K. *QUAY*

1. Physical structure

QUAY was a harsh, rusty sound. It could be heard from up to 50 m away. None of the calling birds was identified as female. *QUAY* was composed of two simultaneously produced elements, which were unrelated in terms of temporal mode and modulated frequency (Figs. 7B, 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 emphasised. The individual mean duration ranged between 286 and 490 ms and the variation was high within individuals (CV: 20.5–26.0%).

2. Behavioural contexts

QUAY was a rare sound heard from solitary birds near the nest site. On an occasion, a male sang and his mate joined in singing from the nest hole. Suddenly the male started to utter *QUAY* several times and switched to *GUF*.

L. *BUF*

1. 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. 7D. 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 emphasised than the fundamental.

2. Behavioural contexts

On one occasion, a bird produced *BUF* between *MEEEW* calls. On the other occasion, a bird was perched near the nest tree.

M. 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.

N. *BYAHBYAH*

1. Physical structure

BYAHBYAH was a strikingly bizarre yowl. No recording was made, but it lasted for a few seconds.

2. Behavioural contexts

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 handler to release them.

O. *PACK*

1. 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 (Fig. 7E).

2. Behavioural contexts

PACK was made when senders 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.

IV. Development of the Vocal Repertoire

In the present section, juvenile vocal repertoire is briefly surveyed in the first year of development after hatching (see p. 7). Nestlings (0–27 days old) had 4 vocal sounds: *LEEE*, *GILILILI*, *CHILILILI* and *KYRRKYRR*. Fledglings (4–8 weeks old) increased the repertoire to 8 vocal sounds: *LEEE*, *GILILILI*, *CHEWLEE*, *BYAHBYAH*, *PUH*, *SOO*, *POOH* and *O-GUF*. Juveniles further added three types of vocalisation, *PY-O*, *BEH*, and *SCHEEE* by the time of autumnal migration. The subsong *O-GUF O-GUF* and transformation of calls from juvenile to adult form also occurs for *CHEEE*, *MEW* and *MEEEW*. Later, another sound PUR appeared during the first year of development. As for nonvocal sound, young birds snap bills to make a sharp sound *PACK*.

Young birds emitted *LEEE* and *GILILILI* from an early stage of development until 13 weeks old (Figs. 8A, B, C). *CHILILILI* appeared late in the nestling stage (Fig. 8D).

CHEWLEE was emitted between 7 and 15 weeks (Figs. 8E, F).

KYRRKYRR was recorded but has not been analysed sonagraphically. It was uttered by nestlings, when they were alone

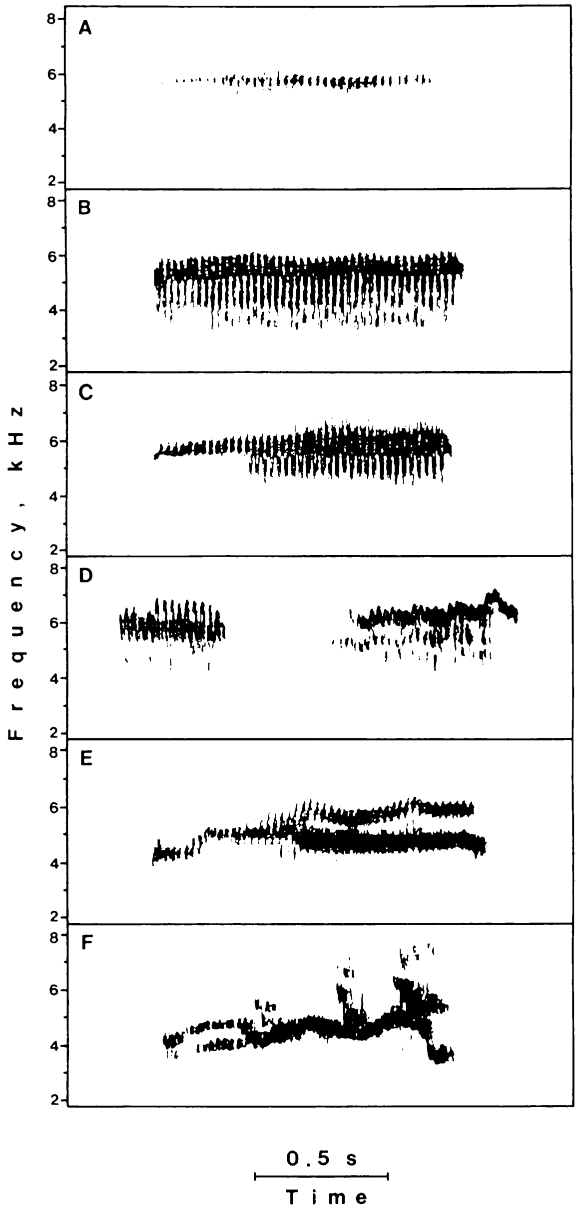


Fig. 8. Sonagrams of juvenile sound 1: *LEEE*, *GILILILI*, *CHILILILI* and *CHEWLEE*. A, *LEEE* produced by a 17-day-old bird. B, *GILILILI* produced by a 30-day-old bird. C, combination of *LEEE* and *GILILILI* produced by a 30-day-old bird. D, two calls of *CHILILILI* produced by a 30-day-old bird. E and F, *CHEWLEE* produced by a 3-month-old bird. (wide-band, 80–8000 Hz)

or handled by people.

BYAHBYAH was produced after 6 weeks at the latest.

PUH, *PY-O*, and *SOO* were uttered by captive males (Figs. 9A, B, C). *PUH* and *SOO* appeared between 8 and 14 weeks, and *PY-O* between 9 and 26 weeks. These calls were commonly heard from a bird playing with some materials such as leaves and pieces of paper. *PUH* was also heard during preening. *PY-O* was emitted by the bird holding a prey as it was approached by people.

SCHEEE was heard from the birds over 8 weeks old (Fig. 9D). They emitted the call during the play session. In the play, they suddenly grabbed up pieces of leaves or at a

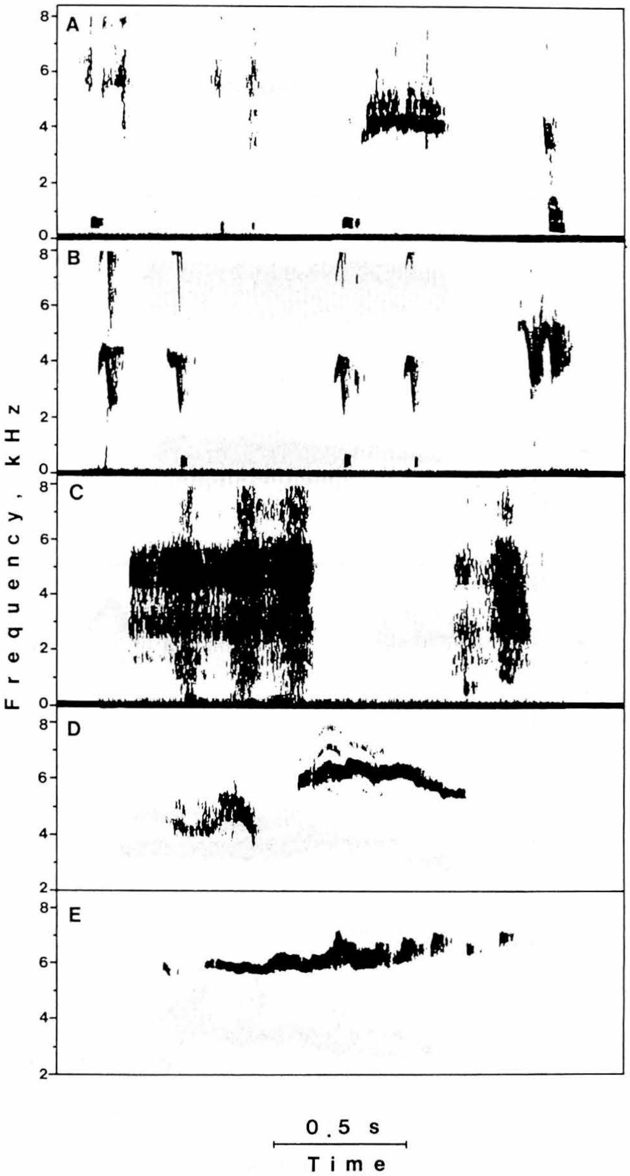


Fig. 9. Sonagrams of juvenile sound 2: *PUH*, *PY-O*, *SOO* and *SCHEEE*. A, *PUH*. A young male called the first three calls during the play with a piece of paper, which simultaneously made noises in higher frequencies. The fourth call was immediately followed by *CHILILILI* in higher frequencies. The last call occurred immediately after *PY-O*. B, *PY-O* was repeated singly or twice in succession. C, long and short bouts of *SOO*. D, *SCHEEE* produced by a 3-month-old male immediately after *CHILILILI*. E, *SCHEEE* produced by a 2-and-a-half-month-old male. (wide-band, 80–8000 Hz).

corner of cage. They opened the wings wide or fluttered vigorously and then called *SCHEEE*. It is speculated that this behaviour is the prototype of copulatory behaviour in adult males. Indeed, *SCHEEE* turned out to be *CHEEE* at 12 weeks.

POOH was first noticed at 7 weeks (Fig. 10 A). The captive bird uttered the call, whenever it saw other birds and aeroplanes flying to pass windows. The behavioural context appear to suggest that *POOH* is the prototype of *MEW* and *MEEEW*. Actually, *POOH* turned to *MEW* and *MEEEW* by the 25 th week.

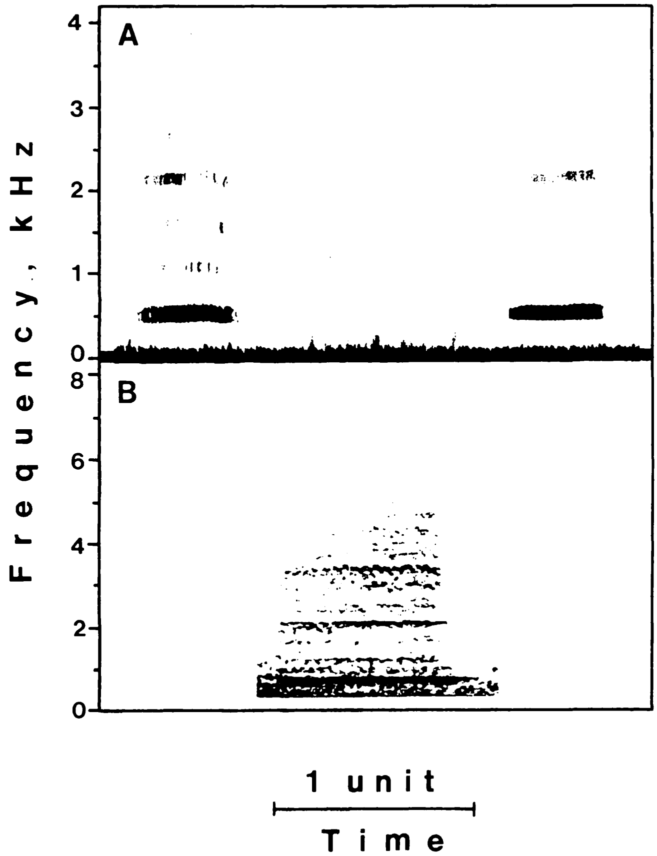


Fig. 10. Sonagrams of juvenile sound 3: *POOH* and *BEH*. A, two calls of *POOH* (wide-band, 40–4000 Hz, unit time of one second). B, *BEH* (narrow-band, 80–8000 Hz, unit time of 0.5 seconds).

BEH was heard between 9 and 26 weeks (Fig. 10B). No clear context was known.

O-GUF was heard after 7 weeks (Figs. 11A, B). The captive juvenile uttered it when it heard people approaching, when unfamiliar objects were presented, and before the pseudo-copulatory behaviour.

The subsong appeared as early as 8 days after fledging in the wild (Figs. 11C, D). It was rather throaty and uncontrolled compared to the clear timber and temporal organisation of adult songs. In the captive male, the subsong emerged between 10 and 14 weeks, when *O-GUF* was delivered in the unit structure, *O-GUF O-GUF*. In the wild, subsongs were heard on a few occasions. Juveniles produced subsongs in response to the male parent's song from some distance away. They flew to the parent afterwards. In captivity juveniles, subsongs were produced spontaneously or induced by playback of recorded songs of conspecific males.

In captivity, the subsong resumed after 27 weeks, and the full song was heard after 32 weeks. In the literature, the full song did not develop until later years. Uki (1973) reported that a high-pitched *WOO* in the unit structure was produced in the third year, and that the full song appeared in the fourth year. Nakanishi (1936) also observed the first full song in the fourth year.

Finally, *PUR* was added to the repertoire at 28 weeks (Figs. 11E, F). The young male often presented food to a human observer. It tended to call *PUR*, as it prepare, carry and present food to the observer. This behaviour was in common with the behavioural context of *HOH* and *HYU* in the adult repertoire.

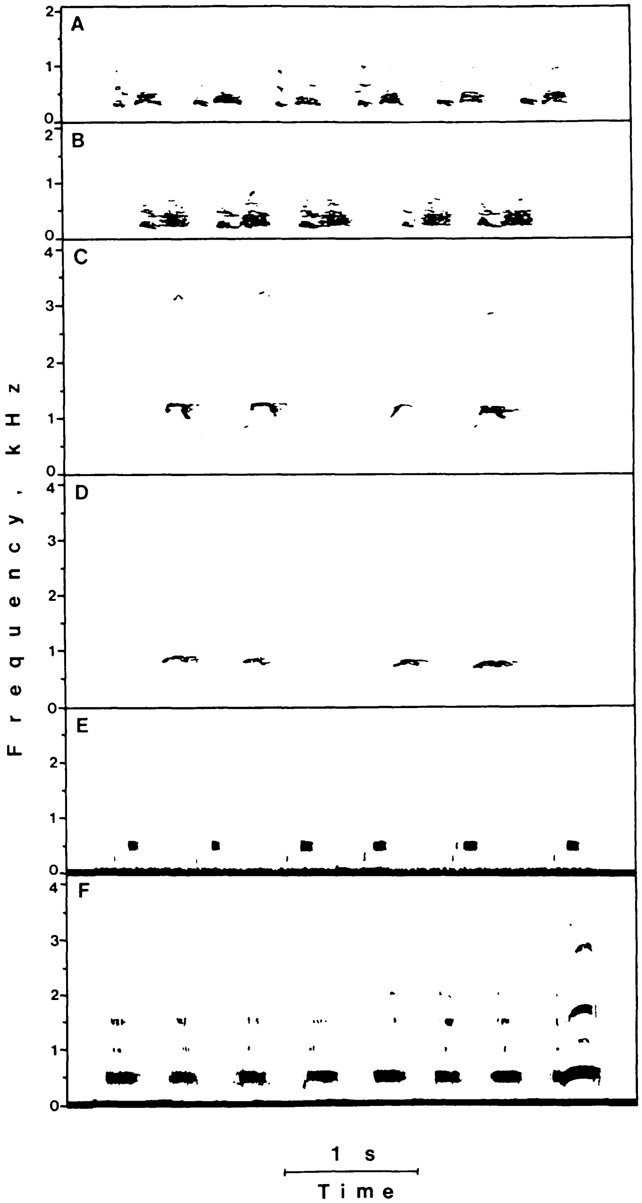


Fig. 11. Sonagrams of juvenile sound 4: *O-GUF*, *K-HOOH* and *PUR*. A, *O-GUF* produced by a 3-month-old bird (narrow-band, 40–4000 Hz). B, *O-GUF* produced by a 6-and-a-half-month-old bird (narrow-band, 40–4000 Hz). C and D, *K-HOO* produced by 1-month-old birds (narrow-band, 40–4000 Hz). E, *PUR* produced by a 6-and-a-half-month-old bird (wide-band, 40–4000 Hz). F, an 11-month-old bird called *PUR* which graded to *K-HOO* towards the end of bout (wide-band, 40–4000 Hz).

V. Discussion

A. Interpretation of messages, meaning and functions

In the present section, messages, meanings and functions of the acoustic signals of the Japanese Brown Hawk Owl are discussed after Smith (1965). Clues to messages should be sought in the physical feature of vocalisations, behavioural contexts and non-behavioural nature of senders, neglecting the responses of other birds. However, assumptions are sometimes necessary to make in view of behaviour of potential receivers.

Here the list of possible messages is given:

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

Behavioural messages
(behavioural supplement)

- probability
- intensity
- relative stability
- direction

Non-behavioural messages

- species
- subspecies
- local population
- individual
- age
- sex
- breeding condition
- pairing condition
- family group
- location

Definitions of respective messages are given by Smith (1977a). Meanings are interpreted from the response of receivers, and functions are inferred from meanings to the receivers. As for the adult vocal repertoire, messages are interpreted for all sounds except *BUF* and light rustling made by the wings. In Table 3, a summary of messages proposed for the most common 9 adult sounds is given.

1. *K-HOO* (the Song)

1) Messages

Identity and mating status

K-HOO is most likely to carry information concerning species' identity. Additional information about the identity of local populations may be difficult for an absence of clear dialects. However, audible differences among individuals and those between the sexes suggest that *K-HOO* may carry information concerning the individual identity and sex of the sender. The result of playback experiment actually supports such information. Further, information about the males' mating status may be encoded in the frequency of singing. Unpaired males tended to produce *K-HOO* more frequently than paired ones (Oba, 1987).

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 singing at an exposed perch seem to facilitate the chance of interactions. However, since singers often performed none of the alternatives, hesitating between selections, *K-HOO* could also encode a message of indecisive behaviour. The singer may be able to send an additional message about attentiveness to other conspecific birds' songs and movement by beaming *K-HOO* in a particular direction.

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

Sites and distance

Since repetition of short, loud elements with an abrupt start and finish renders the vocalisation easily locatable from a distance (Marler, 1957), *K-HOO* appears to contain a message about the singers' momentary location and also the site to which female parents attempt to guide their young. *K-HOO* may convey a message of the long-term location such as the nest and territory. Further, it may carry a message about the distance of the singer, since part A, which attenuates

Table 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	●					●		●	
attack			●						●
escape			●						
copulation or sexual behaviour				●					
association		●							
indecisiveness	●	●	●	●				●	
locomotion							●		
incompatible set of behaviour alternatives	●		●						
site	●								
food					●				
seeking	●			●	●	●			
receptiveness						●			
attentiveness	●								
Behavioural supplement									
probability	●	●	●	●		●		●	
intensity	●	●	●		●	●		●	
relative stability	●	●	●	●		●		●	
direction	●								
Non-behavioural									
species	●						●		
individual	●				●				
sex	●				●		●		
mating status	●								
distance	●								
location	●				●			●	

more quickly than part B, can be used as an indicator of travelling distance.

2) Meanings

The meanings of *K-HOO* may be summarised as instructions on how to interact with the singer in a beneficial way. To conspecific males, male songs may be a territorial *keep out* signal. Since female songs occur only in the presence of the simultaneously singing male during a territorial dispute, they may mean that the female assists her mate in advertising the territory. To females, male songs may mean that a possible mate is available. The own mate's song may provide the female with assurance and reaffirmation of the pair-bond. To juveniles, their parents' songs may be taken as reassurance.

3) Functions

As birds sing, both senders and receivers can choose their location and distance, so that they may pursue an appropriate type of interactions from the following list:

Male song

- 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

Female song

- pair association and co-operation
- sexual stimulation
- family association and cohesion
- territorial defence by association with the male

The range of interactions for both males and females well coincides with that of oscine songs (Catchpole & Slater, 1995). Consequently, relevance to denote *K-HOO* as a song can be highly supported in view of possible functions interpreted from physical structure and behavioural context.

2. *HOH*

HOH may not contain messages about the identity of the sender, since vocalisations 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 as the distance from other individuals shortens. It may also coordinate the breeding behaviour.

3. *GUF*

GUF may encode a message about incompatible behavioural alternatives, attack and escape. The sender 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 sender is aggressive enough to attack. The function may be to control the interaction when the caller's territorial and social status is really threatened. It seems to act as the final threat and deterrent before overt aggression.

4. *OO-COO*

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 sender is sexually receptive. The functions may be to coordinate the sexual behaviour between mates.

5. *POO*

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.

6. *HYU*

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 sender (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 sender. It may function to inform the time of feeding acoustically, so that recipients need not waste time and energy to receive food items.

7. *KRRR*

KRRR may contain a message that the sender seeks for and is receptive to a close range interaction. The message about the probability, intensity, and relative stability in seeking such interaction can be encoded by repetition and amplitude modulation.

Meanings of *KRRR* seem to change with situations. When a male is hunting or holding prey, his mate's *KRRR* may mean that the sender asks for prey. If he is not engaged in hunting, the same call is likely to mean that the sender merely wants a contact. When the sender is preening itself, the meaning of calls may be that the sender is soliciting for preening. Further, to the offspring the call of a parent may mean that parents shortly bring them food.

It is suggested that *KRRR* may function to manipulate the other birds' behaviour, so that the sender may succeed in the close range interaction of different purposes.

8. *CHEEE*

CHEEE may contain a message about the sender's sexual and specific identity and also a message about the location of the sender. To females, *CHEEE* may mean that the male's flight after copulation does not constitute any danger. A possible function may be mate assurance after copulation.

9. *MEW* and *MEEEW*

The caller of both *MEW* and *MEEEW* is believed to be in conflict between the two motivations of fear and aggression. The presence of two distinctive forms and their variations seem to provide behavioural supplemental messages. The message may be that the sender is interactional but indecisive between the two incompatible alternatives, attack and escape. Both calls clearly encode a message about the sender's location.

On hearing *MEW*, young birds may get the meaning that it is dangerous to move. To enemies, the same call may be that their movement is monitored. As for *MEEEW*, the meaning to receivers may be that the caller is intensely antagonistic to them, whether they are conspecific rivals or other species.

It can be suggested that *MEW* functions as an alarm to warn kin in possible danger. *MEEEW* is speculated to be used as a more intense threat.

10. *HOOH*

Message, meanings and functions are difficult to infer from the result. However, *HOOH* is considered not to contain messages about feeding and food.

11. *QUAY*

Message, meanings and functions are difficult to infer from the result.

12. Wing noises

The message, meaning and function of these noises are unknown; however, the former may contain a message of attack.

13. *BYAHBYAH*

BYAHBYAH may contain a message that the caller attempts to avoid interactions. In spite of lack of knowledge concerning the response of receivers, 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.

14. *PACK*

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.

As for the juvenile sounds, it is not easy to interpret messages, meanings and functions, since many of them were only observed in captivity. It is interesting to see some calls appeared in play sessions and eventually transformed to adult calls. In Table 4, it is attempted to show messages proposed for 11 sounds. *LEEE*, *GILILILI* and *CHILILILI* occurred most commonly in the juvenile vocal repertoire. Its function can be suggested to guide parents to feed or contact young birds while controlling their agonistic tendency.

B. Graded vocalisations

As it is often quoted that owls hoot, the

Table 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		●	●				●		●		●
attack								●			
escape				●				●			
association										●	
indecisiveness							●	●	●	●	●
incompatible set of behaviour alternatives								●	●		●
site									●		
care	●										
seeking	●	●							●		
receptiveness	●	●									
attentiveness									●		
exertion and/or play				●	●	●					
Behavioural supplement											
probability			●					●	●	●	
intensity	●	●	●					●	●	●	
relative stability	●	●	●					●	●	●	
direction									●		
Non-behavioural											
species	●								●		
individual									●		
sex									●		
age	●	●							●		
location	●								●		

Note: *LEEE etc* includes *LEEE, GILILILI, CHILILILI* and *CHEWLEE.*

Japanese Brown Hawk Owl certainly hoots. Considering the simple vocal apparatus in owls (Miller, 1934), their vocalisations cannot be as complicated and elaborate as those of oscines. However, careful listeners can tell that there are different kinds of hooting: *K-HOO, HOH, GUF, OO-COO, POO* and *HYU.* They appear to be graded each other while each of them keeps a unique sound quality. How are they graded in the physical structure? How are such differences utilised in a system of vocal communication? Is the physical structure relevant to the behavioural context? What is the mechanism in development such graded vocalisations?

1. Physical dimensions

Compared for the general structure in Table 5, the common feature throughout the graded vocalisations is that elements are always repeated in a bout. The two-part

Table 5. Comparison of physical structure between graded vocalisations.

Feature	*K-HOO*	*HOH*	*GUF*	*OO-COO*	*POO*	*HYU*
Hierarchical structure						
Part A	●	(●)	(●)	●	—	—
Part B	●	●	●	●	●	●
Unit	●	—	—	—	—	●
Bout	●	●	●	●	●	●
Frequency modulation						
Part A	A, F, DA	None	None	D, F, AD & AFD	—	—
Part B	AF, AFD & AD	AF, AFD & AD	AFD & AD	AFD & AD	AF, A, F	AF, AFD & AD
	(C, R)	(L, C)	(L, C)	(L, C)		(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: ●, present; (●), the presence could not be denied; —, absent. Emphasised harmonics are in brackets.

structure of elements distinguish *K-HOO*, *HOH*, *GUF* and *OO-COO* from *POO* and *HYU*. The unit structure is found only in *K-HOO* and *HYU*. Types of frequency modulation is another feature to distinguish graded vocalisation. Having only A and F types, *POO* is separated from all the rest that exhibit AFD & AD types. The latter is then separated by the location of inflection. *K-HOO* and *HYU* are inflected rightward from central point, while the others leftward from centre. It is speculated that *K-HOO* and *HYU* are homologous or homogeneous in the physical structure. Harmonics patterns are considerably different among the graded vocalisations to suggest that tonal quality provides an individually distinct feature.

In Fig. 12, the distribution of graded vocalisations in the frequency and temporal dimensions is compared for parts. Individual means are plotted, and outermost points are connected to show the general range. As for part A, male sounds are arranged from *OO-COO* to K-HOO via *HOH* as maximum and minimum frequencies increase (Fig. 12 A). Similarly, they show a gradual constriction of the duration range in the same order (Fig. 12B). Since female songs are produced generally higher in frequency, their vocalisations are divided in the two separate ranges. Whereas *HOH*, *GUF* and *OO-COO* cannot be singled out, their relative locations to *K-HOO* are maintained (Figs. 12C, D).

As for part B, male vocalisations are also arranged diagonally from *OO-COO*, *GUF*, *HOH* to *HYU* or *K-HOO* in the frequency dimensions. Here, *HYU* has a narrower frequency width than *K-HOO* (Fig. 12E). With regard to the duration and interval (short interval for *K-HOO* and *HYU*) dimension, *HOH* and *OO-COO* occupy wide ranges, while *K-HOO*, *GUF* and *HYU* show independent smaller ranges. It results in complex pattern of overlapping (Fig. 12F). As for females, the diagonal arrangement in the frequency dimensions are similarly noticed from *OO-COO* to *K-HOO* except for *GUF*. As mentioned above, the female song is higher in frequen-

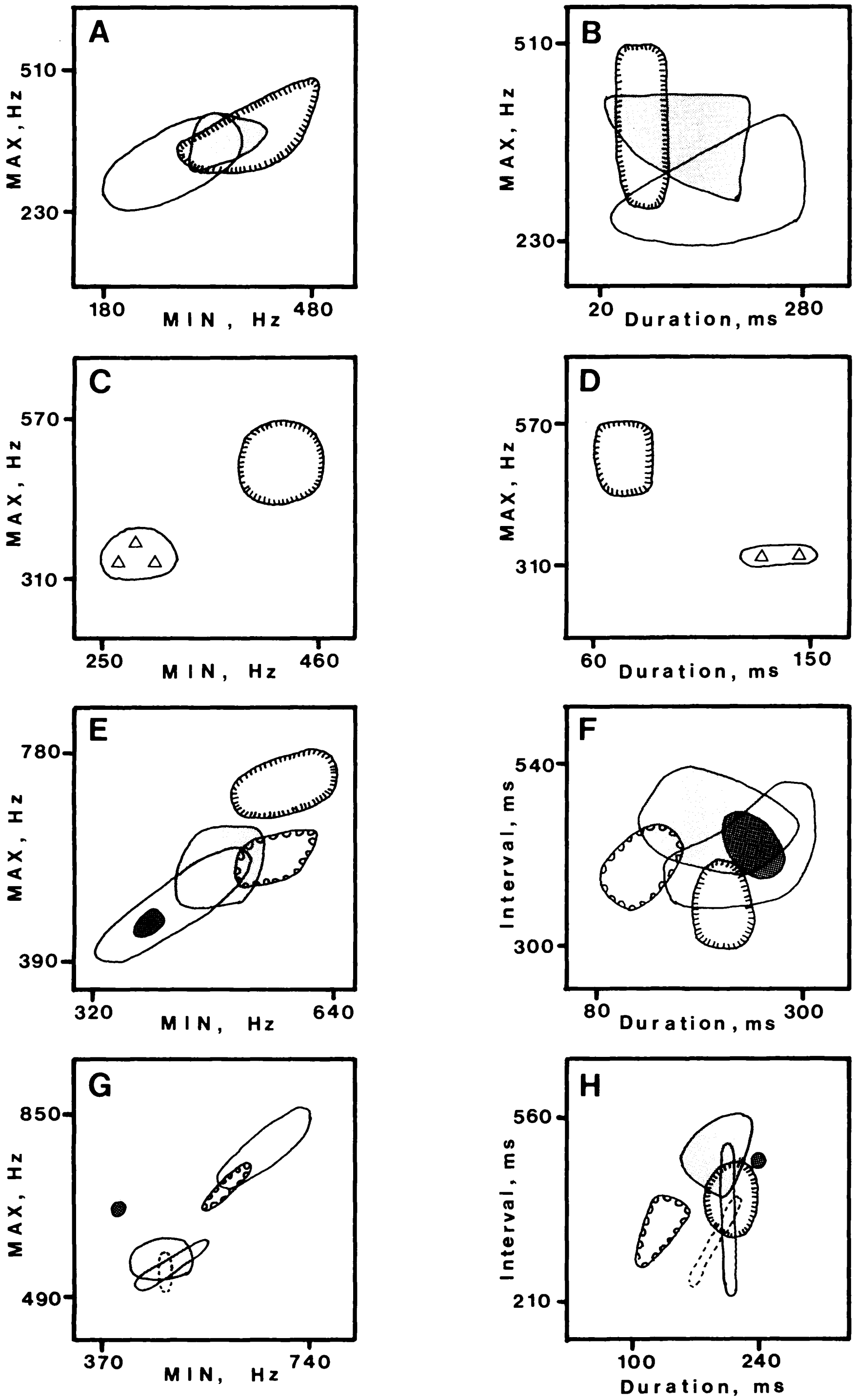


Fig. 12. Distribution of graded vocalisations in temporal and frequency dimensions. A and B, males' part a. C and D, females' part a. E and F, males' part b or element without part structure. G and H, females' part b or element without part structure. Graded vocalisations: *K-HOO* (toothed), *HOH* (shadowed), *GUF* (dark), *OO-COO* (plain), *HYU* (semi-circled), *POO* (broken), combined distribution of *HOH*, *GUF* and *OO-COO* (triangles). For *K-HOO* and *HYU*, the interval in F and H is short one.

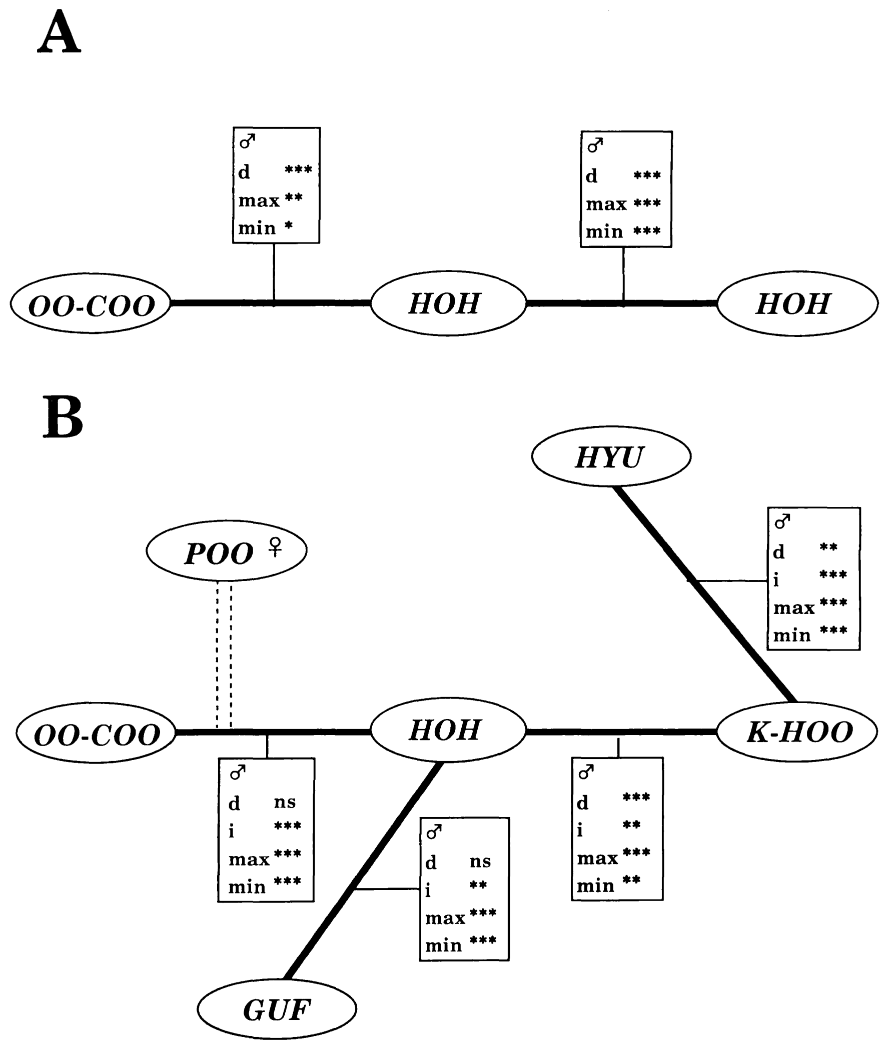


Fig. 13. Relationships among the graded vocalisations 1: physical dimensions. A, part a. B, part b. d, duration; i, duration of interval; max, maximum frequency; min, minimum frequency. Statistical probabilities for differences (two-way ANOVA with *a priori* test): ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ns, $p \geqq 0.05$.

cy, the female vocalisations are separated into the two groups. *POO* is closely related to *OO-COO* and *HOH*. *GUF* is shifted to the higher range. *HYU* is gradually shifted to lower frequency from *K-HOO* (Fig. 12G). As for the temporal dimension, the relative locations of *K-HOO*, *HOH*, *GUF* and *HYU* are similar to those of males. *POO* is clearly separated from *HOH*, but overlaps a little with *OO-COO*. (Fig. 12H).

To summarise, the relationships among the graded vocalisations are proposed in Fig. 13. In males, each vocalisation is significantly different from the others in many of the physical features including duration, interval, maximum and minimum frequencies for both parts. A series from *OO-COO*, *HOH* to *K-HOO* is a common trend in both parts. For part B, there are two branches, one from *HOH* to *GUF* and the other from *K-HOO* to *HYU*. Apart from the fact that the female songs are discretely higher in frequency, the general relationships among female vocalisations follow the males'. *POO* is related to *OO-COO* more than *HOH*.

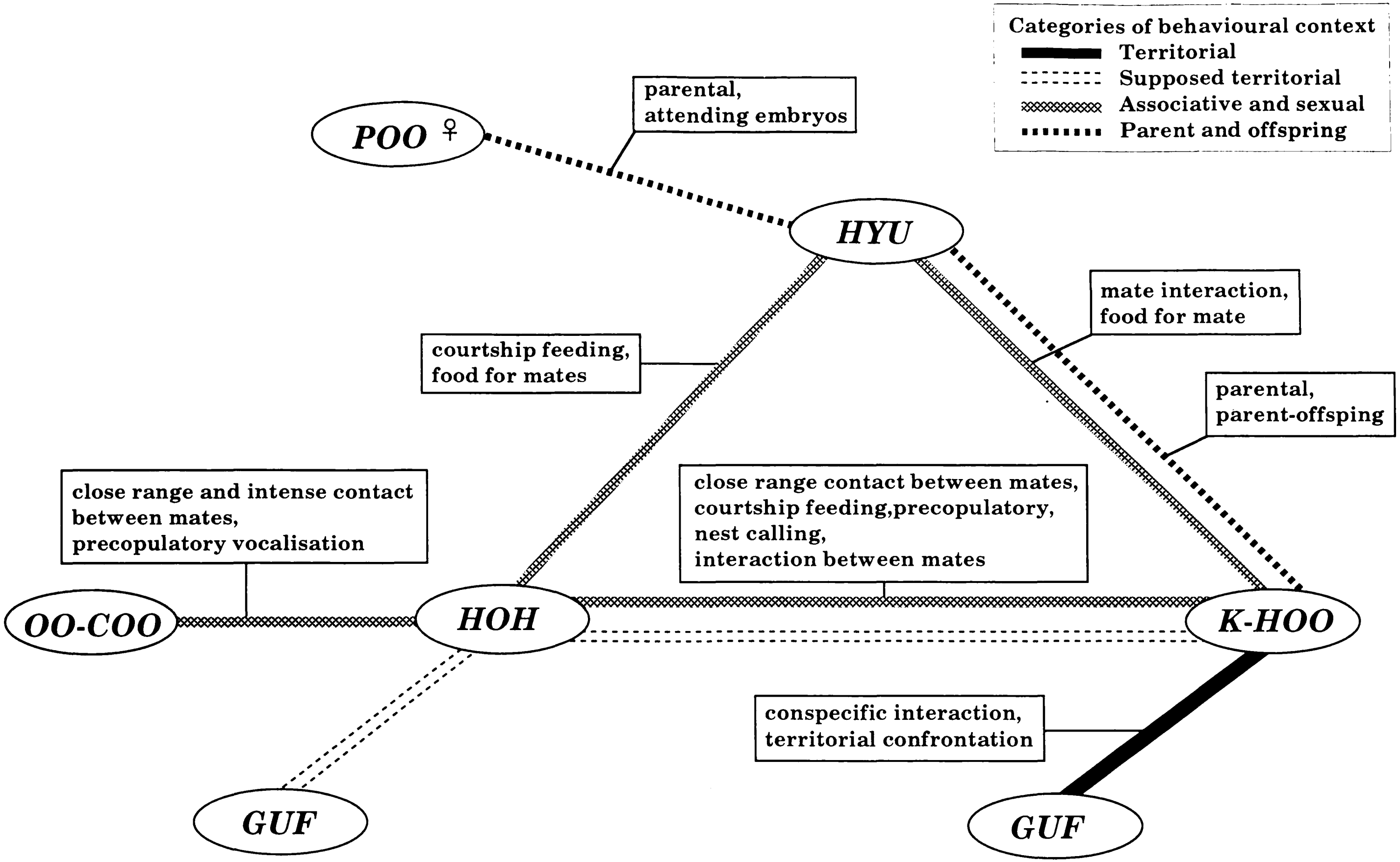


Fig. 14. Relationships among the graded vocalisations 2: behavioural aspects.

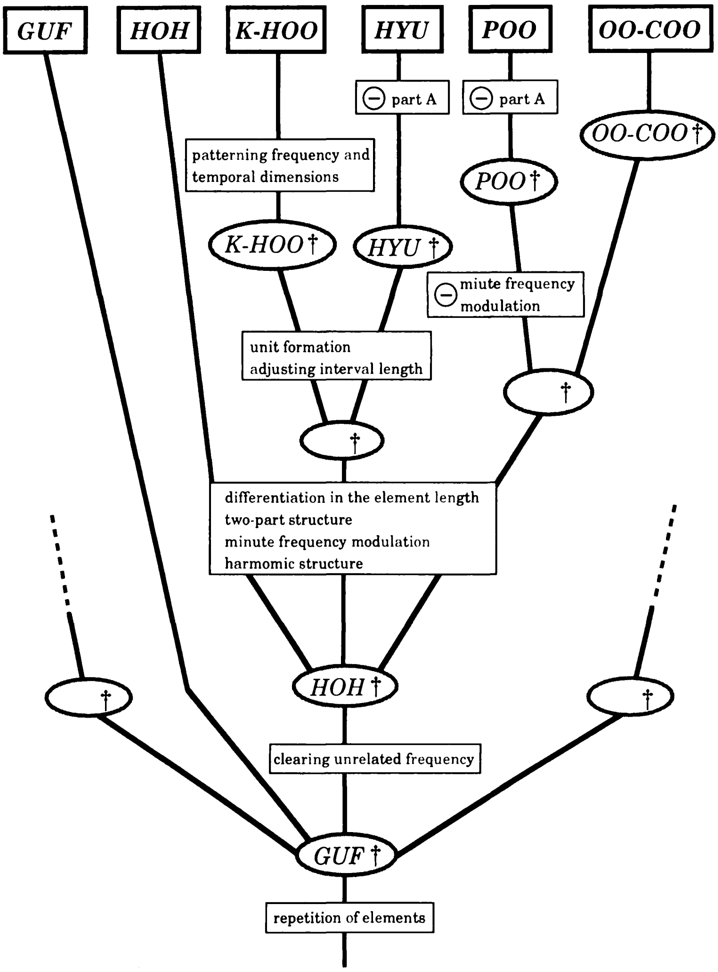


Fig. 15. A diagram of developmental history of the graded vocalisations. Vocalisations: square, present form; oval, derivative sound during the development;—+, extinct form; ⊖, missing features.

2. Behavioural aspects

Behavioural contexts of graded vocalisations can be classified into the following three categories of interaction between conspecific birds: territorial relationships, associative and sexual relationships between mates, and relationships between parent and offspring. In Fig. 14, each vocalisation is placed in a relative position according to their affinities and differences of contexts. Although *GUF* directly stems from *K-HOO* in the figure, it is highly suggested that *HOH* comes between the two in the territorial context as indicated by the dotted line. When the birds are involved in territorial confrontation, they briefly emit *HOH* as the song turns to the fierce call of *GUF* (Oba, 1987). Such momentary changes in vocalisations were not managed in the observation for the present analysis.

3. Development of vocal repertoire

As shown in Fig. 12, all graded vocalisations are found in 180–780 Hz in males and in a slightly higher range of 250–850 Hz in females. The duration of element or part B is in 80–300 ms in males and 100–240 m in females. The interval or short interval is 300–540 ms in males and 210–560 ms in females. Due to the physical constraint from their vocal apparatus, the owl sound should certainly be limited within a narrow band of quite a low frequency. It naturally follows that such a low-frequency sound can neither be short in length nor delivered quickly.

To increase the vocal repertoire in such conditions, one way is to select discreteness by allocating an isolated small range to each vocalisation. It is relatively easy if the potential range of frequency is wide and high. The other way is to pursue gradation by dividing the range with gradual overlap among different vocalisations. In the present case of the limited ranges of frequency and time are given, gradation is the feasible mechanism to accommodate 5–6 vocalisations.

How could gradation occur in the evolution of acoustic signals? A hypothesis is that the owls differentiate the physical structure of an original sound to gain derivative sounds, from which the eventual set of graded vocalisations of more complex structure develop. Although it is difficult to know the true original, the simplest and least organised vocalisation like *GUF* could be. The actual process of differentiation occurs in temporal organisation, structural refinement and specialisation. The level of temporal organisation advances with the repetition of elements, and differentiation in the element length, adjusting the interval length, and grouping of two calls as a unit. The structural refinement advances with clearing unrelated frequencies and adding the different set of harmonics to the fundamental frequency. As a result, the tonal quality of sound is adjusted from harsh or atonal to pure-tone-like for diversity of timbers (Jeans, 1937). Specialisation like the two-part structure and minute frequency modulations add the accent and impression of sound. The total pattern of frequency and temporal structure of element provides the song with a clue to individual identity (Oba, 1987). In Fig. 15, a diagram is given to summarise the proposed history of the graded vocalisations.

4. Motivational mechanism

By comparing the two relationship diagrams (Figs. 13 and 14), there are good correspondences between physical dimensions and behavioural contexts, to suggest the design of physical structures of vocalisations is directed by a factor behind the behavioural context. Morton (1977) suggested that the physical structures of vocalisations have significance for understanding vocal expression in vertebrates, and that in general the sounds are considered to reflect differences inmotivation. He coded the term motivation-structural rule, suggesting the relationship between sound frequency and motivation. In his model, vocalisation structures are predicted in the two physical dimensions, one for the sound frequency band ranging from low to high and the other for the sound quality ranging from harsh or atonal to pure-tone-like. An aggressive motivation is expressed with a low and harsh sound, and a fearful or appeasing one through a high and tonal sound. Further, the way of frequency modulation in an element is indicative of the two motivations. A rise in frequency expresses lowered aggressive tendencies and motivation tends toward fear. A drop in frequency shows increased aggressive tendencies and fearful and appeasing motivation tends to decline.

In Fig. 16, the graded vocalisations are examined for the Morton's model (1977). They are distributed in the upper 6 blocks, covering the whole range of aggressive tendencies and up to medium fearful tendencies. Apart from *POO*, each of the other graded vocalisations is located in the central block and extends toward other blocks. Morton suggested that sounds in the central block show up and down in frequency, which expresses a neutral or adaptively indecisive motivation and functions in a wide ranges of contexts. In the present case, it is suggested that these vocalisations can be used neutrally or indecisively in territorial, associative or sexual, and parent-offspring contexts, while they can express the changing motivational state by manipulating the frequency modulation types.

GUF is additionally located in the upper middle and right blocks. The downward slope in frequency indicates that motivation is tending toward aggression. Then, being the lowest harsh sound, *GUF* reaches an aggressive endpoint, inducing actual physical combats in a territorial encounter. In females, however, *GUF* is emitted in a relatively higher frequency range and located in the middle right block to express fearful or appeasing tendencies. Females usually avoid aggressive encounters.

In the territorial context, male *K-HOO* is

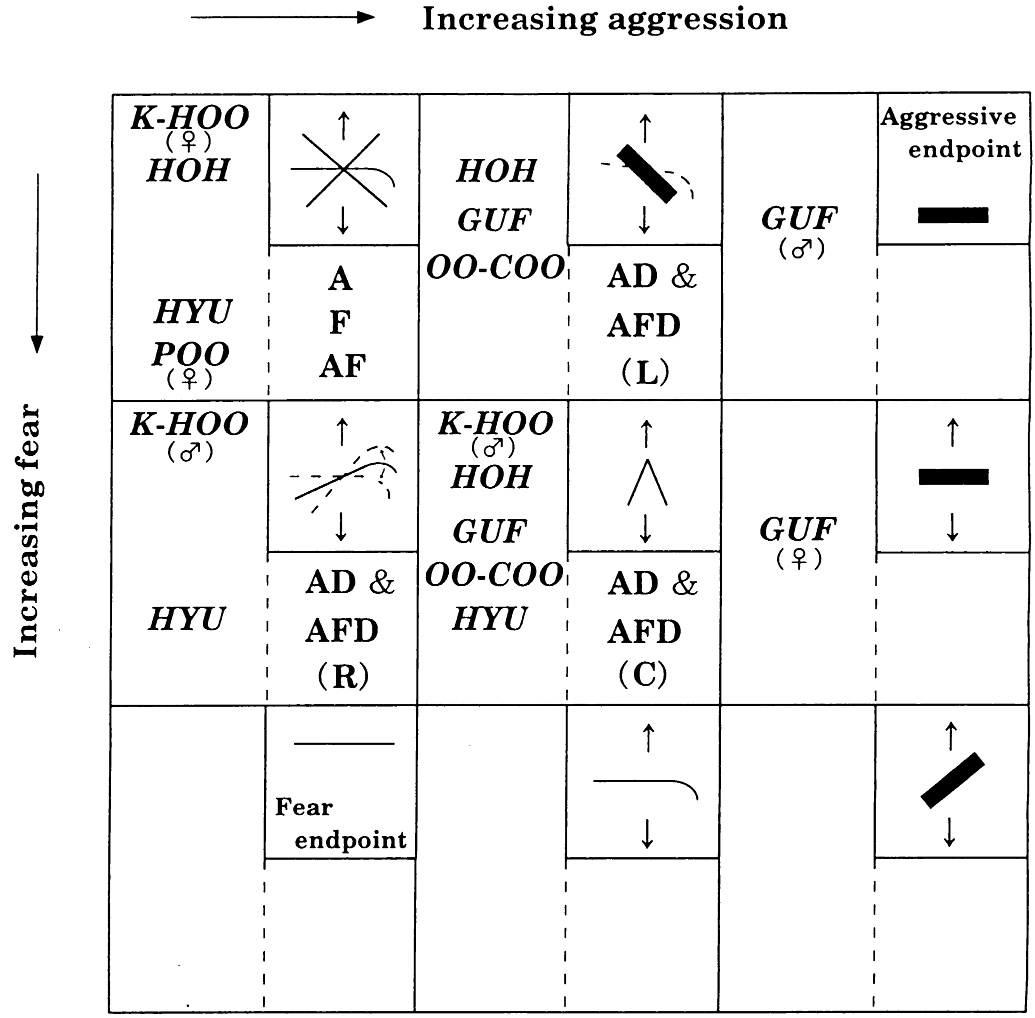


Fig. 16. Examination of the graded vocalisations under the motivation-structural rule. Each block includes a hypothetical sonagram (vertical scale, frequency; horizontal scale, time) with thin lines to indicate a pure-tonal sound and thick lines to show a harsh or atonal sound. The arrows mean that the sound can move up and down between the low and high frequency endpoints (Morton, 1977). Underneath is given the relevant frequency modulation type of part B (Table 1). To the left, the relevant types of graded vocalisations are listed for each block.

further located in the left middle block, which generally expresses low aggressive tendencies closer to the fear endpoint. *HOH* is then located in the upper middle and left blocks to intermediate between *K-HOO* and *GUF.* Contrary to *K-HOO,* it expresses increased tendency to aggression. The motivation-structural rule well supports the correspondence between the physical structure and motivational level in the interchangeable use of *K-HOO, HOH* and *GUF.*

In the associative and sexual context, *OO-COO* is additionally located in the upper middle expressing a motivation tending toward aggression. Here the sender tends to be the receiver in precopulatory duetting performances. *HYU* is located in the upper left and middle similarly to *K-HOO.* It expresses low aggressive tendencies or appeasing motivation, as the sender awaits the mate for courtship feeding. The motivation-structural rule again supports the correspondence between the physical structure and motivational level in the interchangea-

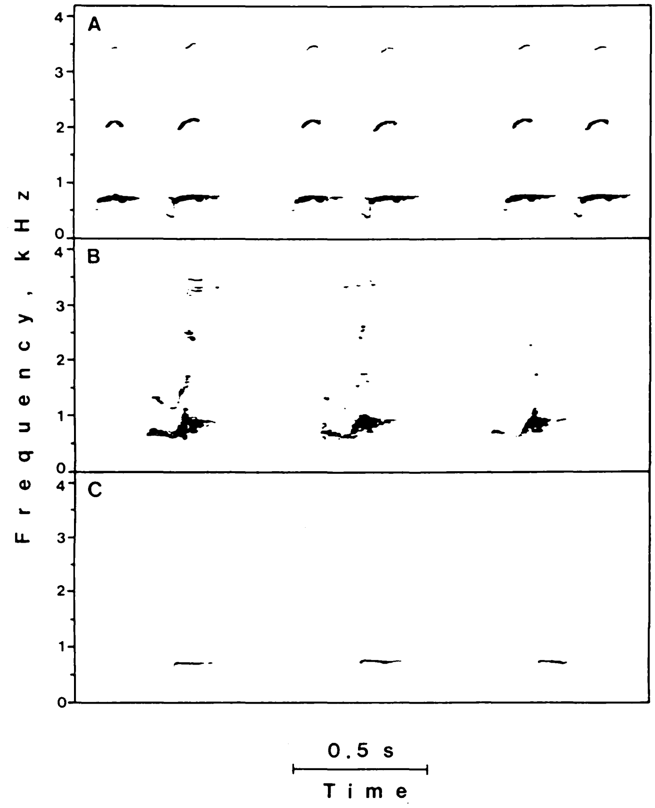


Fig. 17. Differences in the subspecific song of the Brown Hawk Owl. A, *K-HOO* recorded from a Japanese bird by the author in 1980; B, *HOO-OIP* recorded from an Indian bird by Marshall in 1974; C, *HOOP* recorded from a bird of Mindanao Island in the Philippines by Marshall in 1971.

ble use of *HYU* and *HOH* in courtship feeding, that of *HOH* and *OO-COO* in precopulatory vocalisation and the wide use of *K-HOO* in associative behaviour between mates.

In the parent-offspring interaction, *POO* is located in the upper left block for its frequency modulation. It expresses the least aggressive and fearful tendencies, as females call to attend eggs. The motivation-structural rule also supports the correspondence between the physical structure and motivational level in the use of *K-HOO* and *HYU* in parental behaviour.

Finally, the female *K-HOO* is located in the upper left block, expressing low motivational level both in aggression and fear. Female use *K-HOO* in less aggressive interactions.

In the present section, relationships in the graded vocalisation have been discussed for the present repertoire and its evolution. The examination of present forms and their background factors in view of physical and motivational mechanisms throws light on possible causes and functions of vocalisations.

C. Comparisons

1. Vocal repertoire of *Ninox*

There are distinct differences in the subspecific song of *Ninox scutulata*: type A, *K-HOO*; type B, *HOO-OIP*; type C, *HOOP* (Fig. 17). Type A is emitted in a unit of two elements as found in the northern subspecies, *N. s. japonica* and *N. s. ussuriensis*. Although Yuri and Aragaki (1975) described the song of *N. s. totogo* in a unit of three elements, it is considered a casual variation of type A (Yonashiro, pers. comm.). In type B, elements are repeated in succession. The first part *HOO* is lower pitched than the second part *OIP*, while Henry (1971) described otherwise for the call of Sri Lankan birds. Type B belongs to southern subspecies, *N. s. lugbris*, *N. s. hirsuta*, *N. s. obscura*, *N. s. burmanica* and *N. s.*

Table 6. Geographical distribution of song 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 & 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 & Nicobar Islands	B	Butler, 1899ab; Abdulali, 1964, 1978; Sálim & Ripley, 1969; Marshall pers. comm.
Burma	B	Stanford & Ticehurst, 1939; Smythies, 1953; Sálim & Ripley, 1969
Thailand	B	Lekagul & Cronin, 1974; Holmes, 1974*; Marshall pers. comm.*
Malay Peninsula	B	Medway & Wells, 1976; Kersley, 1972*; Marshall pers. comm.*
Sumatra	B	Mashall pers. comm.*
Borneo	(B)	Hose, 1893; Smythies, 1968.
Java	(B)	Bartels, 1928; Hoogerwerf, 1949.
Mindanao	C	Marshall pers. comm.*

scutulata, and possibly *N. s. bornensis* and *N. s. javanensis*. Type C is a monotonous song repeating single elements and it is suggested to belong to *N. s. randi* (Table 6). The discreteness observed between the different types of songs and its corresponding geographical isolation of breeding populations suggest that the need for a study of the subspecific status of *Ninox* owls.

In general, the vocal behaviour of other subspecies is not known. It should be noted that the pair of *N. s. ussuriensis* was observed to perform a duet using *K-HOO*. One of them had higher-pitched song than the other (Panov, 1973). Vocalisations similar to *MEEEW* were reported from *N. s. lugubris* (Jerdon, 1862), *N. s. hirsuta* (Wait, 1921) and *N. s. burmanica* (Smythies, 1953).

In other *Ninox* species, vocalisations have been described phonetically in three species. The Powerful Owl *N. strenua* has at least six types of adult vocalisation. The song is powerful *WHO-WHOO*, and the pair sang in duetting performances out of the nesting season. Other vocalisations are 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 vocalisation. The song is *WOOK-WOOK*, which gradually varied to *ER-WOOK-WOOK*. They performed singing in a coordinated duet in summer. Other vocalisations are 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 vocalisation: a cricket-like trill used for contact, *WHOOP-WHOOP* which developed during the first winter, a scream and a conversational note (Barnard, 1911; White, 1917; 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 vocalisation. The song *MORE-PORK* varied in the physical structures, such as a drop in sound frequency while singing, variations in clearness, tempo and number of repetitions, and seasonal changes in tone. Male songs were sometimes accompanied by monotonously repeated female songs. Other vocalisations are 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; Cheney, 1915; Stuart Dove, 1922; Fleay, 1925; Stidolph, 1925; Wilkinson, 1927; Fleay, 1940; Bryant, 1941; Harrison, 1973; Van der Weyden & Ginn, 1973).

It is possible to comment on the general design of *Ninox* vocal repertoire based upon the present study of the Brown Hawk Owl and these three species. The minimum set of adult vocal repertoire appears to include the following five types: the song, shrieking, screaming, a cat-like sound, and trilling. The song is delivered in a unit composed of two elements. Gradation and variation is the usual case for physical structures of song. Songs are produced by both male and female birds, and females tend to sing at a higher pitch than males. Duetting between the mates of a pair is common. In the juvenile repertoire, a cricket-like, shrill trill or whistle seems to be in common. Beak snapping is also believed to be included in the repertoire.

2. Vocal repertoire of the Strigiformes

In the Strigiformes (a total of 133 species over 24 genera), adult vocalisations have been described for 87 species from 21 genera. Only one type of vocalisation, generally the song, is known in 26 species and 2–4 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;

Table 7. 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	-	-	-	Ligon 1967; Smith *et al.* 1982.
Bubo bubo	9	1	4	1	König, 1972; Leibundgut 1973.
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	Wendland, 1963; Southern, 1970; 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.
Ninox connivens	7	1	1	-	MacGillivray, 1914; Fleay, 1940, 1942.
N. novaeseelandiae	7	-	-	-	M'lean, 1911; Stuart Dove, 1922; Stidolph, 1925; Van der Weyden & Ginn, 1973.
N. scutulata japonica	13-14	3	4	1	This study.
Sceloglaux albifacies	9	-	-	-	König, 1972; Harrison, 1973; Van der Weyden & Ginn, 1973.
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	Bergmam & Ganso, 1965; Schönn, 1976.
Micrathene whitneyi	9	-	1	-	Ligon, 1967.
Aegolius funereus	9	1	2	7	Kuhk, 1941; König, 1972; Van der Weyden & Ginn, 1973.

Note: V, vocal sounds; NV, non-vocal sounds; *, sonagraphical study; -, unknown. Diurnal species are underlined.

Higuchi & Momose, 1980; Scott, 1980). In Table 7, the size of the vocal repertoire is listed for the 27 species including the Brown Hawk Owl, which have or have been reported to have at least five types of vocalisation. Although more detailed studies are required to obtain the general picture of strigidine vocalisations, adult birds have up to fourteen vocal and up to three non-vocal sounds. Nestlings have up to four vocal and one non-vocal sound. The Japanese Brown Hawk Owl can be ranked one of the highest in the vocal repertoire size.

The initial prediction was that the nocturnal owls should depend upon acoustic signalling much more than diurnal birds, as they have to communicate in the darkness. Thorpe (1961) presented call vocabularies in a wide range of birds including a gull, a fowl, a dove and several songbirds. The range of vocabulary size was 6–15 in adults and 1–3 in nestlings. It means that the owl repertoire size is not much different from other birds. It is interesting that a smaller repertoire size of 6–7 is found in the owls of diurnal habits, including the Snowy Owl *Nyctea scandiaca*, Short-eared Owl *Asio flammeus* and Hawk Owl *Surnia ulula*. However, another diurnal species, the Burrowing Owl *Athene cunicularia*, contrarily displays the highest number of vocalisations, to assess the prediction difficult. The details of ecology and behaviour need to be reviewed prior to any conclusion.

Sexual difference in songs have been reported for a variety of owls in *Otus*, *Bubo*, *Pulsatrix*, *Strix*, *Asio*, *Ninox*, *Glaucidium*, *Micrathene*, and *Athene*. In general, female songs tended to be higher-pitched than male songs. (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 also differ between the sexes, although there is no clear overall trend.

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アオバズク *Ninox scutulata japonica* の音声のレパートリーと その自然誌の記録

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アオバズク *Ninox scutulata japonica* の音声のレパートリーについて，主として野生の個体の行動の詳しい観察と音声録音を基に，飼育個体のデータも参考にして研究を行った．成鳥には少なくとも13種類のボーカル音がある．これには本種のさえずりである *K-HOO* のほかに，*HOH, GUF, OO-COO, POO, HYU, KRRR, CHEEE, MEW, MEEEW, HOOH, QUAY, BUF* が含められるが，飼育鳥の観察から *BYAH-BYAH* も追加される可能性がある．また，非ボーカル音としては3種類あり，翼をたたきつけて出すクラッピング，翼を飛翔中に静かに揺するラスリングと嘴をパチンといわせる *PACK* である．音声のレパートリーは孵化後1年間に次第に発達する．巣内雛には4種類のボーカル音 *LEEE, GILILILI, CHILILILI, KYRRKYRR* と，1種類の非ボーカル音 PACK があった．巣立ち雛になるとボーカル音は8種類に増え，*LEEE, GILILILI* のほかに *CHEWLEE, BYAH-BYAH, PUH, SOO, POOH* と *O-GUF* が新しく加わった．親鳥から独立した幼鳥では *PY-O, BEH, SCHEEE* と *PUR* がさらに加わった．幼鳥は10週間後頃になると，*O-GUF O-GUF* とぐぜるようになった．このほかにも音声が幼鳥型から成鳥型へ変化し，*POOH* は *MEW* に，*SCHEEE* は *CHEEE* になった．

これらの音声は，ソナグラフにより物理的構造を分析するとともに，発信者と受信者の双方について，音声を出す前，出している最中，出した後の行動やその他の状況から，行動の脈絡を解析した．これらは，

Smith (1977a) の考察にそって，音声に含まれる発信者についての情報（メッセージ）と，受信者にとっての意味の解釈を試み，さらに音声の機能についての考察を行った．とくに，*K-HOO* をアオバズクのさえずりとする観点から議論した．

成鳥の音声のレパートリーの中で，*K-HOO*, *HOH*, *GUF*, *OO-COO*, *POO* と *HYU* の 6 種類はそれぞれよく似た音で，その物理的構造は周波数や時間構成について勾配があった．これらの音声を物理的な面で比べても，また行動的な面で調べても，相互の関係を示す図式はきわめて似ており，音声のレパートリーの発達と背景にある動機づけのメカニズムについて考察を行った．勾配音は，動機づけ構造モデル (Morton, 1977) に合致するものである．

日本産の鳥と東南アジアに広く分布する各亜種，同属種について音声のレパートリーを比較した結果，Ninox 属に共通する最小の組み合わせは，さえずり，鋭い金切り声，大声の叫び声，ネコがニャンというような声とふるえ声の 5 種類である．さらに，フクロウ目の 21 属 87 種について概観した結果，27 種について 5 種類以上の音声が確認されており，成鳥のレパートリーの最大数はボーカル音が 14，非ボーカル音が 3 であった．幼鳥ではボーカル音が 1–4，非ボーカル音が 1 であった．本研究における日本産のアオバズクのレパートリーは，この最大数に達するものである．

本論文では，1974–1981 年に行われたオリジナルの観察と日本語の文献を含む過去の文献に基づいて，アオバズクの記載，分類，分布，棲息環境，行動，摂食，捕食行動，繁殖，番関係，巣およびなわばりについて概要をまとめた．

Appendix A. Physical Structure of Vocalisations 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 p. 10. For types of frequency modulation, the number of occurrences in a sample is shown. See Table 1 (p. 11) for categories of frequency modulation. A, part A; B, part B; x, absent; xx, few samples.

A-1. *K-HOO* (the song): temporal features

		Duration (A)			Duration (B)			Short interval			Long interval		
Individual		**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 song): 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	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 song): 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 song): types of frequency modulation

Individual	Types of part A					Types of part B					
	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. Binomial test: *, $p < 0.05$; **; $p < 0.025$; ***, $p < 0.01$; ****, $p < 0.001$.

A-5. *K-HOO* (the song): 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:

$$sk = 3\ (M - Md) / S$$

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

	Maximum (A)			Minimum (A)			Maximum (B)			Minimum (B)		
Individual	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								
	A	F	AF	AFD & AD			FD	D	O
Individual				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

	Duration (A)			Duration (B)			Interval		
Individual	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

	Maximum (A)			Minimum (A)			Maximum (B)			Minimum (B)		
Individual	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

		Types							
	A	F	AF	AFD & AD			FD	D	O
Individual				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

	Duration (A)			Duration (B)			Interval		
Individual	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

	Maximum (A)			Minimum (A)			Maximum (B)			Minimum (B)		
Individual	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

	Types of part A						Types of part B								
	A	F	D	AFD	DFA	O	A	F	AF	AFD & AD			FD	D	O
Individual				&AD	&DA					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

	Duration			Interval		
Individual	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

	Maximum			Minimum		
Individual	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

	Types								
	A	F	AF	AFD & AD			FD	D	O
Individual				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 (A)			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

		Maximum			Minimum		
Individual		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

	Harmonics				
Individual	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

	Types								
	A	F	AF	AFD & AD			FD	D	O
Individual				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			Maximum frequency			Minimum frequency		
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	937	100	28.3	587	11	32	530	14	42
	1160	74	21.2	509	15	49	418	23	75

Appendix B. Behavioural Contexts of Vocalisations 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 *. Those with a probability level of less than 0.05 (binomial test) are underlined. Sample numbers are as follows:

		Sexes		
Vocalisation	Phase	T	M	F
K-HOO	PR	446	258	8
	SI	612	313	13
	FO	522	285	10
HOH	PR	140	65	23
	SI	206	73	28
	FO	157	64	25
HYU	PR	33	9	11
1976-1978	SI	47	9	10
	FO	40	9	10
HYU	PR	41	35	6
1979-1981	SI	41	35	6
	FO	41	35	6
KRRR	PR	346	103	139
	SI	381	106	144
	FO	374	103	149

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

CO	Confront rivals
At	Attack rivals
RET	Retreat from rivals
O(v)	Vocalisation, v, of neighbouring territorial males or rivals
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)	Vocalisation, v, of the mate
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 post-fixed 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 bob their heads
YFD	Juveniles are near or on the ground and are approached by a potential enemy
J(v)	Vocalisation, v, of juveniles
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
AT	*	*	0	0	0	0	1	2	0
RET	*	1	0	0	0	0	0	0	0
O (*K-HOO*)	9	13	0	18	26	8	6	10	0
AO	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
A5	3	5	13	1	1	0	3	4	10
-A5	1	*	0	*	*	0	4	3	0
A6	*	*	0	0	0	0	*	*	0
-A6	0	0	0	0	0	0	*	0	0
A7	1	*	0	0	0	0	2	1	0
A8	1	1	0	*	0	0	2	2	10
AE	*	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	1	*	0
N3	*	*	0	1	1	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	1	1	0
N2m	0	0	0	*	*	0	0	0	0
N3m	*	*	0	*	*	0	0	0	0
N4m	5	5	0	4	7	0	4	5	0
N5m	*	*	0	0	0	0	0	0	0
FLY	*	0	0	0	0	0	*	0	0
SY	*	0	0	1	0	0	1	0	0
DY	0	0	0	0	0	0	*	0	0
FY	*	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	2	0	0	5	0	0
H	3	2	13	0	0	0	2	3	0
HF	*	0	0	1	1	0	1	0	0
PF	0	0	0	0	0	0	*	*	0
E	1	1	13	*	*	0	1	1	0
PRE	1	1	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	24	22	10

B-2. Behavioural contexts of *HOH*

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
AO	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 (*LEEE* & *GILILILI*)	0	0	0	0	0	0	1	0	0
H	2	3	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	*	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	*	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
AO	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) Observations during 1979–1981

	PR			SI			FO		
Behaviour	T	M	F	T	M	F	T	M	F
AO	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 binomial 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	1	*	0	1	*	0	1
AO	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	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
-A6	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	*	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
N4m	3	10	1	4	12	1	4	13	1
N5m	0	0	0	*	1	0	1	*	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	1	0	0
FY	*	0	0	0	0	0	3	1	1
FP	0	0	0	0	0	0	*	0	1
HM	0	0	0	0	0	0	*	0	0
J (*LEEE* & *GILILILI*)	0	0	0	*	0	0	3	0	2
H	5	7	4	*	0	0	3	2	5
HF	7	2	6	10	5	11	7	1	12
-HF	2	0	4	2	1	1	*	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	*	1	0
P	4	0	3	7	3	6	5	0	3
L	1	0	1	*	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 near the nest of a widowed female (caller); RM3, A replacing male was near a widowed female (caller); RM(*v*), A replacing male produced vocalisation, *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* & *GILILILI*)	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 binomial test was not applied.