AN ECOLOGICAL STUDY OF THE TIMALIINAE (MUSCICAPIDAE) OF TAIWAN

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ABSTRACT—The altitudinal distribution, ecological niche and breeding season of each of 16 species of Timaliinae in Taiwan are reported, and the ecological isolation of coexisting congeneric species and present status of distribution of the lowland inhabitants are discussed.

KEY WORDS: Timaliinae, forest birds, altitudinal distribution, ecological isolation.

INTRODUCTION

The Timaliinae are all lovely songsters of the grasses, mountain forests and lowland woods.There are 257 species in the world (Howard and Moore, 1980). The Oriental region are with 114 species in 25 genera found in China (Cheng, et al; 1987). The 16 species (9 genera) of the Timaliinae of Taiwan (tab.1) include 5 endemic species and 10 endemic subspecies (Hachisuka and Udagawa, 1951). These authors reviewed the literature and reported on measurements, distribution and habits of each species. Chai (1977) and Kobayashi (1987) have also reported on their field studies of the Timaliinae in Taiwan.

The Timaliinae live in various types of original and secondary forests, including coniferous forests, broadleaf forests, mixed forests, forest plantations and orchards. Taiwan is a mountainous island. Six vegetation zones have been described varying along a gradient from sea level to alpine elevation and from tropical to subarctic climates (Su, 1984). They are *Ficus-Machilus* (tropical) Zone from sea level to 500m, *Machilus-Castanopsis* (subtropical) Zone from 500m to 1500m, *Quercus* (temperate) Zone from 1500m to 2500m, *Tsuga-Picea* (cool-temperate) Zone from 2500m to 3100m, *Abies* (cold-temperate) Zone from 3100m to 3600m, and Alpine Vegetation (subarctic) Zone from 3600m to the summit.

Taiwan's growing human population and the utilization of natural forest resources in recent decades have resulted in great reduction in habitat for many species of birds. The purpose of this study is to review the present status of the Timaliinae in Taiwan.

METHODS

For the analysis of altitudinal distribution, ecological niche and breeding season, the literature on the Timaliinae (Kano, 1940; Hachisuka and Udagawa, 1951; Kobayashi, 1978; Kobayashi and Cho, 1981; Chang, 1985; Sha, 1986) and records of specimens deposited in the National Museum of Natural Science, Taichung and in Taiwan Museum, Taipei were reviewed. Additional information was provided by the author's extensive notes from field studies (1972-1990), including surveys of forest avifauna (Chen and Yen, 1973-75), throughout Taiwan and its dependent isles (fig.1).

RESULTS

Timaliinae are geographically distributed throughout the main island of Taiwan and are not found on the dependent isles (Momiyama, 1932; Kano, 1932). The altitudinal distribution of the Timaliinae shown in fig.2 can be divided roughly into three zones. The lower elevation zone is from sea level to the mountains of 1200m (tropical to subtropical). *Garrulax canorus* and *Yuhina zantholeuca* usually restrict themselves to this area, but the latter may disperse to as high as 2200m after breeding season. The intermediate elevation zone is from 1000m to 2500m (upper subtropical to

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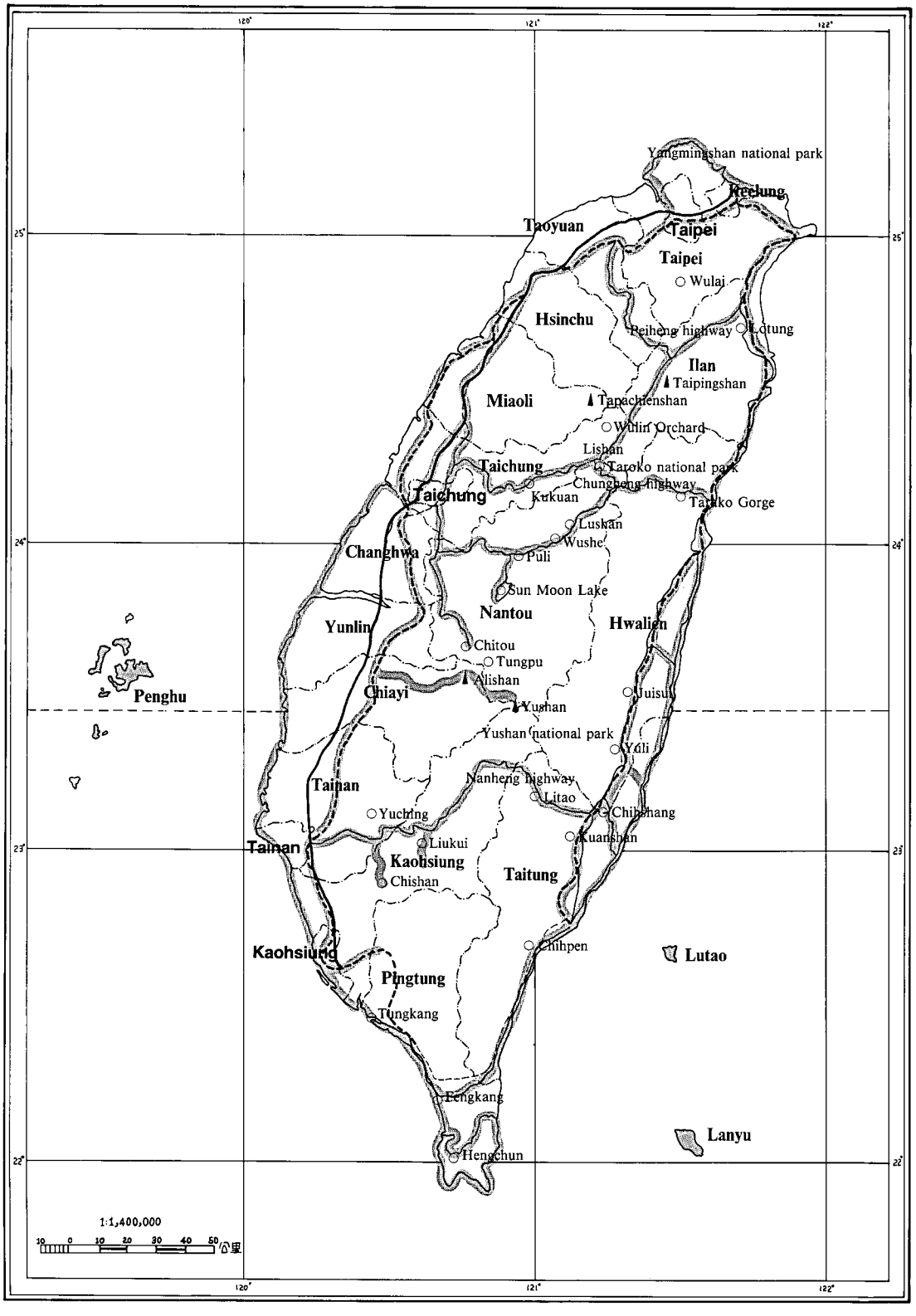

Figure 1. Areas of field trips by the author.

Table 1. List of the Timaliinae of Taiwan

Species	*(•) = Endemic Species*	*(••) = Endemic Subspecies*
•• *Pomatorhinus erythrogenys erythrocnemis Gould*		• *Liocichla steerii Swinhoe*
•• *Pomatorhinus ruficollis musicus Swinhoe*		• *Actinodura morrisoniana Ogilvie-Grant*
•• *Pnoepyga pusilla formosana Ingram*		•• *Alcippe cinereiceps formosana (Ogilvie-Grant)*
•• *Stachyris ruficeps praecognita Swinhoe*		•• *Alcippe brunnea brunnea Gould*
•• *Garrulax albogularis ruficeps Gould*		•• *Alcippe morrisonia morrisonia Swinhoe*
•• *Garrulax poecilorhynchus poecilorhynchus Gould*		• *Heterophasia auricularis (Swinhoe)*
•• *Garrulax canorus taewanus Swinhoe*		• *Yuhina brunneiceps Ogilvie-Grant*
• *Garrulax morrisonianus (Ogilvie-Grant)*		*Yuhina zantholeuca griseiloris (Stresemann)*

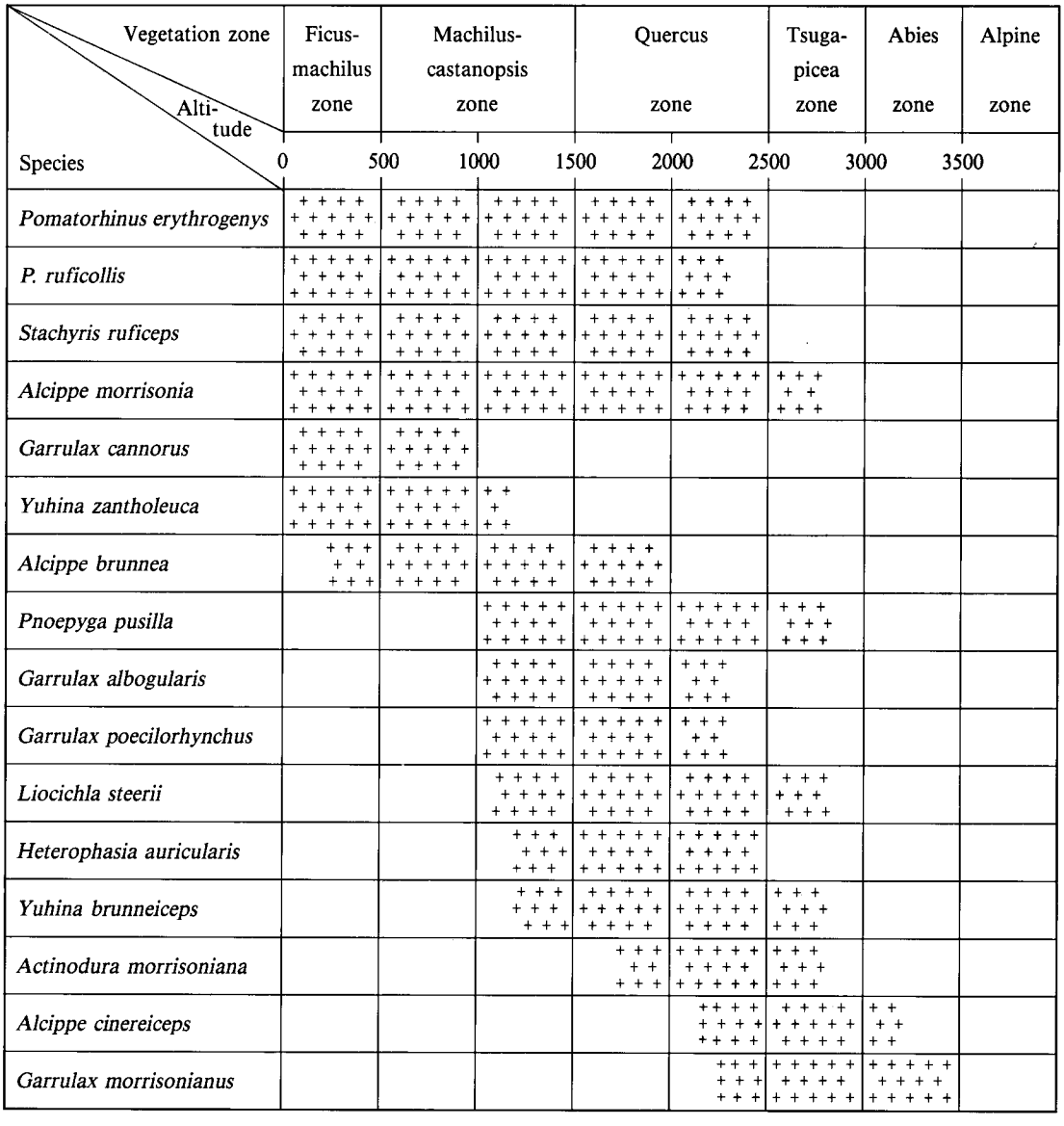

Figure 2. Vegetation zones and altitudinal distribution of the Timaliinae.

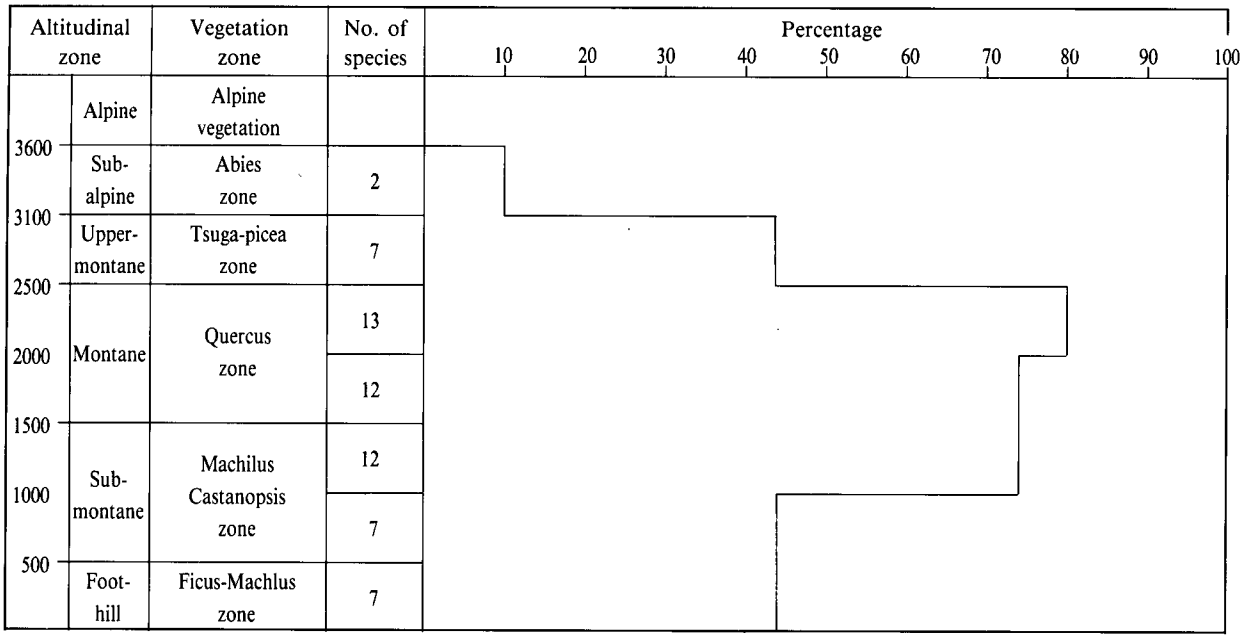

Figure 3. Distribution of the Timaliinae along the altitudinal gradient.

temperate), in which six species *(Pnoepyga pusilla, Garrulax albogularis, G. poecilorhynchus, Liocichla steerii, Heterophasia auricularis,* and *Yuhina brunneiceps)* are generally confined except during winter when they may descend to the lower zone. *P.pusilla, L.steerii,* Heterophasia auricularis, and *Y.brunneiceps* can be found as high as 2800m but may descend to the lower zone during winter. There are five species *(Pomatorhinus erythrogenys, P.ruficollis, Stachyris ruficeps, Alcippe brunnea* and *A.morrisonia)* with a distribution range bridging the lower and intermediate elevation zones. The upper elevation zone is from 2000m to the summit (upper temperate, cool and cold temperate to subarctic), in which three species *(Garrulax morrisonianus, Actinodura morrisoniana* and *Alcippe cinereiceps)* are confined except during winter when they may descend to the intermediate elevation zone.

Seven species are found in the lowland; all 16 species are found in the intermediate elevation zone between 1000m and 2500m; 7 species are found above 2500m; and only two species are found at 3100m. Therefore, the species-density compared with altitude is a bell-shaped curve (fig.3).

The amplitude of vertical range is quite large among the Timaliinae of Taiwan. The two species confined to the lower elevation zone have an amplitude of vertical range of between 1000m and 1200m. Those species generally confined to the intermediate elevation zone have an amplitude of vertical range of between 1200m and 1800m. Those species confined to the upper elevation zone have an amplitude of vertical range of between 1000m and 1200m. Those species that live in both lower and intermediate elevation zones have an amplitude of vertical range of between 1800m and 2800m. *Alcippe morrisonia* has the largest range (2800m), overlapping three zones. The average amplitude for the 16 species is 1666m, whereas all the land breeding birds of Taiwan have an average amplitude of 1333m (Chai, 1977).

Four strata of the forest (undergrowth, lower tree, middle tree, and canopy) are distinguished for indicating the ecological niche of each species (fig.4). There are 4 species *(Pomatorhinus ruficollis, Pnoepyga pusilla, Alcippe cinereinceps* and *A.brunnea)* which restrict their activities to the dense undergrowth of the forest. Another six species *(Pomatorhinus erythrogenys, Stachyris ruficeps, Garrulax poecilorhynchus, G.canorus, G.morrisonianus* and *Liocichla steerii)* live in both the undergrowth and the lower tree stratum. Three species *(Garrulax albogularis, Actinodura morrisoniana* and *Alcippe morrisonia)* utilize both middle and lower strata, and another three species

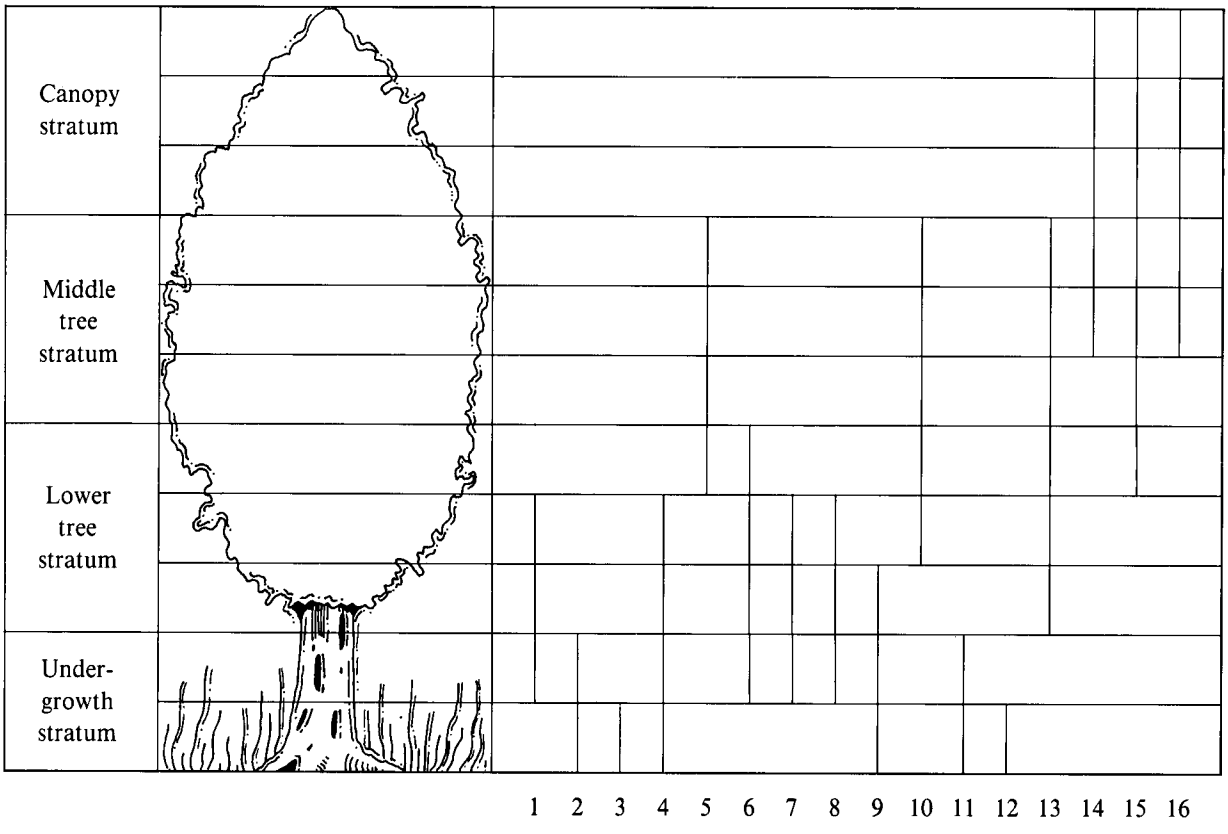

Figure 4. The ecological niche of each studied species.

1. *Pomatorhinus erythrogenys*
2. *Pomatorhinus ruficolllis*
3. *Pnoepyga pusilla*
4. *Stachyris ruficeps*
5. *Garrulax albogularis*
6. *Garrulax poecilorhynchus*
7. *Garrulax canorus*
8. *Garrulax morrisonianus*
9. *Liocichla steerii*
10. *Actinodura morrisoniana*
11. *Alcippe cinereiceps*
12. *Alcippe brunnea*
13. *Alcippe morrisonia*
14. *Heterophasia auricularis*
15. *Yuhina brunneiceps*
16. *Yuhina zantholeuca*

(Heterophasia auricularis, Yuhina brunneiceps and *Y.zantholeuca)* utilize both canopy and the middle strata.

The social habits of the Timaliinae in the non-breeding season may be characterized as solitary, forming small flocks, or gregarious. Species such as *Pnoepyga pusilla* and *Garrulax canorus,* which limit their activities to dense bushes or undergrowth of forest, may be solitary, or 2 or 3 individuals may form a small flock as do *Pomatorhinus erythrogenys, P.ruficollis* and *Alcippe brunnea.* The species that confine their activities to both the undergrowth and the lower tree stratum, or the lower and middle tree strata may form a larger flock of 8 to 10 individuals, as do *Garrulax albogularis, G.poecilorhynchus, G.morrisonianus, Liocichla steerii, Actinodura morrisoniana* and *Heterophasia auricularis.* Those species which are smaller in size and are active in the canopy or on the edges of trees, such as *Stachyris ruficeps, Alcippe morrisonia, Yuhina brunneiceps* and *Y. zantholeuca,* are gregarious and often mix with other small species to form large flocks moving among trees.

The breeding data for the Timaliinae in Taiwan

	Species	Month												Size of Clutch
		1	2	3	4	5	6	7	8	9	10	11	12	
Lower hill habitants	*G. canorus*				———	———	———	———						3 - 4
	Y. zantholeuca				———									4
	Pomatorhinus erythrogenys			———										4
	P. ruficollis				———	———	———							3
	Stachyris ruficeps				———	———	———	———						3 - 5
	A. brunnea				———	———	———							2 - 3
	A. morrisonia				———	———	———	———						2 - 4
Middle mountain habitants	*Garrulax albogularis*													
	G. poecilorhynchus					———								2 - 3
	Heterophasia auricularis													
	Yuhina brunneiceps				———	———								2 - 3
	Pnoepyga pusilla					———	———	———						2
	Liocichla steerii					———	———	———	———					2 - 3
Upper mountain habitants	*Actinodura morrisoniana*													
	Alcippe cinereiceps					———	———	———						2
	G. morrisonianus							———						2

Figure 5. The breeding season and clutch size of the Timaliinae in Taiwan.

are quite limited, and there is no information on breeding for three species. Fig.5 shows that the breeding season is related to the altitudinal distribution. The lower hill inhabitants begin their breeding season in March and April. The middle and upper mountain inhabitants begin their breeding season in May or later.

There is a peculiar breeding habit of communal nesting of *Yuhina brunneiceps*. Several pairs have been found building one nest, and incubating time in turn (Yamashina, 1938; Yu and Lin, 1985).

Clutch size also is related to the altitudinal distribution, the lower hill inhabitants having 2 to 5 eggs per clutch, the middle mountain inhabitants having 2 to 3 eggs per clutch, and the upper mountain inhabitants having 2 eggs per clutch (fig.5).

The results of the examination of stomach contents are as shown in tab.2; the staple food items are insects and plant seeds. There was some gravel in the stomachs of some species, such as *Pnoepyga pusilla, Garrulax poecilorhychus, C.canorus, G.morrisonianus* and *Liocichla steerii,* and tiny pieces of wood in the stomach of *G.poecilorphychus*. These species are active in the undergrowth of forest, and sometimes may dig in the ground for food. The species of tree foragers that are active in the canopy and middle tree stratum have no gravel in their stomachs.

Two lower inhabitants, such as *Garrulax canorus* and *Yuhina zantholeuca,* formerly were widely distributed in the island, but they are now limited to a smaller area. *Y.zantholeuca* can be seen, for example, at Sun Moon Lake and Lienhuachih, Nantou County; Kukuan, Taichung County; Chishan and Sanping, Kaohsiung County; Tai-an,

Table 2. The stomach contents of Timaliinae in Taiwan

Food items / Species	Insects	spiders	snails	seeds	gravels	small pieces of wood
Pomatorhinus erythrogenys	v					
Pomatorhinus ruficollis	v			v		
Pnoepyga pusilla	v	v	v	v	v	
Stachyris ruficeps	v			v		
Garrulax albogularis						
Garrulax poecilorhynchus	v			v	v	v
Garrulax canorus	v			v	v	
Garrulax morrisonianus	v			v	v	
Liocichla steerii	v			v	v	
Actinodura Morrisoniana	v			v		
Alcippe cinereiceps	v			v		
Alcippe brunnea	v		v	v		
Alcippe morrisonia	v			v		
Heterophasia auricularis	v			v		
Yuhina brunneiceps	v			v		
Yuhina zantholeuca	v			v		

Miaoli County; Shihmen, Taoyuan County, where some relics of original forests may be found.

DISCUSSION

The altitudinal distribution of the Timaliinae shows two critical intersections of life zones in the vertical range of the Taiwan mountains: one is between 1000m and 1200m, and the other, a wider belt, between 2000m and 2500m. These critical intersections appear to restrict the altitudinal distribution of some species of Timaliinae. The number of species of breeding birds of Taiwan increases from the lowlands to a peak between 1200m and 1500m and then decreases with increasing altitude (kano, 1940; Chai, 1977). The number of species of the Timaliinae is lower in the lower elevation zone (7 species) and above 2500m elevation (7 species), but there is no distinct peak in the intermediate elevation zone where 10-12 species can be found at any given elevation.

The number of Timaliinae species utilizing forest undergrowth, lower tree, middle tree, and canopy strata are 10, 10, 6 and 3 species, respectively. The vertical distribution of ecological niches of the birds is positively correlated with the species diversity of vegetation and food resources found in these strata.

There are four genera of the Timaliinae in which more than one species can be found in Taiwan. The coexisting congeneric species are usually separated by some ecological factors that keep them from competing. The ecological factors include the separation by differences in range, habitat, and food or foraging behavior (Lack, 1971). The phenomenon of isolation to avoid competition within the genus in the Timaliinae of Taiwan can be explained as follows:

Genus *Pomatorhinus*--though the two species, *P.erythrogenys* and *P.ruficollis,* occupy almost the same distributional and altitudinal range in Taiwan (fig.2), they live in different habitats: the former are found in the dense undergrowth of forests, and the latter occur in more open area such as grassland. They are also different in bill, weight, and size. The bill, weight, and length of wing of *P.erythrogenys* are 31mm, 68.7g, and 93.2mm(89-97), respectively, and of *P.ruficollis* are 20.7mm, 39.3g.(33-43.7), and 82.2mm(80-86), respectively. The differences in bill or body size can ensure ecological isolation (Lack, 1971).

Genus *Garrulax*--There are four species of this genus in Taiwan. *G.canorus* is a lower hill and open grassland inhabitant. *G.albogularis* and *G. poecilorhynchus* are middle mountain and broadleaf forest inhabitants. *G.morrisonianus* is an inhabitant of upper mountain pine woods. The ecological isolation of these species is generally

characterized by differences in altitude and habitat. The two species occurring in the middle mountains are separated by vertical stratum with *G. albogularis* active in the middle tree stratum and *G.poecilorhynchus* in the lower tree stratum (fig.4).

Genus *Alcippe*--three species are found in Taiwan. They are separated by differences in altitude, habitat, and vertical stratum. *A.brunnea* occur both in lower hills and middle mountains, and breed in the undergrowth of broadleaf forest. *A. cinereiceps* are found in the upper mountains and breed mainly in alpine bamboos and undergrowth of pine woods. The ecological isolation of the two species is clearly characterized by differences in altitude and habitat. *A.morrisonia* have a wider distributional range which overlaps considerably in altitudinal range with *A.brunnea* and *A.cinereiceps,* but have different activity and breed in the middle tree stratum.

Genus *Yuhina*--there occur two forms, *Y.zantholeuca* and *Y.brunneiceps,* separated by altitudinal range with a small zone of overlap. *Y. zantholeuca* inhabit the lower hills and tropical forest, whereas *Y.brunneiceps* inhabit the middle mountains and subtropical forests.

There is a paucity of breeding data on the Timaliinae of Taiwan. According to available data, the breeding season of the lower hill habitants begins much earlier than middle and upper mountain habitants. This is probably due to climatic effects of warmer temperatures on food resources in the lower hills. Longer breeding seasons with multiple broods may be expected at lower elevations. *Garrulax canorus* and *Pomatorhinus ruficollis,* lower hill habitants breed twice and sometimes thrice a year (Swinhoe, 1863).

The human population of Taiwan increased 3.4 times within the past 40 years, from about six million people in 1950 to about twenty million people in 1990. The population pressure and the great reduction in forest resources have caused serious loss of bird habitats. About 0.34 million ha. (18%) of the virgin forests had been cut by the end of 1987 (Peng, 1989). Deforestation has caused the shrinkage of the distribution range of the lower hill Timaliinae, generally limiting them to isolated patches of woods.

Garrulax canorus was previously abundant everywhere on the plains and lower hills (Swinhoe, 1863; Ogilvie-Grant and La Touche, 1907), but has suffered the pressures of habitat destruction and hunting. As the natural environment has been converted to cultivated land and *G.canorus* continues to be captured for sale as a cage bird, this species has become a threatened bird and needs protection. Other species of Timaliinae at higher altitudes have not suffered as high hunting pressure as *G.canorus,* and are still abundant or common. As the lower hill inhabitants faced the pressure of habitat destruction, they have developed a larger amplitude of distribution and are found at higher altitudes. This probably is due to deforestation at higher altitudes favorable to extension of their habitats.

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台灣畫眉亞科的生態學研究

顏重威

摘 要

本文報告台灣畫眉亞科16種的高度分布，生態職位和繁殖季節。另外，也討論其同屬內種的生態隔離和棲於低原地帶的分布現況。

關鍵詞：畫眉亞科、森林鳥類、高度分布、生態隔離。