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Distribution and Ecology of Birds of Japan[1]

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ABSTRACT: The effects of island biogeography are clearly seen in the avifauna of Japan. Species composition and distribution reflect Japan's geographic, climatic, vegetational, topographical, and geological characteristics. It is a country composed primarily of mountainous, forested islands that lies off the coast of a continent rich in bird life. Though Japan has a wide range of climates and diverse forest habitats, the terrestrial and freshwater avifauna is depauperate when compared with species, family, and order diversity on the nearby continent, which is both larger in total area and more diverse in habitats. However, the bird groups that do have higher species diversity in Japan than in the Asian mainland are seabirds. The large, productive ocean area and small, isolated islands provide them with foraging and nesting sites, and the long geographic range of Japan allows seabirds from both northern and southern regions to nest in the Islands. Island biogeography also affects the ecology of many terrestrial species. Niche shift and expansion of foraging and parasitic behaviors are seen in populations established on islands where the species composition does not include certain competitors. The terrestrial species resident on small islands have developed unique breeding behavior, in comparison with their conspecifics on larger islands, such as smaller clutch size, exaggerated begging behavior, and longer parental care in small-island populations of Varied Tits, *Parus varius* Temminck & Schlegel.

JAPAN LIES ALONG the east side of the Asian continent. The long island chain stretches from Hokkaido in the north to the South-West Islands in the south (Figure 1). The characteristics of Japanese avifauna have been described (e.g., Blakiston 1883, Austin and Kuroda 1953, Brazil 1991), but most of those authors focused on taxonomic aspects and did not discuss ecological relationships. The distribution and ecology of birds are affected by the environmental features of birds' habitat.

In this paper, we review the characteristics of Japanese avifauna from the ecological point of view. First, we describe the physical environment on which the Japanese avifauna depends; then we examine its influence on species distribution. Second, the species composition of Japan is compared with that of the Asian mainland. We pay particular attention to the composition at the order, family, and species levels. The comparison yields differences that are explained by the differences in area sizes and habitat between Japan and the mainland.

Last, we report some ecological phenomena from our fieldwork. Characteristics such as foraging and breeding behavior are influenced by the presence or absence of other competing species. Species existing in areas without competitors show ecological shifts with morphological changes allowing them to take advantage of resources left available by the absence of competition. Further, breeding behavior changes for large- and small-island populations are described, and climatic explanations are suggested.

Features of the Japanese Environment

The Japanese island chain and the Asian continent are separated by the Japan Sea, at

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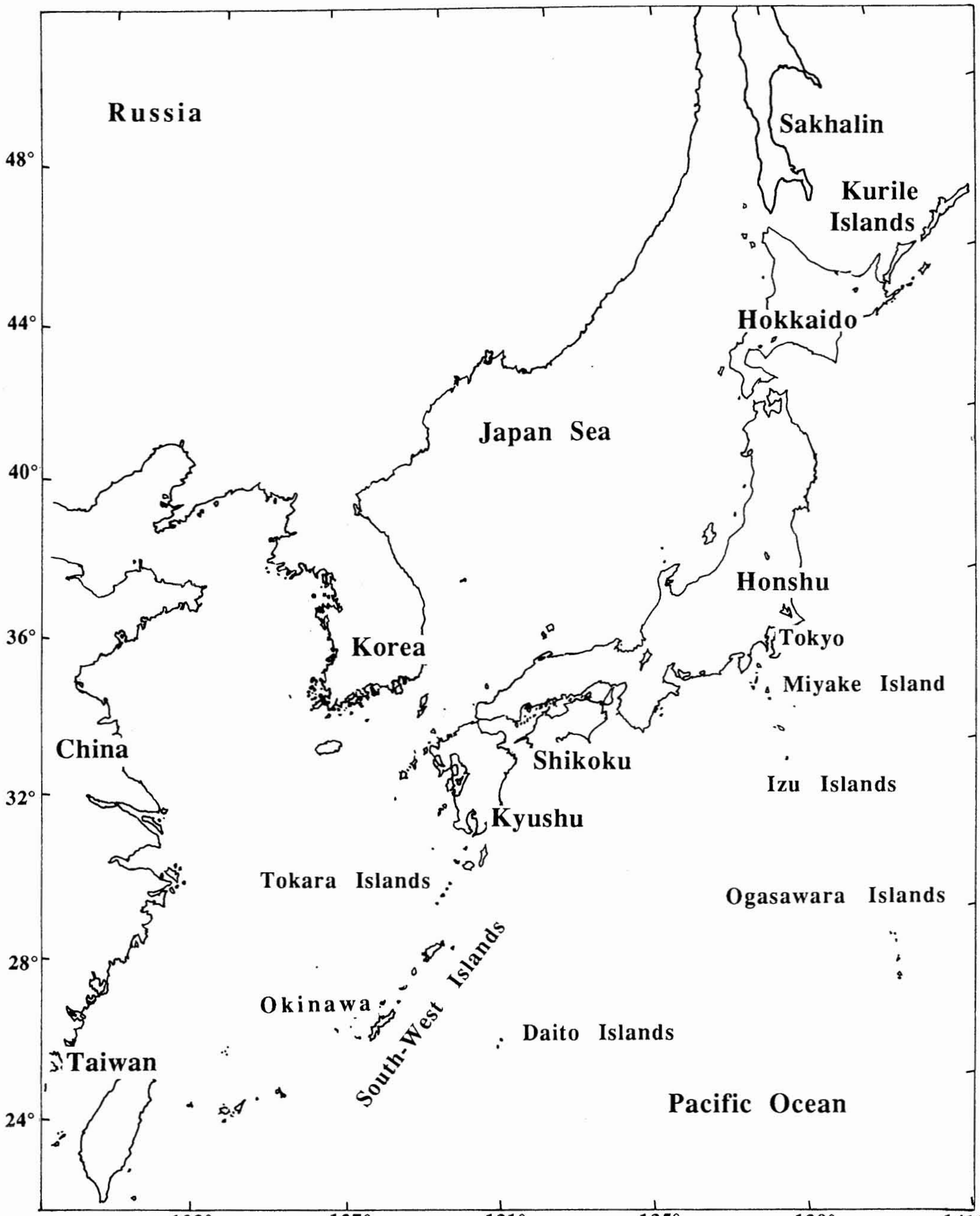

FIGURE 1. Japan, neighboring islands, and nearby continental Asia.

distances ranging from 200 to 800 km. The more than 3,500 Japanese Islands cover an area from Sakhalin in the north, to Taiwan in the south, the Kurile Islands in the east, and the Korean Peninsula in the west.

The shapes and sizes of the Japanese Islands have changed many times in geologic history, and most of the Japanese Islands were connected to the Asian continent at one time (Minato et al. 1965). Honshu, Shikoku, and Kyushu were isolated from the continent and from Hokkaido, which was the last main island to be separated from the continent, after the latest Pleistocene of ca. 20,000 yr ago. Since that time, all the islands have been isolated from the continent and from each other.

Japan's terrestrial habitat is heavily vegetated. Forests cover 68% of the land area. The topography of Japan is extremely mountainous, with 70% of the land area in mountain ranges. The altitudinal range is from sea level to 3,776 m.

Japan lies in three climate zones because of its long north–south geographic range, between 24° and 46° N latitude. There are subtropical, temperate, and subarctic climate regions. The Ryukyu Islands, which are the southernmost islands of the Japanese island chain, lie in the subtropical zone. The islands extending northward from the Ryukyus to the southern tip of Kyushu are called the South-West Islands. The majority of the main islands and land area of Japan lies in the temperate zone. Northern Hokkaido and several associated islands belong to the subarctic region north of 45° N latitude.

The southern South-West Islands are covered with subtropical broad-leaved and mangrove forests. The northern South-West Islands are covered with temperate mixed evergreen forests intergrading with typically southern vegetation. In this latitudinal range, but to the east and much more remote, are the Daito and Ogasawara (Bonin) Islands. They are on the order of 1000 km from the large northern islands of Japan and have no neighbors within 500 km.

The temperate zone includes most of the main islands of Kyushu, Shikoku, Honshu, and southern Hokkaido, between 31° and 42° N latitude. The vegetation consists of two main types, broad-leaved evergreen forests in the south and deciduous forests in the north. The majority of Hokkaido and adjacent islands is vegetated with typically subarctic mixed forest of deciduous and coniferous trees.

There are both warm and cold currents in the ocean surrounding Japan. Kuroshio, a southern warm current, flows north and divides at the southern tip of Kyushu, flowing into both the Sea of Japan and the Pacific Ocean. The cold Oyashio Current moves south from the subarctic, along the coast of eastern Hokkaido and northern Honshu. These interacting currents have made the coastal and marine regions of Japan extremely productive (Ching 1991).

Features of the Avifauna Relative to Environmental Features

The distribution of avifauna in Japan is a function of the physical environment, particularly its island nature. The avifauna of the Islands varies seasonally and regionally. However, forest species predominate throughout the Islands. The forest landscape supports a majority of Japan's terrestrial bird species. Approximately 100 of the 150 land and freshwater bird species are woodland dwellers, such as hawks, pheasants, woodpeckers, thrushes, warblers, flycatchers, finches, and buntings.

The seasonal climate of much of Japan means that many species are migratory. Some are winter or summer visitors, and others, such as shorebirds, visit Japan only as a migration stopover. Thus, Japan's species composition changes between summer and winter. The number of species that arrive each season closely matches the number that leave during the period (Figure 2).

Regional species composition results from the geographic situation of the area. The avifauna of the South-West Islands is influenced by the tropical area and temperate regions. Tropical species such as the Cinnamon Bittern, *Ixobrychus cinnamomeus* (Gmelin); Malay Night Heron, *Gorsakius melanolophus* (Raffles); Purple Heron, *Ardea purpurea* L.; Barred Buttonquail, *Turnix suscitator* (Gmelin); White-breasted Waterhen, *Amaur-*

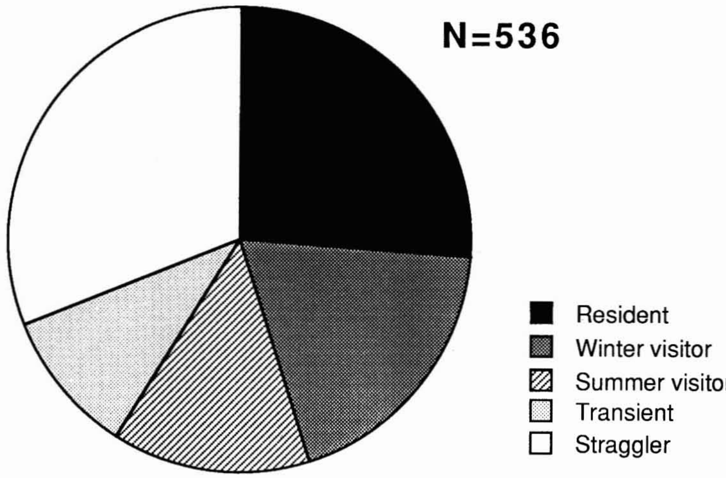

FIGURE 2. Residential status of Japanese birds as a proportion of five categories. Based on Wild Bird Society of Japan (1982) and Takano (1985).

ornis phoenicurus (Pennant); and Red-capped Green Pigeon, *Sphenurus formosae* (Swinhoe) (Brazil 1991), intergrade with Palearctic species such as Woodcock, *Scolopax rusticola* L.; Japanese Robin, *Erithacus akahige* (Temminck); and Carrion Crow, *Corvus corone* L., in the northern South-West Islands.

In the subarctic region of Hokkaido, drastic seasonal variation in temperature drives many birds south for the winter. But many breeding and resident species of Hokkaido are closely related to the northern climate and do not live elsewhere in Japan. The White-tailed Sea Eagle, *Haliaeetus albicilla* (L.); Common Merganser, *Mergus merganser* L.; Tufted Puffin, *Lunda cirrhata* (Pallas); Hazel Grouse, *Tetrastes bonasia* (L.); Blakiston's Fish Owl, *Ketupa blakistoni* (Seebohm); Three-toed Woodpecker, *Picoides tridactylus* (L.); and Willow Tit, *Parus palustris* L., are breeders not seen south of Hokkaido. These species are found on the adjacent Asian continent, suggesting that Hokkaido was still connected to the continent after Honshu had been separated. The biogeographical line separating Hokkaido and Honshu is called Blakiston's line (Tokuda 1970).

Regional differences in avifauna are clear, but the effects of island biology are just as strong, though less obvious without study. The distribution of species within each region varies. Island size, island distance from emigration sources, and chance, as well as island geology have determined the presence or absence of species. The number of species on each island differs. For example, in the South-West Islands, 47 species have been identified as resident, but only 17 of these are found on five or more of the six major islands of this group (Ikehara 1991). Figure 3 shows the species-area relationship of the Japanese Islands. The number of breeding species increases as the area of an island increases. However, in remote islands more than 300 km distant from any main island of Japan, fewer species are present than expected from the size of the island. These are good examples of island biogeographical theories (MacArthur and Wilson 1963, 1967).

The relationship between island size, remoteness, and species presence is demonstrated by the colonization patterns of woodpeckers (Higuchi 1980). The likelihood of their presence on small islands increases with island size and proximity to one of the main islands (Figure 4). For example, the Japanese Pygmy Woodpecker, *Dendrocopus kizuki* (Temminck), is commonly found on islands with an area of 10–99 km^2 located less than 10 km from a main island. One

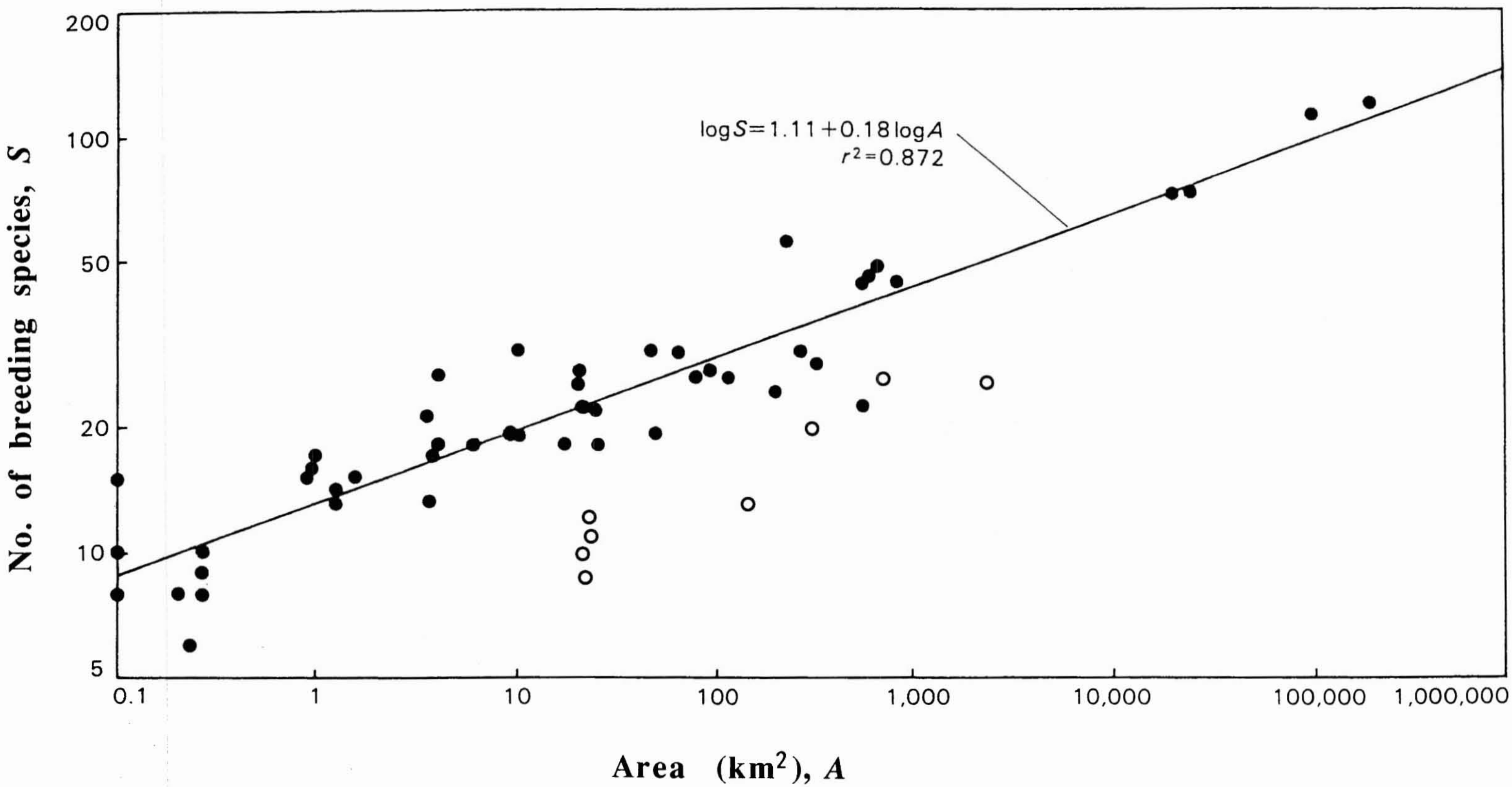

FIGURE 3. The relationship between the number of breeding species and sizes of Japanese Islands. Open circles represent remote islands that are >300 km from any main island of Japan. Scales of the axes are logarithmic (from Higuchi 1979).

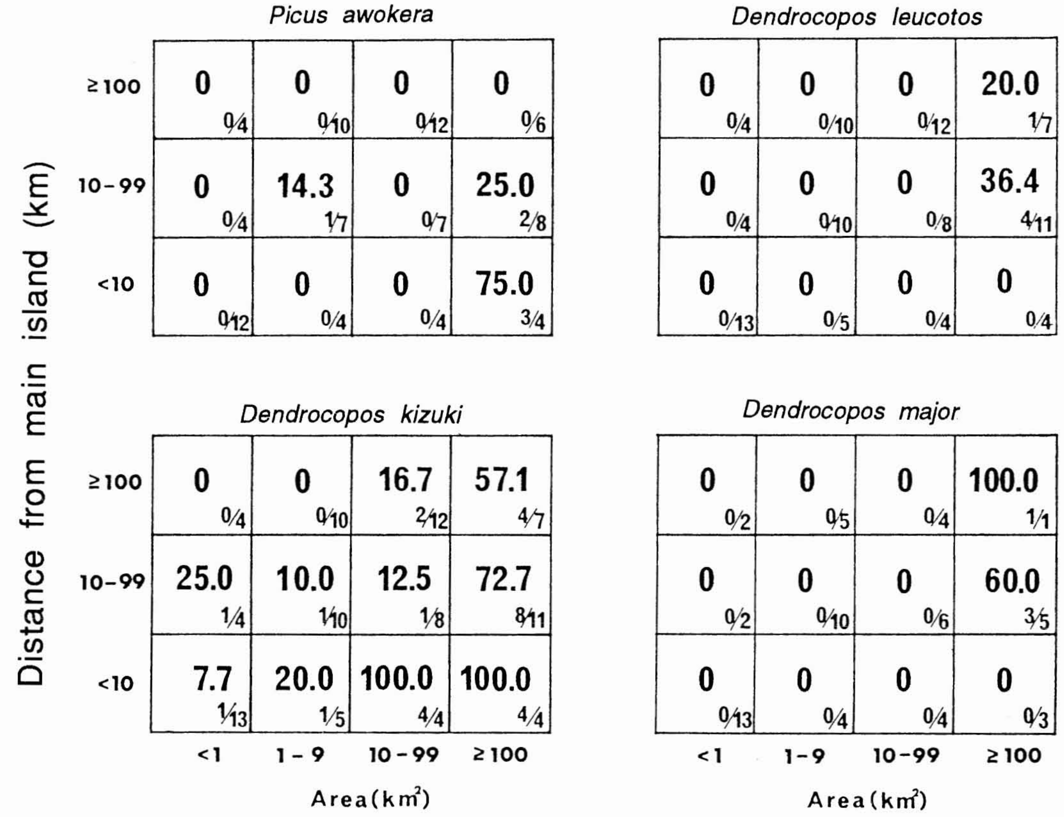

FIGURE 4. Frequency distribution of the occurrence of woodpeckers in relation to the size and remoteness of islands. Islands are placed into 12 classes based on island sizes and distances from the nearest main island. Occurrence rates (%) are calculated by dividing the number of islands in each class where the woodpeckers breed by the total number of islands in that class. The fraction shown at the lower right in each category is the number of islands surveyed (from Higuchi 1980).

hundred percent of those islands have this species, but only 12.5% of islands the same size located 10–99 km distant from a main island do. The Japanese Green Woodpecker, *Picus awokera* Temminick, occurs on three main islands and the outlying small islands that were connected to the main islands in the latest Pleistocene. The White-backed Woodpecker, *D. leucotos* (Bechstein), is found only on islands greater than 100 km^2 in area.

Japan has a rich endemic avifauna, with 22 endemic residents or breeders. There are two methods by which endemic species have arisen: through speciation and through isolation of relictual populations. The formation of relictual populations usually comes about through environmental change and interspecific competition. Many species now considered endemic were widespread in the past. During times of environmental change or interspecific competition with newly established closely related species, these species retreated from their ranges and were effectively isolated in small areas to which they are now endemic. It is not easy to distinguish which of these two processes, speciation or isolation, is responsible for endemic Japanese birds. A useful characteristic for determining which process occurred is the distribution of the species. Endemic species that speciated within an area have close relatives in neighboring regions. Relict species are characterized by a discontinuous distribution of relatives, because they retreated from a wide range to small pockets of suitable habitat.

Many terrestrial Japanese endemic species show the trait of discontinuous distribution and are considered relicts. Ijima's Willow Warbler, *Phylloscopus ijimae* (Stejneger), breeds only on the Izu Islands off Honshu and on the Tokara Islands in the South-West Islands, 500 km away from the Izus. These island populations are probably a more primitive species than many other *Phylloscopus* species occurring elsewhere and used to be widely distributed (Martens 1980, 1981, Higuchi and Kawaji 1989). Similarly, the Lidth's Jay, *Garrulus lidthi* Bonaparte, of Amami Island has no nearby relatives on the mainland or Japan, but is closely related to the Black-throated Jay, *G. lanceolatus* Vigors, of the Himalayas (Yamashina 1941, Short 1973, Morioka 1974) (Figure 5). The Copper Pheasant, *Syrmaticus soemmerringii* (Temminck), occurs on Kyushu, Shikoku, and Honshu, but its nearest relatives live on Taiwan (the Mikado Pheasant, *S. mikado* [Ogilvie-Grant]), in tropical China in Yunnan Province (Mrs. Hume's Pheasant, *S. humiae* [Hume]), and in the mountains of central eastern China (Elliot's Pheasant, *S. ellioti* [Swinhoe]) (Higuchi 1987, Sibley and Monroe 1990).

In contrast, another member of the pheasant family obviously speciated within Japan. The Green Pheasant, *Phasianus versicolor* Vieillot, is endemic on Japan's main islands (except Hokkaido), and its closest relative, the Common Pheasant, *P. colchicus* L., occurs on the Asian mainland (Delacour 1977, Johnsgard 1986). These nearby populations of a close relative show that the Green Pheasant speciated in Japan.

The origins of some Japanese endemics are unclear. For example, the Japanese Wagtail, *Motacilla grandis* Sharpe, is closely related to the widely distributed White Wagtail, *M. alba* L., and this distribution pattern suggests that the Japanese Wagtail speciated

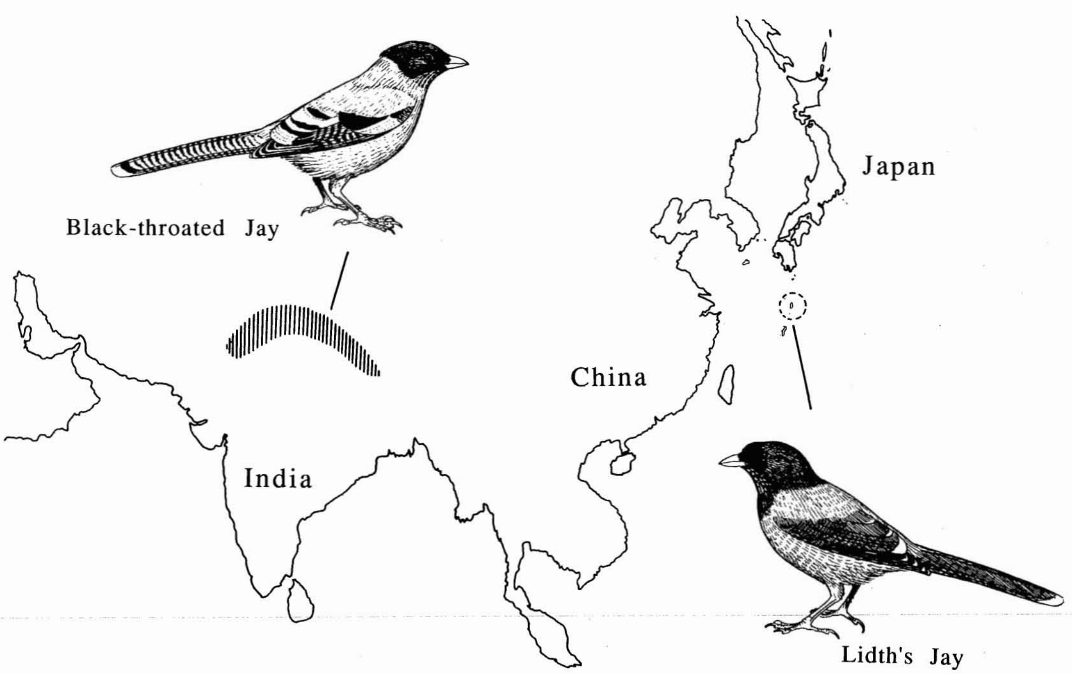

FIGURE 5. Distributions of the closely related Lidth's Jay (*Garrulus lidthi*) and the Black-throated Jay (*G. lanceolatus*) in Japan and the Himalayas, respectively. The discontinuous distribution is characteristic of relict species.

in Japan from the continental White Wagtail. However, the plumage and the courtship behavior of the Japanese Wagtail is most similar to that of the Large Pied Wagtail, *M. maderaspatensis* Gmelin, of India. These characteristics suggest that these two species are closer to each other than to the White Wagtail (Higuchi and Hirano 1988), and their discontinuous distribution suggests that they are relict species. Which of these interpretations is correct is yet to be discovered.

The biota of Japan is rich in relict endemics. Besides birds, there are many relict amphibians, reptiles, and mammals (Imaizumi 1962, 1985, Hikita 1985).

Comparison of the Avifauna of China and Japan

The most important biogeographic features of Japanese avifauna are those associated with the island environments. This becomes clear when the Japanese avifauna is compared with the neighboring continental avifauna. We use China's breeding bird species as a representative of the avifauna of the Asian continent. China is a political region, and its size and habitats are remarkably different from those of Japan, but we compare the two regions for three reasons: (1) mainland China is a major source for birds immigrating to Japan, (2) some closely related species exist in Japan and on the mainland as far away as the Himalayas (e.g., Lidth's Jay and Black-throated Jays), and (3) the general distribution of China's avifauna has been well studied by Cheng (1976, 1987) and Fan (1990). As is common for continental island chain avifauna, the birds of Japan are a subset of continental avifauna. Japan's main habitats are forest and coastal/marine, and overall we find less diverse habitats in Japan; the species composition and diversity reflect this. The large area and variety of habitats in China support an equally large and diverse avifauna, and though most of the Japanese Islands used to be connected to the continent, the avifauna is depauperate.

The species diversity (and diversity of orders and families) found on Japan is less than that found on the Chinese mainland (Appendix). The number of breeding species recorded in Japan is 248, and there are 972 in China. There are no breeding bird orders in Japan that are not also present in China. Twenty orders are present in China, and 18 in Japan. The orders missing from Japan are Psittaciformes (parrots) and Trogoniformes (trogons), both tropical. Japan's comparative lack of extensive tropical avifauna explains much of the difference between the Islands and the mainland at both the order and family levels.

There are 22 families, containing a total of 82 species, breeding in China and not in Japan. Fourteen of these families typically are tropical, and 56 (85%) of their 66 species present in China live in tropical habitats. Some of these tropical families are Psittacidae (parrots), Trogonidae (trogons), Bucerotidae (hornbills), Capitonidae (barbets), Eurylaimidae (broadbills), and Irenidae (leafbirds). Timaliinae, which is sometimes treated as a separate family (e.g., Ali and Ripley 1971, King and Dickinson 1975), is also a tropical group missing from Japan and is represented by 124 species in China. Several other families absent from Japan contain grassland or arid-adapted species, such as Pteroclididae and Otidae.

There is only one family present in Japan that is absent from China. Meliphagidae is represented by a single endemic species from the Ogasawara Islands, the Bonin Islands Honeyeater, *Apalopteron familiare* (Kittlitz). However, there is some taxonomic uncertainty about its status (Higuchi 1978).

At the species level, the avifauna of Japan is quite depauperate. The largest differences come from families that exist in both China and Japan, but that have fewer closely related species present in Japan (Table 1). We find that even in predominantly forest-associated families, such as the Fringillidae (finches) and Phasianidae (pheasants), Japan has drastically fewer species. Finch species in China number 47, but there are only 11 in Japan. Even more drastic is the difference in pheasant species, 54 and 7 for China and Japan, respectively.

In China, many more congeneric species exist. For example, in the family Columbidae (pigeons), there are 27 species (eight in Ja-

TABLE 1

SOME EXAMPLES OF BIRD FAMILIES HAVING FEWER BREEDING SPECIES IN JAPAN THAN IN CHINA

FAMILY	NO. OF SPECIES	
	CHINA	JAPAN
Accipitridae	41	13
Phasianidae	54	7
Columbidae	27	8
Cuculidae	17	4
Strigidae	22	7
Picidae	28	11
Pycnonotidae	16	2
Corvidae	27	7
Muscicapidae		
(1) Turdinae	72	13
(2) Timaliinae	124	0
(3) Sylviinae	79	15
(4) Muscicapinae	35	5
Paridae	16	5
Ploceridae	13	2
Fringillidae	47	11

TABLE 2

COMPARISON OF BREEDING SPECIES OF HAWK AND EAGLE GENERA PRESENT IN BOTH JAPAN AND CHINA

GENUS	NO. OF SPECIES	
	CHINA	JAPAN
Haliaeetus (Sea Eagles)	4	1
Aquila (Eagles)	4	1
Spizaetus (Hawk-eagle)	1	1
Spilornis (Serpent-eagle)	1	1
Pernis (Honey Buzzard)	1	1
Milvus (Kite)	1	1
Butastur (Buzzard)	1	1
Buteo (Soaring Hawk)	3	1
Circus (Harrier)	6	1
Accipiter (Forest Hawk)	6	3

pan). Ten of these are genus *Columba*, six *Streptopelia*, and eight *Treron (Sphenurus)*. These genera have only three, three, and two species in Japan, respectively. Family Accipitridae (hawks) is similar: Japan has 10 genera, and China has 18. Japan has one-half to one-third the species diversity within hawk genera existing in both China and Japan for which there is more than a single species present in China (Table 2). Genus *Accipiter*, a forest-adapted genus of hawks, shows one-half the species diversity present in China. Even for that woodland-adapted genus the species diversity is less than that in China. For Columbidae, Accipitridae, and many other families, the family is represented in Japan, but the diversity at the genus and species levels is low.

The species diversity of China is greater than Japan's because of the greater number of closely related species that live in China's great diversity of habitats and larger total area. China's land area is 26 times greater than Japan's (Table 3). As a landscape, China provides arctic, subarctic, temperate, subtropical, and tropical climates. China has many high mountains and plateaus of more than 5000 m altitude, whereas Japan's highest mountain is less than 4000 m in altitude. In China, desert, grassland, taiga, tundra, agriculture, rivers, and mountain ranges occur in many climate zones, a much greater diversity and total area than in Japan.

The potential of bird families to establish populations in Japan is limited by the lack of habitat diversity. Because a viable population cannot exist on an island without the appropriate type and amount of habitat, Japan's islands lack many of the species that are present on the Asian mainland because of a lack of some habitat types and the small area of others.

Japan has no arid regions such as deserts or barren plateaus and thus lacks a diversity of arid-adapted species such as larks (Alaudidae) and sandgrouse (Pteroclididae). China has 10 species of larks, mostly living in areas described as rocky, steppe, or grassland (De Schaunsee 1984), whereas Japan has one species, the Skylark (*Alauda arvensis* L.). The presence of three species of sandgrouse in China further attests to the diversity of habitats. Japan has no breeding species of this arid-adapted family, widespread in desert and arid regions of the Old World. Old World Warblers (Sylviinae) also have arid-adapted species present in China [*Sylvia minula* Hume and *S. nana* (Hemptich & Ehrenberg)], but not in Japan. Similarly, finches have species present in China, ranging in habitats from open grasslands, woodlands,

TABLE 3

COMPARISON OF THE PHYSICAL FEATURES OF JAPAN AND CHINA

PHYSICAL FEATURES	JAPAN	CHINA	LARGER/SMALLER RATIO
Area (km^2)	372,197	9,561,000	25.7
Climatic zones	Subarctic–subtropical	Arctic–tropical	
Highest altitude (m)	3,776	8,848	2.3
Largest river			
Water area (km^2)	15,760	1,775,000	112.6
Length (m)	322	5,200	16.1
Range of terrestrial habitats	Grassland–forest	Desert–forest	
Length of coast line (m)	28,000	18,000	1.6

semideserts, barren plateaus, or forests up to treeline. Japan has a primarily woodland subset of Fringillidae.

China's vast area and variety of habitats has produced speciation within the Order Galliformes on a scale unmatched in Japan. The Galliformes is a group of nonmigratory grouse, pheasants, and quail common in forest and mountain habitats. China has 54 species, including 16 endemics, which are resident in habitats from semidesert to alpine meadows over 5000 m (Tang 1989). Their endemicity shows that they responded to the variety of habitats by adapting to them. In Japan Phasianidae is represented by three native species and one introduced. Two of these are endemic to Japan, and the third is found in China as well. Even if those species living at altitudes and climates not found in Japan are not considered, there are over 20 species more in China. Although a land mass 26 times smaller is expected to have fewer species, Japan is depauperate in Galliformes, even for this primarily woodland subset of the pheasant family (those found at comparable altitudes in Japan and nontropical).

The majority of Galliformes live only on the large, main islands of Japan, which have a relatively homogeneous habitat when compared with China and lack severe isolation that could pressure them to speciate within Japan.

It is clear that the pattern of existing avifauna in Japan is heavily affected by its island biogeography. Its birds are a subset of mainland avifauna, and the composition is depauperate in terrestrial species. The only bird groups with a greater number of species in Japan than the mainland are those that utilize the marine or coastal habitats. In direct contrast with the families that are depauperate in Japan, seabirds have found the islands much more accessible. Japan's coastline is 1.6 times longer than China's. The isolation of islands by the sea is an asset for them, not a barrier. Four families from two orders have a total of 20 breeding species throughout Japan, 15 more than China (Table 4). The sea areas of China do not have a diverse or populous seabird population and are especially depauperate in species that breed only on small islands. There are only two species of seabirds common in Chinese waters, the Streaked Shearwater, *Calonectris leucomelas* (Temminck), and Bulwer's Petrel, *Bulweria bulweria* (Jardine & Selby) (Melville 1984). These common seabirds of China are coastal breeders and are also widespread in Japan.

TABLE 4

SOME EXAMPLES OF BIRD FAMILIES HAVING MORE BREEDING SPECIES IN JAPAN THAN IN CHINA

FAMILY	NO. OF SPECIES: CHINA	NO. OF SPECIES: JAPAN
Diomedeidae	1	3
Procellariidae	2	5
Hydrobatidae	1	5
Alcidae	1	7

Twenty species of Procellariiformes and Alcidae nest on Japanese isles. Different species utilize different regions of Japan's geographic range. Northern alcid species such as Rhinoceros Auklets, *Cerorhinca monocerata* (Pallas), and Spectacled Guillemots, *Cepphus carbo* Pallas, nest on the coast of Hokkaido or northern Honshu, but never range south of those points. At the other extreme, the northernmost range boundary for Audubon's Shearwaters, *Puffinus lherminieri* Lesson, and Wedge-tailed Shearwaters, *P. pacificus* (Gmelin), is southern Japan. The latter two species breed only on small islands and find ample nest sites on the Ogasawara Islands, 900 km south of Honshu.

One seabird species is endemic to Japan, and one is an endemic breeder. The Japanese Murrelet, *Synthliboramphus wumizusume* (Temminck), is endemic, and the Short-tailed Albatross, *Diomedea albatrus* Pallas, has its last known breeding sites on Japan's Torishima and Senkaku Islands. Both are endangered because of human perturbation in the past.

The environment of Japan is ideal for seabirds. For coastal- or islet-breeding species, there are suitable breeding areas in a large range of geographic locations, and as a result, both northern Alcidae and southern Procellariiformes can nest in Japan. The rich oceans and small land area are benefits to seabirds, which have quality foraging areas to support breeding.

Ecological Features of Land Birds on Small Islands

Populations of birds on small islands have developed ecological and behavioral traits that differentiate them from populations on larger islands in Japan. These ecological characteristics have been investigated in studies on foraging, breeding, and parasitism of several species (Higuchi 1976, Higuchi and Momose 1981, Higuchi and Sato 1984). Characteristics that differ between populations of the same species can be caused by differences in species composition of congenerics or by abiotic factors. Some examples are given below for ecological characteristics such as wide niche utilization, host expansion/shift of parasites, and morphological changes resulting from species composition. Further, the case of the Varied Tit, *Parus varius*, is discussed with regard to ecological and behavioral differences caused by abiotic factors.

ECOLOGICAL SHIFTS BASED ON SPECIES COMPOSITION. Some populations show increased niche width in the absence of other species. For example, the Bonin Islands Honeyeater (*Apalopteron familiare*) exhibits foraging behavior similar to that of birds not occurring sympatrically. The Ogasawara (Bonin) Islands lack tits, nuthatches, small robins, and woodpeckers (Paridae, Sittidae, Muscicapidae, and Picidae, respectively). The honeyeater exhibits foraging behavior similar to

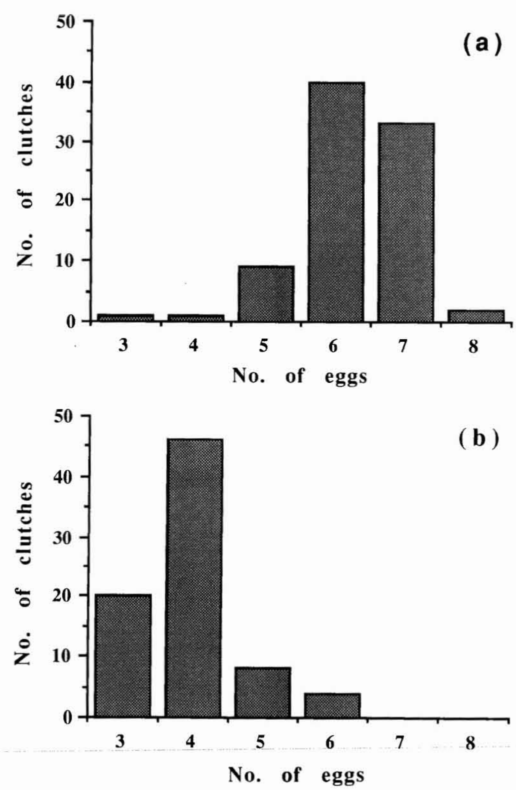

FIGURE 6. Clutch sizes of the Varied Tit (*Parus varius*) on Honshu (*a*) and Miyake Island of the Izu Islands (*b*), Japan (after Higuchi 1976).

that of tits among twigs and leaves, to that of nuthatches or woodpeckers on trunks and branches, and to that of small robins on the ground (Higuchi 1978). It is probable that the absent species have not colonized the Ogasawara Islands because of their great distance from the Japanese main islands (900 km south of Honshu). A similar case of foraging behavior expansion is known in the Brown Trembler, *Cinclocerthia ruficauda* (Gray), on Dominica Island of the West Indies (Zusi 1969).

Host changes are found among *Cuculus* cuckoos on islands where they do not occur sympatrically. There are four breeding species of cuckoos in Japan. They are all brood parasites, and their main host species are segregated within their range of sympatry.

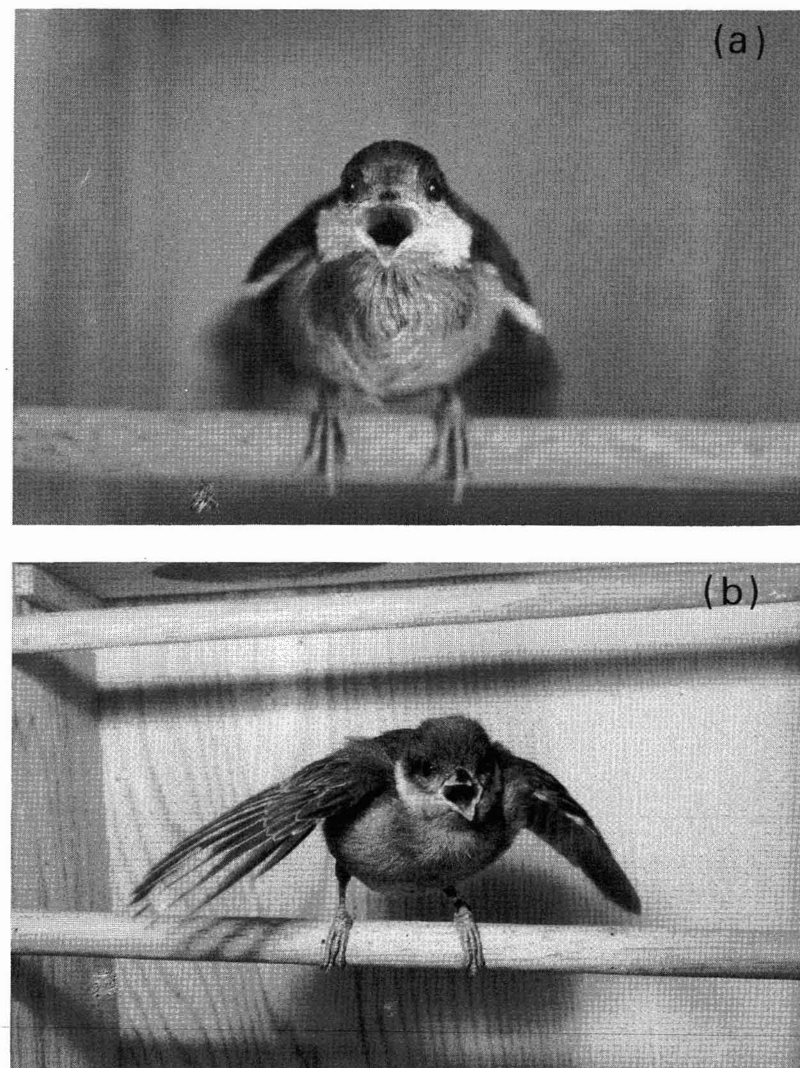

FIGURE 7. Begging postures of Honshu (*a*) and Miyake Island (*b*) Varied Tit (*Parus varius*) fledglings (from Higuchi and Momose 1981).

However, on some islands, host shifts or host expansions are found in the absence of closely related species of cuckoos (Higuchi 1986).

Host expansion is found in central Japan between large- and small-island populations of the Little Cuckoo, *Cuculus poliocephalus* Latham. Populations on Honshu and on the small Izu Islands demonstrate this. Honshu has four breeding species of cuckoos, which segregate host choice between 12 species or more. Honshu Little Cuckoos mostly parasitize two species. The Izu Islands have only the Little Cuckoo, and they lay eggs in nests of seven or more different species, including those parasitized by Himalayan Cuckoos, *C.*

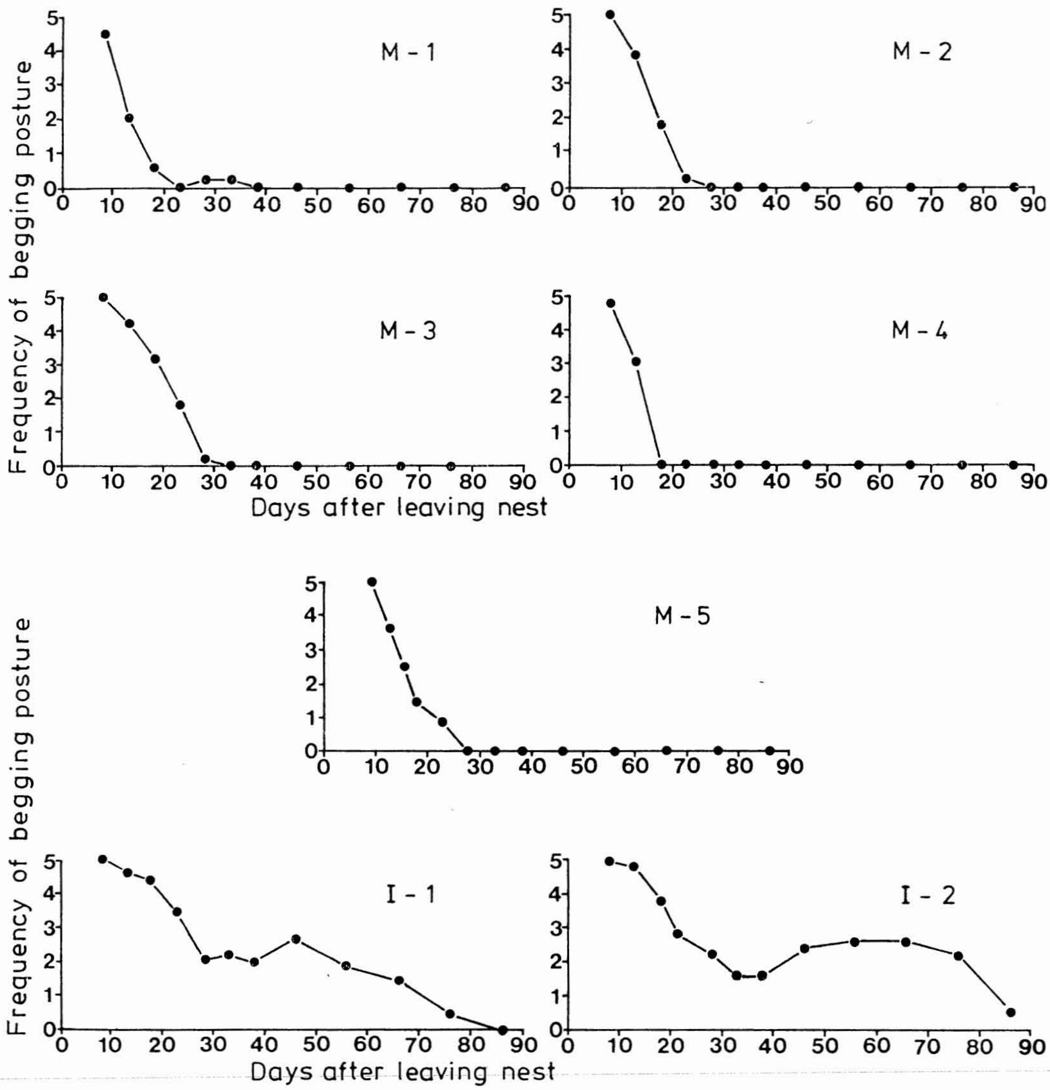

FIGURE 8. The decline with age of the begging posture in main-island (M-1 to M-5) and small-island (I-1 and I-2) captive fledglings (Higuchi and Momose 1981). The ordinate indicates the number of mealworms eaten that were accompanied by the begging posture in five trials each day. Begging behavior declined sharply with age in Honshu young, but it lasted for a longer period, ca. 3 months, in small-island young.

saturatus Blyth, and Common Cuckoos, *C. canorus* L., on Honshu (Higuchi 1979).

Host shifts and changes in egg mimicry occur where the species composition of brood parasites is different. On Honshu, Little Cuckoos often parasitize Bush Warblers, *Cettia diphone* (Kittlitz), and lay a chocolate brown egg closely matching that of the warbler host. Sympatric Himalayan Cuckoos do not parasitize the Bush Warbler and lay eggs that are white with brown spots. However, in most parts of Hokkaido there are no Little Cuckoos, and eggs of the Himalayan Cuckoo population are chocolate brown or orange-brown, like those of the Bush Warbler and its Honshu parasite, the Little Cuckoo, and completely unlike the eggs of Himalayan Cuckoos on Honshu (Higuchi and Sato 1984).

Egg mimicry is facilitated by the distinguishing ability of the hosts (Harrison 1968, von Haartman 1981, Mason and Rothstein 1987, Davies and Brooke 1988). Experiments performed with Brush Warblers showed that they were more likely to reject eggs that were least like their own egg's chocolate brown color (Higuchi 1989). The host shifts and subsequent morphological changes seem to be common phenomena on the Japanese Islands, where each island has a different species composition.

TABLE 5

DURATION OF POSTFLEDGING CARE FOR HONSHU AND MIYAKE ISLAND POPULATIONS OF VARIED TITS (*Parus varius*)

DURATION (DAYS AFTER FLEDGING)	NO. OF CASES	
	HONSHU	MIYAKE ISLAND
5–9	2	
10–14	3	
15–19	4	1
20–29	2	
30–39		2
40–49		2
50–59		1
60–69		2
70–80		1

From Higuchi and Momose (1981).

ECOLOGICAL AND BEHAVIORAL DIFFERENCES RELATED TO ABIOTIC FACTORS. The ecology and behavior of island populations are also subject to interpopulation variation caused by abiotic factors. The Varied Tit (*Parus varius*) shows different breeding characteristics between the Honshu (228,000 km^2) and Miyake Island (Izu Islands) (55 km^2) populations. Clutch size is smaller on the Izu Islands than on Honshu; the most common number of eggs is four on Miyake Island and six on Honshu (Figure 6). The fledglings from these small-island clutches exhibit an exaggerated begging behavior. Main-island Varied Tit young flutter their half-open wings or shake the posterior tips of the wings sideways, whereas young from the Izu Islands stretch both wings sideways and flutter them vertically (Figure 7). The begging behavior of small-island young can be sustained up to 3 months after fledging, 2 months longer than that of main-island young (Figure 8). Parental care is prolonged for a similar length of time on small islands (Table 5).

These ecological and behavioral differences between island populations may be the result of ecological factors, such as the difference in primary production between large and small islands. Seasonal fluctuation in food productivity is expected to be smaller in the marine climate of the small Izu Islands. Temperate marine islands are similar to tropical regions in that the food supply is relatively stable throughout the year and the population is usually near carrying capacity. The breeding density of Varied Tits is two to three times as high in the Izu Islands as in Honshu (Higuchi 1976), thus the small increase of food during the breeding season, when divided among the large numbers of pairs, does not provide a large excess for breeding (Figure 9) (Ricklefs 1980, Perrins and Birkhead 1983). Under such conditions of lower food availability, smaller clutch size will produce more young than larger clutch size. Fledglings begging more furiously and for longer periods would increase their chance of survival because the parents would continue to feed them. Thus, smaller clutch

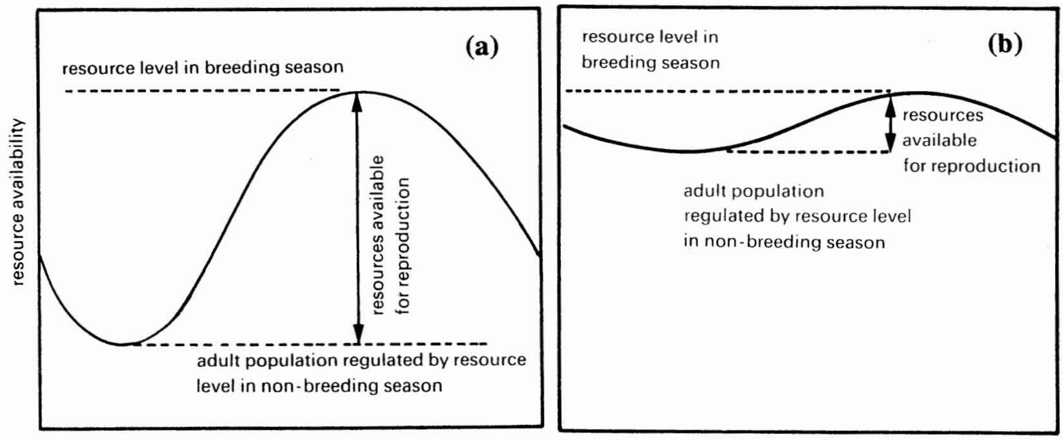

FIGURE 9. Resource availability in main-island (*a*) and small-island (*b*) populations. Clutch size is proportional to the ratio of the resource levels in breeding and nonbreeding seasons (after Ricklefs 1980 and Perrins and Birkhead 1983).

size, exaggerated begging behavior, and prolonged parental care of small-island Varied Tits are adaptations to these ecological conditions (Higuchi and Momose 1981). Honshu Varied Tit populations experience a larger seasonal flush of food, which allows a larger clutch size. A larger brood is optimal if the parents can feed the young successfully, which is more likely with greater food resources.

These patterns of interspecific variation in populations are influenced by the particular environment found on islands. Host shifts and morphological changes seen in cuckoo species are a result of the presence or absence of congenerics. Similarly, behavioral differences are related to climate differences of islands and the available food resources. The biogeographic relationship between islands and birds strongly affects the ecology and behavior of island avifauna.

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LITERATURE CITED

ALI, S., and S. D. RIPLEY. 1971. Handbook of the birds of India and Pakistan, Vol. 6. Oxford University Press, London.

AUSTIN, O. L., and N. KURODA. 1953. The birds of Japan: Their status and distribution. Bull. Mus. Comp. Zool. Harv. Univ. 109(4): 279–613.

BLAKISTON, T. W. 1883. Zoological indications of ancient connection of the Japan Islands with the continent. Trans. Asiatic Soc. Jpn 2:126–140.

BRAZIL, M. A. 1991. The birds of Japan. Christopher Helm, London.

CHENG, T. 1976. Distributional list of Chinese birds, 2nd ed. Scientific Press, Beijing.

———. 1987. A synopsis of the avifauna of China. Paul Parey Scientific Publishing, Hamburg.

CHING, K. 1991. Temperate deciduous forests in East Asia. Pages 539–555 *in* E. Rohrig and B. Ulrich, eds. Ecosystems of the World 7, Temperate deciduous forests. Elsevier Science Publishers, Amsterdam.

DAVIES, N. B., and M. DE L. BROOKE. 1988. Cuckoos versus reed warblers: Adaptations and counteradaptations. Anim. Behav. 36:262–284.

DELACOUR, J. 1977. The pheasants of the

World, 2nd rev. ed. Saiga Publishing Co., Surrey, U.K.

DE SCHAUNSEE, R. 1984. The birds of China. Oxford University Press, Oxford.

FAN, Z., ED. 1990. Species of Chinese birds. Liaoning Science and Technology Press, Shenyang.

HARRISON, C. 1968. Egg mimicry in British cuckoos. Bird Study 15:22–28.

HIGUCHI, H. 1976. Comparative study on the breeding of mainland and island subspecies of the Varied Tit, *Parus varius*. Tori Bull. Ornithol. Soc. Jpn. 25:11–20.

———. 1978. Ecology and evolution of birds. Shisaku-sha, Tokyo (in Japanese).

———. 1979. The ecology of island birds. Saiensu (Japanese ed. of Sci. Am.) 9(8): 74–88 (in Japanese).

———. 1980. Colonization and coexistence of woodpeckers in the Japanese Islands. Misc. Rep. Yamashina Inst. Ornithol. 12: 139–156.

———. 1986. Adaptations for brood parasitism in *Cuculus* cuckoos. Pages 1–31 *in* S. Yamagishi, ed. Breeding strategies of birds, Vol. 2. Tokai University Press, Tokyo (in Japanese).

———. 1987. The nature and birds of Japan. Yacho 52(4): 16–21 (in Japanese).

———. 1989. Responses of the Bush Warbler *Cettia diphone* to artificial eggs of *Cuculus* cuckoos in Japan. Ibis 131:94–98.

HIGUCHI, H., and T. HIRANO. 1988. Breeding season, courtship behavior, and territoriality of White and Japanese Wagtails *Motacilla alba* and *M. grandis*. Ibis 131: 578–588.

HIGUCHI, H., and N. KAWAJI. 1989. Iijima's Willow Warbler *Phylloscopus ijima* of the Tokara Islands, a new breeding locality, in southwest Japan. Bull. Biogeogr. Soc. Jpn. 44:11–15.

HIGUCHI, H., and H. MOMOSE. 1981. Deferred independence and prolonged infantile behaviour in Varied Tits, *Parus varius*, of an island population. Anim. Behav. 29:523–528.

HIGUCHI, H., and S. SATO. 1984. An example of character release in host selection and egg colour of cuckoos *Cuculus* spp. in Japan. Ibis 126:398–404.

HIKITA, T. 1985. Japan is a country of salamanders. Anima 13(3): 39–42 (in Japanese).

IKEHARA, S. 1991. Report on the survey and conservation of the birds of the Nansei Islands. Pages 211–229 *in* World Wildlife Fund-Japan, eds. Study of essential factors for preservation of wildlife in Nansei Islands. Japanese Environment Agency, Tokyo.

IMAIZUMI, Y. 1962. The relationships between endemic species and geographic isolation in Japanese mammals. Shizenkagaku to Hakubutsukan 29:39–46 (in Japanese).

———. 1985. Origin of the Japanese fauna. Anima 13(3):28–34 (in Japanese).

Johnsgard, P. A. 1986. The pheasants of the World. Oxford University Press, Oxford.

King, B. F., and E. C. DICKINSON. 1975. A field guide to the birds of South-East Asia. Collins, London.

MACARTHUR, R. H., and E. O. WILSON. 1963. An equilibrium of insular zoogeography. Evolution 17:373–387.

———. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

MARTENS, J. 1980. Lautausserungen, verwandtschaftliche Beziehungen und Verbreitungsgeschichte asiatischer Laubsanger (*Phylloscopus*). Fortschr. Verhaltensforsh. 22.

———. 1981. Searching the evolutionary process of *Phylloscopus* Willow Warblers through their song. Anima 98:25–31 (in Japanese).

MASON, P., and S. ROTHSTEIN. 1987. Crypsis versus mimicry and the color of Shiny Cowbird eggs. Am. Nat. 130:161–167.

MELVILLE, D. 1984. Seabirds of China and the surrounding seas. Pages 501–511 *in* J. P. Croxall, P. G. H. Evans, and R. W. Schreiber, eds. ICBP Technical Publication No. 2. International Council for Bird Preservation, Cambridge.

MINATO, M., M. USHIKU, and M. FUNABASHI. 1965. The geologic development of the Japanese Islands. Tsukiji-Shokan, Tokyo.

MORIOKA, H. 1974. Avifauna of the Ryukyu Islands and its origin. Mem. Natl. Sci. Mus. (Tokyo) 7:203–211 (in Japanese with English summary).
ORNITHOLOGICAL SOCIETY OF JAPAN. 1974. Check-list of Japanese birds, 5th & rev. ed. Gakken, Tokyo.
PENG, Y., D. YAN, and B. KUANG. 1981. A distributional list of Yunnan birds. Yunnan Science and Technology Press, Kumin.
PERRINS, C., and T. BIRKHEAD. 1983. Avian ecology. Blackie and Sons, Glasgow.
RICKLEFS, R. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38–49.
SHORT, L. L. 1973. Notes on Okinawa birds and Ryukyu Islands zoogeography. Ibis 115:264–267.
SIBLEY, C. G., and B. L. MONROE, JR. 1990. Distribution and taxonomy of birds of the world. Yale University Press, London.
TAKANO, S., ED. 1985. Birds of Japan in natural color. Yama-to-keikoku-sha, Tokyo (in Japanese).
TANG, C. 1989. The distribution of pheasants and partridges in China. Pages 16–17 *in* D. Hill, ed. Pheasants in Asia. Institute of Zoology, Academia Sinica, Beijing.
TOKUDA, M. 1970. Biogeography. Tsukiji-shokan, Tokyo (in Japanese).
VON HAARTMAN, L. 1981. Co-evolution of the Cuckoo *Cuculus canorus* and a regular Cuckoo host. Ornis Fenn. 58:1–10.
WILD BIRD SOCIETY OF JAPAN. 1982. A field guide to the birds of Japan. Wild Bird Society of Japan, Tokyo.
YAMASHINA, Y. 1941. On the three endemic birds in the Ryukyu Islands—Their classificatory position and zoogeographical meaning. Trans. Biogeogr. Soc. Jpn. 3:319–328.
ZHAO, Z., ED. 1988. The birds of Northeast China. Liaoning Science and Technology Press, Shenyang.
ZUSI, R. 1969. Ecology and adaptation of the Trembler on the island of Dominica. Living Bird 8:137–164.

APPENDIX

NUMBER OF BREEDING SPECIES FOR EACH ORDER AND FAMILY IN CHINA AND JAPAN

ORDER	FAMILY	NO. OF SPECIES: CHINA	NO. OF SPECIES: JAPAN
Podicipediformes	Podicipedidae	5	3
Procellariiformes	Diomedeidae	1	3
	Procellariidae	2	5
	Hydrobatidae	1	5
Pelecaniformes	Phaethontidae	1	1
	Pelecanidae	1	0
	Sulidae	2	1
	Phalacrocoracidae	3	4
	Fregatidae	2	0
Ciconiiformes	Ardeidae	19	16
	Ciconiidae	3	1
	Threskiornithidae	2	1
Anseriformes	Anatidae	27	13
Falconiformes	Accipitridae	41	13
	Falconidae	9	3
Galliformes	Phasianidae	54	7
Gruiformes	Turnicidae	3	1
	Gruidae	6	1
	Rallidae	16	10
	Otididae	3	0
Charadriiformes	Jacanidae	2	0
	Rostratulidae	1	1
	Haematopodidae	1	0
	Ibidorhynchidae	1	0
	Charadriidae	9	5
	Scolopacidae	12	5
	Recurvirostridae	2	1
	Glareolidae	2	1
Lariformes	Laridae	20	10
	Alcidae	1	7
Columbiformes	Pteroclididae	3	0
	Columbidae	27	8
Psittaciformes	Psittacidae	4	0
Cuculiformes	Cuculidae	17	4
Strigiformes	Tytonidae	2	0
	Strigidae	22	7
Caprimulgiformes	Caprimulgidae	5	1
Apodiformes	Apodidae	9	3
Trogoniformes	Trogonidae	3	0
Coraciiformes	Alcedinidae	9	4
	Meropidae	6	0
	Coraciidae	2	1
	Upupidae	1	1
	Bucerotidae	3	0
Piciformes	Capitonidae	8	0
	Picidae	28	11
Passeriformes	Eurylaimidae	2	0
	Pittidae	5	1
	Alaudidae	10	1
	Hirundinidae	9	5
	Motacillidae	13	6
	Campephagidae	10	1

APPENDIX (continued)

ORDER	FAMILY	NO. OF SPECIES CHINA	NO. OF SPECIES JAPAN
Passeriformes (continued)			
	Pycnonotidae	16	2
	Irenidae	6	0
	Bombycillidae	1	0
	Laniidae	10	3
	Orolidae	5	0
	Dicruridae	7	0
	Sturnidae	15	2
	Artamidae	1	0
	Corvidae	27	7
	Cinclidae	2	1
	Troglodytidae	1	1
	Prunellidae	7	2
	Muscicapidae		
	(1) Turdinae	72	13
	(2) Timaliinae	124	0
	(3) Sylviinae	79	15
	(4) Muscicapinae	35	5
	Paridae	16	5
	Sittidae	9	1
	Certhiidae	4	1
	Remizidae	2	0
	Dicaeidae	6	0
	Nectariniidae	12	0
	Zosteropidae	3	1
	Meliphagidae	0	1
	Estrildidae	4	0
	Ploceidae	13	2
	Fringillidae	47	11
	Emberizidae	18	8
	Aegithalidae	4	1
Totals 20	78	996	254

Compiled from Ornithological Society of Japan (1974) and Wild Bird Society of Japan (1982) for Japanese birds and from Cheng (1976, 1987), Peng et al. (1981), Zhao (1988), and Fan (1990) for Chinese birds.