Endemicity and Altitudinal Stratification in Distribution of Megascolecid Earthworms in the Centro-western Taiwan

台灣中西部地區蚯蚓之特有性及其垂直分布

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Abstract

Earthworm surveys were conducted in the centro-western Taiwan from the coastal plain at 50m in elevation near the Tatu Estuary to Mt. Hohuan at 3,200m in the Central Mountain Range in 1999, 2000 and 2003. A total of 34 species of megascolecid earthworms were collected, consisting of 19 native species and 15 exotic species. Most of the native species were woodland earthworms, dwelling primarily in the mountain range and its peripheral hills. They showed altitudinal stratification in the distribution; each species had its specific geographical area with the highest and the lowest altitudinal ranges. Apparently, elevation defines the distributional ranges, and is one of the important factors for autochthonous speciation of the native species. In contrast most of the exotic species were farmland earthworms commonly found in the coastal plain and at the foot of peripheral hills, and showed the altitudinal stratification only in the highest altitudinal ranges. Apparently, their species-specific adaptability to climatic and environmental conditions in the hill and mountain regions defines the highest altitudinal ranges of their distribution. With the decrease in elevation, number of native species decreased while number of exotic species increased, suggesting the presence of species shift from native forms to exotic forms in the earthworm communities, and the shift was higher at low elevations than at high elevations.

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摘 要

自1999年至2000年於中央山脈西側集集至合歡山區以及2003年於集集至大肚溪口共採得34種蚯蚓，其中特有種19種、外來種15種。特有種在海拔高度上有其特定之分布上下限，形成不同物種垂直分層的現象；外來種則自平地至山區皆有分布，僅分布上限因物種而有所不同。高海拔處之特有性較低海拔處爲高。海拔高度下降，則蚯蚓特有種種數隨之減少，而外來種種數隨之增加，顯見物種組成有自特有種轉換成外來種之趨勢，此趨勢又以低海拔處較高海拔處明顯。

Key words : earthworm, native species, exotic species, species diversity, elevation

關鍵詞：蚯蚓、特有種、外來種、物種多樣性、海拔

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Introduction

Megascolecid earthworms are one of the dominant terrestrial macro-invertebrates in the eastern and southeastern Asia, and their altitudinal distributions have been reported sporadically. The highest elevation that has been recorded so far is for *Amynthas asiaticus* (Michaelsen), which occurs at 3,415 to 4,268m in Tibet (Michaelsen 1902). It is followed in decreasing order by *Amynthas corticis* (Kinberg) at 3,659m in Sichuan of China (Gates 1972); *Perionyx hingstoni* Stephenson at 3,354m at Mt. Everest (Stephenson 1925); *Amynthas wulinensis* Tsai, Shen and Tsai and *Amynthas tessellatus* Shen, Tsai and Tsai at 3,200m at Mt. Hohuan of Taiwan (Tsai *et al*. 2001; Shen *et al*. 2002); *Amynthas omeimontis kinabalu* Sims and Easton and *Pheretima darnleiensis* (Fletcher) at 3,100m, and *Pheretima saba* Sims and Easton and *Metapheretima elongata* (Perrier) at 2,750m at Mt. Kinabalu of Borneo (Sims and Easton 1972); *Metapheretima bulmeri* (Gates), *Amynthas kaironkensis* (Gates), and *Amynthas schraderi* (Gates) at 2,530 to 2,560m in New Guinea (Gates 1970); *Metaphire langbiangi* (Michaelsen) and *Amynthas dactilicus* (Chen) at 2,400m, respectively, in Vietnam (Michaelsen 1934) and at Mt. Omei in Sichuan of China (Chen 1946); and *Amynthas yamizoyamensis* (Ohfuchi) at 1,022m at Mt. Yamizo of Japan (Ohfuchi 1935). According to literature there is a decreasing trend in highest altitudinal ranges with the increase in latitude in the distribution of megascolecid earthworms in the eastern and southeastern Asia. Also, there are evidences of high endemicity and altitudinal stratification in their distribution in highlands (Sims and Easton 1972).

Taiwan is an island situated between the tropical zone and the subtropical zone in the western Pacific. The Central Mountain Range runs from north to south, and is cut deeply by valleys and mountain peaks of 3,000m to nearly 4,000m in elevation. It is the area of highly diverse habitat with rich flora and fauna, and homes of most of native animals. Prior to the 1970s most of the areas of the mountain range were not easily accessible to man, and earthworms that had been studied were only those collected from coastal plains and peripheral hills (Kobayashi 1938a, 1938b; Gates 1959; Tsai 1964). In the past few decades, cross-island highways were constructed across the mountain range, from where some earthworms have been reported (Chen and Shih 1996; Tsai *et al*. 1999, 2000b, 2000c, 2001, 2002, 2004; Shen *et al*. 2002, 2003b).

This study was intended to relate the distribution of terrestrial earthworms to elevations with respects to native and exotic species, and to determine their altitudinal stratification in the centro-western Taiwan.

Materials and Methods

In 1999 and 2000 we conducted earthworm surveys on the western slope of the Central Mountain Range and its peripheral hills from Chichi at 250m in elevation to the peak Wulin of Mt. Hohuan at 3,200m along Rt. 14 A in the central Taiwan (Tsai *et al*. 2001; Shen *et al*. 2003b). This highway was only primary road that reaches to Mt. Hohuan in the Nantou County. With its secondary mountain roads it was only place accessible for earthworm collection in the mountains. The earthworms were collected from mountain slopes wetted by spring waters, and from the piles of soil and detritus at road sides and in roadside rainwater drainage ditches. The earthworms collected in the latter were those apparently washed down from the mountains by heavy rainwater, trapped in the ditches and aggregated in the piles of soils and detritus. They were easily collected and might be good representatives of the earthworm communities in the mountains above.

In 2003 we made another survey along Rts. 14 and 139 on the coastal plain from Chichi to the area around 50m in elevation near the mouth of the Tatu River flowing into the Taiwan Strait (Fig. 1). As there was no natural forest in the coastal plain, we collected earthworms on dry lands and drainage ditches in betel nut plantations, fruit orchards, bamboo plantations, schools, villages, and parks.

The coastal plain region was mostly flat farmlands (rice paddies, vegetable gardens, fruit orchards, bamboo plantations, and some betel nut plantations) at elevations of 50 to 200m. It was an area of intensive agricultural activities and human disturbances. The peripheral hill region was at elevations from 250 to 700m, and covered mostly by betel nut plantations, fruit orchards, and sparsely distributed broadleaf forests. The mountain region started from 700m in elevation at the east of Puli to 3,200m at the peak Wulin. The region was covered with mixing broadleaf and coniferous forests at lower elevations and coniferous forests and Yushan cane (*Yushania niitakayamensis* (Hayata)) forests at higher elevations, with sparsely distributed fruit orchards and vegetable gardens. The climates in the study area were subtropical condition in the coastal plain and the peripheral hills, warm temperate condition at low

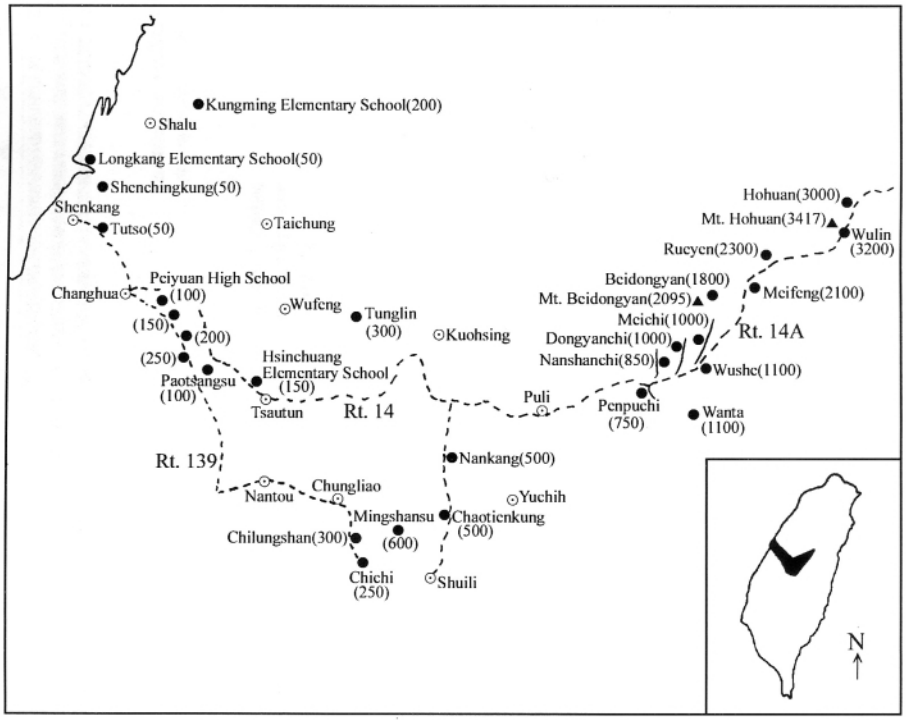


Fig. 1. Localities of earthworm collections (solid circles) in the centro-western Taiwan (open circles with black center dots, urban centers; solid triangles, mountains; elevations in meter in parentheses).

elevations of the mountain range, and cold temperate condition with snowfall in winter at high elevations. The elevations were measured by an altimeter and corrected by a map with elevations. Earthworms collected were fixed in a 10% formalin-water solution for two days to a week, and then preserved in a 75% ethyl alcohol-water solution. Each individual was identified to species.

A native species is a species that occurs naturally in a restricted geographical area, and thus, it is certainly speciated locally and autochthonous (= endemic, indigenous) (Gates 1972). In contrast, an exotic species is a foreign species introduced to a particular geographical area. It is equivalent to a peregrine species, that is a species of wide distribution in Michaelsen's term (Edwards and Bohlen 1996), but it is more commonly characterized as an anthropochorous species, defined as a species transported by humans, usually unintentionally (Gates 1972). In this study the native species is one that occurs only in Taiwan, while the exotic species is one that occurs not only in Taiwan but also in other parts of the world, particularly, in the neighboring Mainland China and Southeast Asia (Tsai *et al*. 2000a).

The number of species of earthworms collected at an elevation was used as a species-diversity indicator for that particular elevation. Its altitudinal trend was determined using the linear regression analysis for each of the three groups of the earthworms: native species, exotic species, and total species (native + exotic). For each group, cumulative numbers of species were established with the increase in elevation. The numbers were converted to percent cumulative numbers and then to probits (Finney 1971). The probit-elevation regressive equation was established using the linear analysis. The constant and slope of the equation was compared among the three groups with the *t*-test (Zar 1984). For examining the changes in the earthworm community structure in relation to elevation, the similarity matrix was established at each of the elevations for total species, using Sorensen's similarity coefficient (S) (Krebs 1989). It was calculated with the formula $S = 2a / (2a+b+c)$, where a is the number of the same species occurring at the two elevations x and y, b is the number of species occurring only at elevation x, and c is the number of species only at elevation y. Based on the similarity coefficients, a dendrogram was established using UPGMA clustering (Everitt 1980).

Results

A total of 2,163 specimens were collected from 43 collections at 27 localities and 17 elevations. They were consisted of 19 native species and 15 exotic species (Table 1). Their distributions in relation to elevations are shown in Fig. 2.

Native species

Native species were widely distributed from the coastal plain at 150m in elevation to the peak Wulin of Mt. Hohuan at 3,200m in the Central Mountain Range (Fig. 2). Each species occupied a species-specific geographical area with the highest altitudinal range and the lowest altitudinal range, indicating the presence of altitudinal stratification in the distribution. According to the patterns of the altitudinal distribution, the native species were divided into five groups as follows:

Group 1: elevations 300 to 3,200m, common and widely distributed in the peripheral hills (subtropical climate) and the Central Mountain Range (warm and cold temperate climates). It was consisted of *Amynthas wulinensis* (Tsai *et al*. 2001), *Amynthas tessellatus* (Shen *et al*. 2002), and *Metaphire bununa* (Tsai *et al*. 2000b). *A. wulinensis* and *A. tessellatus* were found in elevations from 700-800 to 3,200m. They showed an increasing altitudinal cline in the characters of body length, segment number and setal numbers for the former species (Tsai *et al*. 2001), and of genital papillae and associated accessory glands for the latter species that had two distinct subspecies, *A. t. tessellatus* and *A. t. paucus*, at the boundary elevations of 1,000 to 1,100m (Shen *et al*. 2002). *M. bununa* was one of the large earthworms (86-352 mm in length) in the peripheral hills (300 to 600m) of Chungliao, Kuohsing, and Chichi. It was not found in the coastal plain and at the foot of the peripheral hills (250m) in Chichi, where large exotic *Amynthas aspergillus* (Perrier) was common. *M. bununa* made large piles of casts on roadsides, grasslands and woodlands, and was a common species of earthworm walking or killed on highways. At Mt. Hohuan it was a common dweller in the Yushan cane (*Yushania niitakayamensis* (Hayata)) forest. Although the number of specimens collected was small, they tended to show a V-shaped vertical cline in total

Table 1. Species and numbers of native and exotic megascolecid earthworms collected at 17 elevations in the centro-western Taiwan, 1999, 2000 and 2003

	Elevation(m)																	
Species	3200	3000	2300	2100	1800	1100	1000	850	750	600	500	300	250	200	150	100	50	Total
Native																		
A. wulinensis	9			12	1			41										63
A. tessellatus	1	2	8		32	1	1	19	2									66
M. bununa		15		6		2		1	10	13	1	6						54
A. hohuanmontis		8																8
A. catenus		12																12
A. exiguus aquilonius		2	10															12
A. proasacceus		25	2															27
A. tantulus			19															19
A. wangi			1															1
A. fenestrus			8		2													10
A. uvaglandularis			10	53	28													91
M. taiwanensis				1	2													3
A. nanshanensis					3			71										74
A. tungpuensis							8	13	1									22
A. penpuensis								12	34									46
A. formosae											1	5	5	2				13
A. binoculatus												1						1
A. sexpectatus												6						6
A. swanus													2		5			7
Number of species (N)	2	6	7	4	6	2	2	6	4	1	2	4	2	1	1	0	0	19
Number of individuals	10	64	58	72	68	3	9	157	47	13	2	18	7	2	5	0	0	535
Exotic																		
A. corticis				104	9	15	1				5	16	16					166
A. gracilis				9		35	6	2	37	49	27	58	75	2	1	9		310
M. californica				38		4			1	11		3	19		5	38		119
A. rockefelleri						1	1				2							4
P. excavatus						7				1		1	51	5		10		75
A. morrisi						1				1		3	1		5	4	4	19
A. lautus								7		6	8	1	19	3	4		6	54
P. corethrurus									1	55	11	136	455	2	22	38	4	724
A. aspergillus										4	7	23	15		5		2	56
P. elongata											1	15	30					46
A. hupeiensis													1					1
A. incongruus													2					2
M. schmardae													3					3
M. posthuma													2		7		30	39
A. papulosus															1		9	10
Number of species (E)	0	0	0	3	1	6	3	2	3	7	7	9	13	4	8	5	6	15
Number of individuals	0	0	0	151	9	63	8	9	39	127	61	256	689	12	50	99	55	1628
Total (N+E)																		
Number of species	2	6	7	7	7	8	5	8	7	8	9	13	15	5	9	5	6	34
Number of individuals	10	64	58	223	77	66	17	166	86	140	63	274	696	14	55	99	55	2163
Number of localities	1	1	1	1	1	2	2	1	1	1	2	2	2	2	2	2	3	24
Number of collections	1	4	1	1	3	2	2	1	1	1	3	8	6	2	2	2	3	43

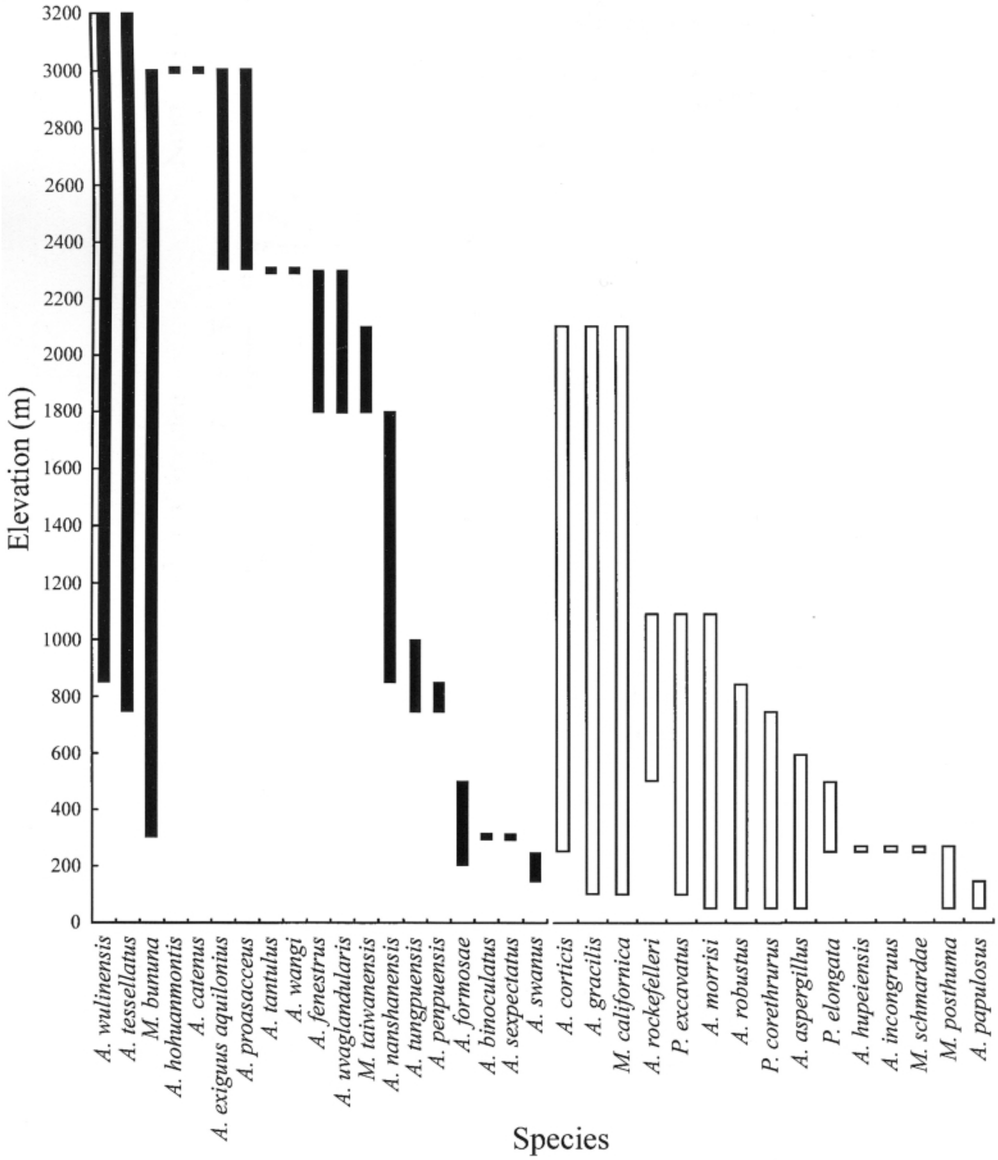
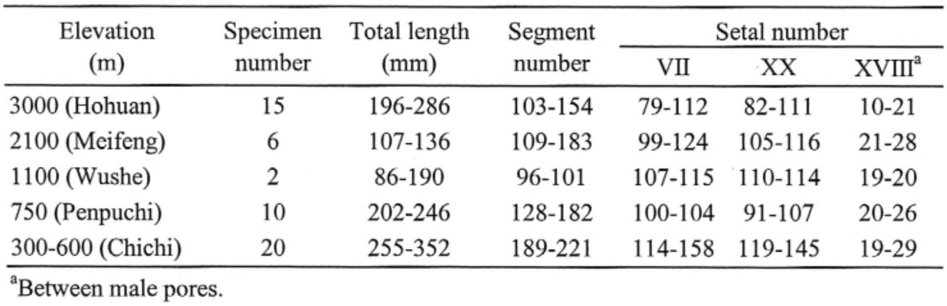


Fig. 2. Altitudinal ranges in distribution of the native species (solid columns) and the exotic species (open columns) of megascolecid earthworms in the centro-western Taiwan.

length and segment number: lowest at 1,100m and highest at 300-600m and 3,000m, while its setal number decreased with the increase in elevation (Table 2).

Group 2: elevations 2,300 to 3,200m in the Central Mountain Range with cold temperate climate. It was consisted of *Amynthas hohuanmontis* (Tsai *et al*. 2002), *Amynthas catenus*, *Amynthas exiguus aquilonius*, and *Amynthas proasacceus* (Tsai *et al*. 2001). The

Table 2. Total length, segment number and setal number of *Metaphire bununa* at different elevations in the western slope of the Central Mountain Range of Taiwan



Elevation (m)	Specimen number	Total length (mm)	Segment number	Setal number		
				VII	XX	XVIII[a]
3000 (Hohuan)	15	196-286	103-154	79-112	82-111	10-21
2100 (Meifeng)	6	107-136	109-183	99-124	105-116	21-28
1100 (Wushe)	2	86-190	96-101	107-115	110-114	19-20
750 (Penpuchi)	10	202-246	128-182	100-104	91-107	20-26
300-600 (Chichi)	20	255-352	189-221	114-158	119-145	19-29

[a] Between male pores.

former two species occurred only at Mt. Hohuan (3,000m), while the latter two species were also found at the Rueyen Nature Reserve (2,300m).

Group 3: elevations 1,800 to 2,300m in the Central Mountain Range with warm temperate climate. It was composed of *Amynthas tantulus, Amynthas wangi, Amynthas fenestrus, Amynthas uvaglandularis* (Shen *et al.* 2003b), and *Metaphire taiwanensis* (Tsai *et al.* 2004). *A. fenestrus* and *A. uvaglandularis* were found from Mt. Beidongyan (1,800m) to Rueyen Nature Reserve (2,300m). They were small- to moderate-sized earthworms, living in grass roots or shallow soil on wet mountain slopes. *M. taiwanensis* was the largest megascolecid earthworm in Taiwan with a size up to 860 mm in length. It was found only in the areas of Mt. Beidongyan and the National Taiwan University's High-Altitude Horticulture Experimental Station in Meifeng (2,100m). *A. tantulus* and *A. wangi* were collected only in the Rueyen Nature Reserve at an elevation of 2,300m, an intermediate in the distribution between Group 2 and Group 3.

Group 4: elevations 750 to 1,800m in the lower mountain region associated with warm temperate climate and the upper hill region associated with subtropical climate. It was consisted of *Amynthas tungpuensis* (Tsai *et al.* 1999), *Amynthas penpuensis* and *Amynthas nanshanensis* (Shen *et al.* 2003b). *A. tungpuensis* was found on the mountain slopes along the Penpu Creek (750m), Nanshan Creek (850m) and Dongyan Creek (1,000m), and *A. penpuensis* along Penpu Creek and Nanshan Creek. *A. nanshanensis* was distributed comparatively widely from Nanshan Creek (850m) to Mt. Beidongyan (1,800m), an intermediate in the distribution between Group 3 and Group 4.

Group 5: elevations 150 to 500m associated with the subtropical climate of lower peripheral hills and the coastal plain. It was consisted of *Amynthas formosae* (Michaelsen), *Amynthas binoculatus* (Tsai *et al.* 1999), *Amynthas sexpectatus* (Tsai *et al.* 1999), and *Amynthas swanus* (Tsai 1964). *A. formosae* was a large earthworm like *M. bununa*, and widely distributed in the peripheral hills from Chiahsien of Kaohsiung (Michaelsen 1922) to Neihu of Taipei (= *Pheretima yushi* Tsai, 1964). *A. binoculatus* was found in Wufeng, Taichung at an elevation of 300m, and *A. sexpectatus* was collected only at Chilungshan near Chungliao, Nantou (Tsai *et al*. 1999). Two specimens of *A. swanus* were collected at the plain area of Chichi and 5 specimens were from the plain near Tsautun, Nantou. Except *A. formosae* that was common, *A. binoculatus, A. sexpectatus* and *A. swanus* were extremely rare in the lower peripheral hills and the coastal plain. They may be considered as the endangered species at the edge of extinction.

Exotic species

The exotic species differed greatly from the native species in their altitudinal distribution. They were common in the coastal plain (subtropical climate) and peripheral hills, and were found in the mountain range only up to an elevation of 2,100m (warm temperate climate). Altitudinal stratification in the distribution was found for the highest altitudinal ranges, but not for the lowest altitudinal ranges (Fig. 2). The above evidences suggest that the exotic species are coastal plain dwelling species and their highest altitudinal ranges in the distribution in Taiwan depend on their species-specific adaptability to altitudinal climates and environmental conditions in the Central Mountain Range and its adjacent peripheral hills.

The highest range of the altitudinal distribution of the exotic species was 2,100m for *Amynthas corticis* (Kinberg), *Amynthas gracilis* (Kinberg) and *Metaphire californica* (Kinberg). They were followed by *Amynthas rockefelleri* (Chen), *Perionyx excavatus* Perrier and *Amynthas morrisi* (Beddard) at 1,100m, *Amynthas robustus* (Perrier) at 850m, *Pontoscolex corethrurus* (Müller) at 750m, *A. aspergillus* at 600m, and *Polypheretima elongata* (Perrier) at 500m. *Amynthas hupeiensis* (Michaelsen), *Amynthas incongruus* (Chen), *Metaphire schmardae* (Horst), *Metaphire posthuma* (Vaillant), and *Amynthas papulosus* (Rosa) occurred only in the coastal plain at 250m or lower.

A. corticis, A. gracilis and *M. californica* were the most common farmland earthworms in the coastal plain, peripheral hills and the Central Mountain Range. *A. corticis* has been found at 2,134m at Mt. Everest (Stephenson 1925) and 3,659m in China (Gates 1972). It was common in the central China (= *Pheretima heterochaeta* (Michaelsen)) (Chen 1933) and in Japan as north as to Hokkaido (Easton 1981). *A. corticis* has been considered as a temperate species of Chinese origin (Tsai *et al*. 2000a). *A. gracilis* was found at 1,829m in the eastern Himalayas, and has been considered to evolve in the temperate zone (Gates 1972). The above three common exotic species share a fairly similar habitat requirement and adaptability to wide ranges of climatic conditions in the coastal plain, peripheral hill and mountain regions.

A. rockefelleri was found from Meichi and Wushe (950 to 1,100m) in the Central Mountain Range and the peripheral hills (500m) near Kuohsing. It has been reported from the plains of Hsinchu (Kobayashi 1938a, 1938b) and Taipei (Tsai 1964). Apparently, it is more or less a coastal plain dweller in the northern Taiwan but a hill and mountain dweller in the central Taiwan. In contrast to *A. rockefelleri, A. papulosus* was found from coastal plain near the Tatu Estuary to the plain near Tsautun, Nantou at an elevation of 150m (Table 1), but it was found in the mountain near Chiahsien of Kaohsiung at an elevation of 400m (Michaelsen 1922). *A.*

papulosus is a hill-dwelling species in the southern Taiwan but a plain dweller in the central Taiwan. *A. rockefelleri* is a warm temperate species perhaps introduced from the central China (Shen *et al*. 2003a), while *A. papulosus* is a tropical species from Southeast Asia (Rosa 1896; Gates 1939).

P. excavatus was found from the plain area at an elevation of 100m to the hill and mountain regions at an elevation of 1,100m (Table 1). In Southeast Asia it is widely distributed from tropical lowlands to the Himalayas at elevations up to 2,744m (Gates 1972). *A. morrisi* was found from the coastal plain near the Tatu Estuary to an elevation of 1,100m in the central Taiwan. It has been found at elevations up to 2,439m in Sichuan, China and at the sea level near Bombay, India to 1,982m in the Himalayas (Gates 1972).

P. elongata was found at 250 to 500m in the peripheral hill region of the central Taiwan. It was found at elevations of 1,650 to 2,750m at Mt. Kinabalu in the tropical Borneo (Sims and Easton 1972), from the sea level to 1,067m in Burma (Gates 1972), and on lowlands of the Riukiu islands (Ohfuchi 1956). Apparently, *P. elongata* is a tropical species originated from Southeast Asia (Gates 1972), and its altitudinal range decreases with the increase in latitude.

The remaining 7 species of the exotic species were commonly found in the coastal plain and the foot of its peripheral hills at elevations of 250m or lower. Like *A. corticis, A. gracilis* and *M. californica,* they are well known exotic (= peregrine) species associated with environments disturbed by human activities, such as banana plantations, betel nut plantations, fruit orchards, bamboo plantations, and city parks (Tsai *et al*. 2000a).

Number of species

Native species were extremely rare in the coastal plain; only 2 species were found at 150 to 250m in elevations (Table 1). In the peripheral hills and the Central Mountain Range, the number of native species increased with elevation, and showed a significantly, positively linearly regressive relationship (Fig. 3A). The maximum number of 7 species was found at 2,300m. Apparently, there was high endemicity of megascolecid earthworms in the Central Mountain Range at elevations of 1,800 to 3,000m.

In contrast to the native species, exotic species were fairly common in the coastal plain; a total of 9 species were collected at elevations of 200m and lower (Table 1). The maximum number of 13 species was found at 250m at the foot of the peripheral hills. With the increase in elevation in the hill and mountain regions, the number decreased to only 3 species at 2,100m. No exotic species were found at elevations at and above 2,300m. In contrast to the positively regressive relationship between the number of native species and elevation (Fig. 3A), the number of exotic species showed a significantly but negatively regressive relationship with elevation (Fig. 3B).

For the total species (native + exotic), the number showed a slightly but insignificantly negative regressive relationship to elevations (Fig. 3C). This suggested that there was a fairly constant number of 8.6 species in average of the earthworms at each elevation in the coastal plain, peripheral hills and Central Mountain Range in the central Taiwan.

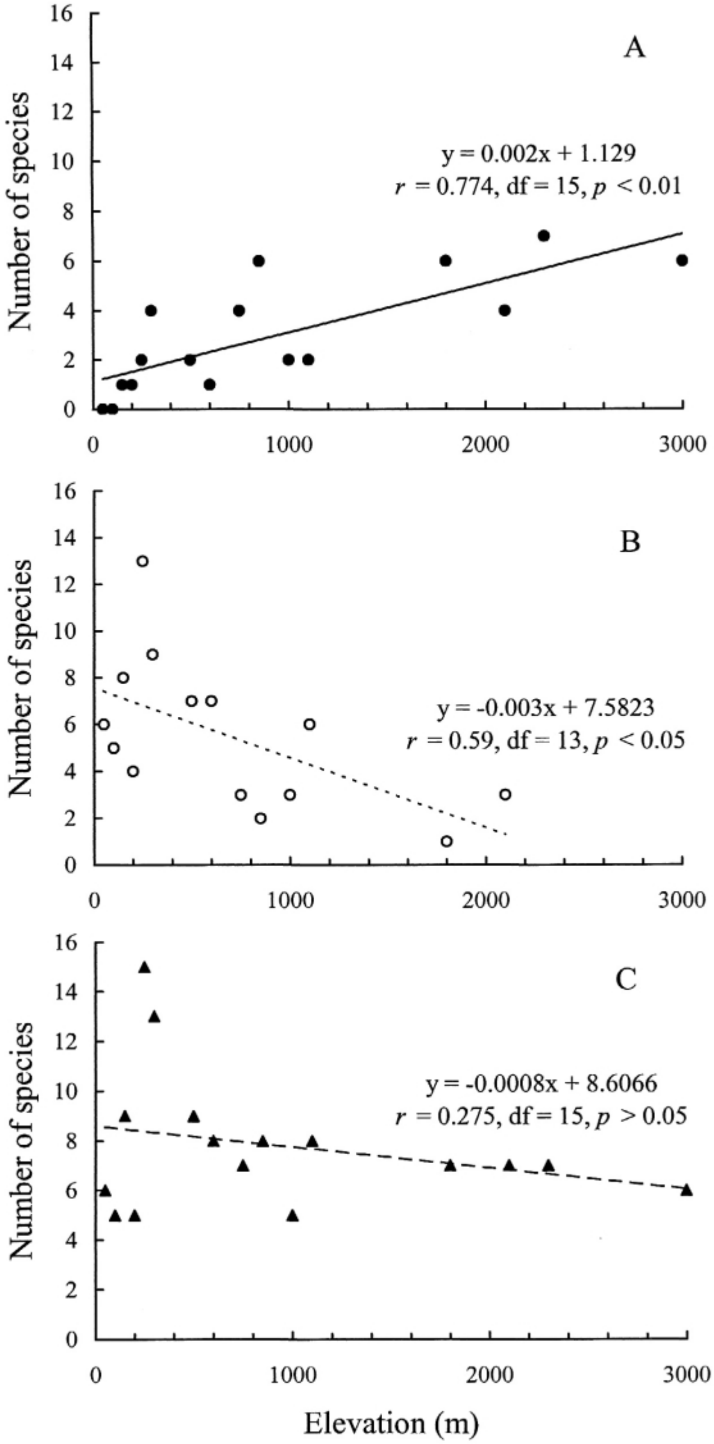
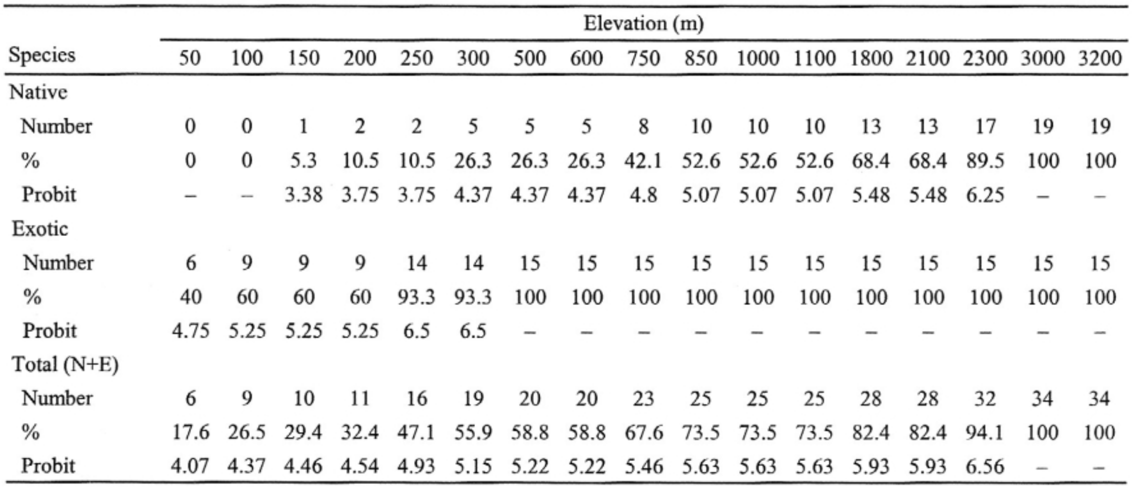


Fig. 3. Relationships between the numbers of species and elevations for the native species (A), the exotic species (B), and the total species (native + exotic)(C) of megascolecid earthworms in the centro-western Taiwan.

Table 3. Probits converted from percentages of cumulative numbers of native species, exotic species and total species (native + exotic) of megascolecid earthworms at 17 elevations in the centro-western Taiwan



Species	Elevation (m)																
	50	100	150	200	250	300	500	600	750	850	1000	1100	1800	2100	2300	3000	3200
Native																	
Number	0	0	1	2	2	5	5	5	8	10	10	10	13	13	17	19	19
%	0	0	5.3	10.5	10.5	26.3	26.3	26.3	42.1	52.6	52.6	52.6	68.4	68.4	89.5	100	100
Probit	–	–	3.38	3.75	3.75	4.37	4.37	4.37	4.8	5.07	5.07	5.07	5.48	5.48	6.25	–	–
Exotic																	
Number	6	9	9	9	14	14	15	15	15	15	15	15	15	15	15	15	15
%	40	60	60	60	93.3	93.3	100	100	100	100	100	100	100	100	100	100	100
Probit	4.75	5.25	5.25	5.25	6.5	6.5	–	–	–	–	–	–	–	–	–	–	–
Total (N+E)																	
Number	6	9	10	11	16	19	20	20	23	25	25	25	28	28	32	34	34
%	17.6	26.5	29.4	32.4	47.1	55.9	58.8	58.8	67.6	73.5	73.5	73.5	82.4	82.4	94.1	100	100
Probit	4.07	4.37	4.46	4.54	4.93	5.15	5.22	5.22	5.46	5.63	5.63	5.63	5.93	5.93	6.56	–	–

Cumulative number of species

Probits of the percent cumulative numbers of native species, exotic species and total species are shown in Table 3. For each of the three groups, the probit showed a positively, linearly regressive relationship to elevation (Fig. 4). When the probit-elevation regressive equations were compared between the native species and the exotic species, the exotic species had the constant of 4.3345 and the slope of 0.0071, that were, respectively, significantly higher than 3.7582 (*t*-value = 6.547, $p < 0.01$) and 0.001 (*t*-value = 3.938, $p < 0.01$) of the equation of the native species. These differences between the two equations suggested that the exotic species were highly dominant in the coastal plain and had more rapid increment in the number of species with the elevation in the coastal plain and the lower peripheral hills, while the native species were rare in the coastal plain and occurred in the entire hill and mountain regions with much slower increment rate in the number of species.

The slope of the probit-elevation regressive equation of total species was 0.0008, that was significantly lower than 0.0071 of the exotic species (*t*-value = 4.280, $p < 0.01$), but not significantly different from 0.001 of the native species (*t*-value = 0.0005, $p > 0.05$). At the same time the constant of the equation of the total species was 4.5699 that was significantly higher but closer to 4.3345 of the exotic species (*t*-value = 3.884, $p < 0.01$) than 3.7582 of the native species (*t*-value = 5.573, $p < 0.01$) (Fig. 4). In other words the total species that represents earthworm community had the equation with the constant closer to that of exotic species but with the slope similar to that of native species. These facts suggest that the changes in the earthworm community with elevation in terms of the increment in cumulative number of species was strongly affected by exotic species in the coastal plain but by native species in the hill and mountain regions.

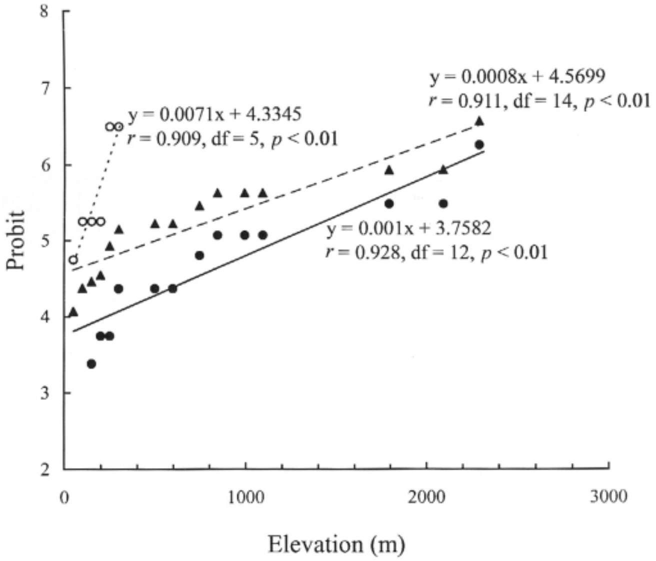


Fig. 4. Probit-elevation relationships for the native species (solid circles and solid line), the exotic species (open circles and dotted line), and the total species (native + exotic, solid triangles and dashed line) of megascolecid earthworms in the centro-western Taiwan.

Table 4. A matrix of Sorensen's similarity coefficients among the megascolecid earthworm communities at 17 elevations in the centro-western Taiwan

Elevation (m)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
3200	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3000	0.250	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2300	0.222	0.462	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2100	0.222	0.154	0.143	1.000	–	–	–	–	–	–	–	–	–	–	–	–	–
1800	0.444	0.154	0.429	0.571	1.000	–	–	–	–	–	–	–	–	–	–	–	–
1100	0.200	0.286	0.133	0.533	0.267	1.000	–	–	–	–	–	–	–	–	–	–	–
1000	0.286	0.182	0.167	0.333	0.333	0.615	1.000	–	–	–	–	–	–	–	–	–	–
850	0.400	0.286	0.133	0.400	0.400	0.375	0.462	1.000	–	–	–	–	–	–	–	–	–
750	0.222	0.308	0.143	0.429	0.143	0.533	0.500	0.667	1.000	–	–	–	–	–	–	–	–
600	0.000	0.143	0.000	0.400	0.000	0.625	0.154	0.375	0.533	1.000	–	–	–	–	–	–	–
500	0.000	0.133	0.000	0.375	0.125	0.471	0.429	0.353	0.375	0.588	1.000	–	–	–	–	–	–
300	0.000	0.105	0.000	0.400	0.100	0.571	0.222	0.286	0.400	0.762	0.727	1.000	–	–	–	–	–
250	0.000	0.000	0.000	0.273	0.091	0.435	0.200	0.174	0.273	0.609	0.583	0.714	1.000	–	–	–	–
200	0.000	0.000	0.000	0.167	0.000	0.308	0.200	0.308	0.333	0.615	0.571	0.556	0.500	1.000	–	–	–
150	0.000	0.000	0.000	0.250	0.000	0.353	0.143	0.235	0.375	0.706	0.444	0.545	0.667	0.429	1.000	–	–
100	0.000	0.000	0.000	0.333	0.000	0.615	0.200	0.154	0.500	0.769	0.286	0.556	0.500	0.600	0.571	1.000	–
50	0.000	0.000	0.000	0.000	0.000	0.143	0.000	0.143	0.154	0.571	0.400	0.421	0.476	0.364	0.800	0.364	1.000

Community structure

Sorensen's similarity coefficients expressing the levels of similarity in the community structure of the earthworms in terms of species composition among 17 elevations are shown in Table 4. The community structure at an elevation tended to show certain similarity with those of its neighboring or nearby elevations, but complete difference (coefficient = 0) from those at elevations of farther distances. For examples, the earthworm community at 3,200m in elevation had some similarity to those at 3,000 to 750m, but completely different from those at 600m and lower, while the community at 50m had some similarity to those at 100 to 1,100m, but completely different from those at 1,800m and higher. At 1,100m the community showed some similarity with those at all elevations above and below. There was a certain trend that the similarity in the earthworm community decreased with the increase in elevation.

A dendrogram expressing the result of the cluster analysis based on Sorensen's similarity coefficients showed that the earthworm communities in the centro-western Taiwan were able to divide into two groups according to their altitudinal distributions (Fig. 5). They were the earthworm communities dominated by native species at high elevations of 750 to 3,200m in the Central Mountain Range, and the communities dominated by exotic species at low elevations of 50 to 1,100m in the coastal plain and peripheral hills.

Discussion

The species of native earthworms were found only in Taiwan and thus, they were certainly speciated within the island. They were found in the Central Mountain Range and its peripheral hills, and rarely found in the coastal plain. Their distributions showed altitudinal stratification; each species had its own specific highest range and lowest range of elevation (Fig.

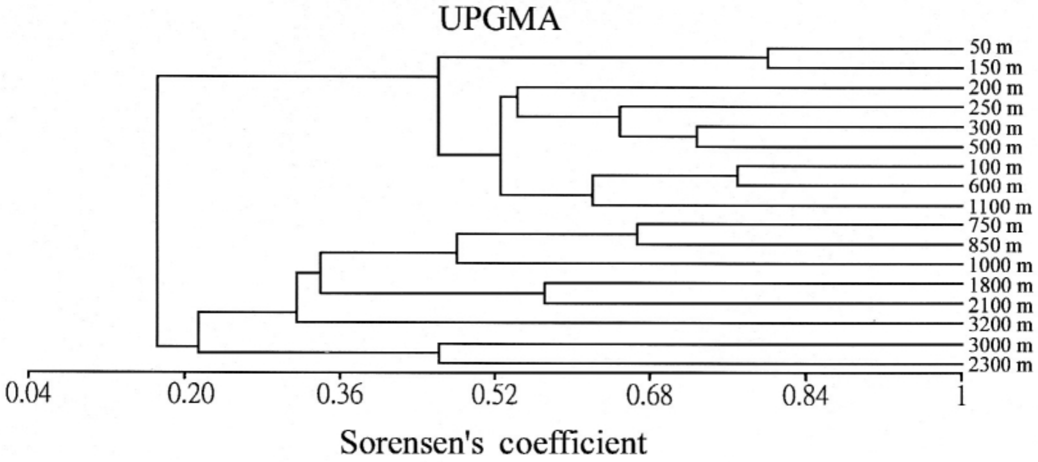


Fig. 5. A dendrogram based on the Sorensen's similarity coefficients among the earthworm communities at 17 elevations in the centro-western Taiwan.

2). Apparently, climatic and environmental conditions associated with elevations define the distribution ranges of the native species, and are one of the important factors for their autochthonous speciation.

The distribution pattern of the exotic species differed greatly from that of the native species (Fig. 2). They are anthropochorous, and likely originated primarily from the southern China and Southeast Asia (Tsai *et al*. 2000a). Apparently, most of them were accidentally introduced to Taiwan with soils and roots of plants brought from abroad. It is reasonable to speculate that they first populated in disturbed lands (farmlands) associated with the human settlements in the coastal plain, and then gradually spread into the peripheral hill and mountain regions along with expansion of human activities, particularly agriculture and horticulture. The highest elevations for their dispersion reached to the elevation of 2,100m, and differed among the species, depending on their adaptability to mountain environments, such as climatic, soil and biotic conditions.

The presence of a positive trend for the native species, a negative trend for the exotic species, but the neutral trend for the total species in the number-elevation relationship equations (Fig. 3) suggested that there was a shift from native species to exotic species in the earthworm communities with the decrease in elevation. The shift was higher at lower elevations than higher elevations. In other words the introduction of exotic species to Taiwan caused the replacement of native species by exotic species rather than the addition of exotic species to the native species for Taiwan's earthworm fauna.

According to the probit-elevation relationship equations (Fig. 4), the cumulative number of the exotic species was estimated to reach to 100% (probit = 10) at an elevation of 798m. In other words, all species of the exotic earthworms were found in the coastal plain and peripheral hills, and thus, those found in the Central Mountain Range were merely an expansion of their distribution (Fig. 2). For the native species the cumulative number to reach to 100% was estimated at an elevation of 6,242m. As the highest peak in the Central Mountain Range is Mt. Yushan of 3,952m, it is predicted that megascolecid earthworms may occur in the entire Central Mountain Range in Taiwan.

Native species have lived in natural environments for their evolutional history. Each of the species has developed its own particular ranges of habitat and environment requirements that were expressed as their altitudinal stratification in distribution in this study. It is reasonable to speculate that the entire island of Taiwan was once covered with tropical forests prior to the massive immigration of Chinese a few centuries ago, and thus, the native earthworms are woodland earthworms. When the woodlands were converted to farmlands, the natural habitat was destroyed, resulting in the extinction of the native earthworms, while the farmlands became favorable places for propagation of exotic species, which are the so-called farmland earthworms. Therefore, the species shift from native species to exotic species found in this study is attributable primarily to the replacement of natural woodland habitat to farmland habitat. Furthermore, intensive use of insecticides and herbicides is another factor contributing to the present scarcity of earthworms in many parts of the island, particularly in the coastal plain.

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Large Insect Diet of the Brown Hawk Owl *Ninox scutulata* in the Central Taiwan

台灣中部褐鷹鴞（*Ninox scutulata*）捕食大型昆蟲類食餌之研究

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Abstract

A total of 2,269 remains of large insects discarded aside by the brown hawk owl *Ninox scutulata* in its noctural feeding were collected at intervals of two weeks under the road lamps in three areas of the peripheral hills of the Central Mountain Range at elevations of 400-700m, November 1999 to December 2001. The results showed that in terms of number of the remains for the study period, insects of the order Coleoptera and Lepidoptera were the most dominant with 844 (37.2%) and 751 (33.1%), respectively. The second dominant group was Homoptera and Orthoptera with 249 (11.0%) and 188 (8.3%). In terms of biomass Coleoptera was the most dominant with a total net weight of 481.1g (37.5%), while Lepidoptera, Orthoptera and Homoptera had 262.9g (20.5%), 253.8g (19.8%), and 204.2g (15.9%). Phasmida, Odonata, Megaloptera, Neuroptera, Lepidoptera, and Homoptera had high utilization rates with 98.4%, 97.6%, 97.3%, 96.0%, 93.4%, and 91.4%. The above six orders of insects were highly utilized by the owl at levels higher than 90.0% of their body weight. The group with lower rates was made up of Coleoptera and Orthoptera at 73.0% and 70.6%.

摘要

研究期間共蒐集2,269個褐鷹鴞捕食大型昆蟲後的食物殘餘，三樣區中以鞘翅目及鱗翅目昆蟲被捕食的數量最多，分別有844 (37.2%)與751 (33.1%)個食物殘餘。其次爲同翅目與直翅目昆蟲，分別有249 (11.0%)與188 (8.3%)個食物殘餘。褐鷹鴞捕食的大型昆蟲生物量以鞘翅目昆蟲最多，達481.1g (37.5%)。鱗翅目、直翅目與同翅目昆蟲居次，所提供之生物量分別是262.9g (20.5%)、253.8g (19.8%) 與204.2g (15.9%)。所有褐鷹鴞捕食的大型昆蟲之中，以竹節蟲目、蜻蛉目、廣翅

目、脈翅目、鱗翅目與同翅目的被利用率最高，利用率分別爲98.4%、97.6%、 97.3%、 96.0%、93.4% 與 91.4% ，這六目昆蟲被利用率均超過90%，可說是被褐鷹鴞利用最澈底的一群。鞘翅目與直翅目昆蟲的被利用率較低，分別只有73.0% 與 70.6%。

Key words : brown hawk owl, *Ninox scutulata*, food remains, large insect, diet

關鍵詞：褐鷹鴞、*Ninox scutulata*、食物殘餘、大型昆蟲、食性

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Introduction

The brown hawk owl (*Ninox scutulata*) is widely distributed in East Asia from the southern Siberia to the Java and Borneo islands of Indonesia. It was also recorded from the northern Australia (König *et al*. 1999; del Hoyo *et al*. 1999). It is composed of 11 geographical subspecies, of which *Ninox scutulata japonica* occurs in Taiwan (König *et al*. 1999; del Hoyo *et al*. 1999). Voous (1988) suggests that *N. s. japonica* is a common resident of Taiwan, but Yao (1995) indicates that it is an uncommon migratory bird wintering in Taiwan, while *N. s. tabago* is a rare resident on the Layun Island. According to our field observation and the bird-watch records of local bird associations of Taiwan, it seems that there are a rare resident population and an uncommon migratory (visitor) population of *N. s. japonica* in Taiwan. For the latter it is still unclear whether it has the wintering and summering populations. The resident population inhabits mainly in peripheral hills of the Central Mountain Range, while the migratory population is found in windbreak areas of the coastal plain from April to October, and each visitor usually stays for a few days.

It has been known that the brown hawk owl feds on large insects, such as beetles, grasshoppers, and cicada, and also, occasionally on small animals, such as mice, bats, birds, lizards, snakes, frogs, and crabs (McCann 1933; Ishizawa 1934; Kawaguchi 1937; Ikeda and Ishizawa 1949; Abe *et al*. 1979; Tomita 1990). The brown hawk owl prefers hunting near road lamps, since a substantial number of insects are attracted under light, their power box and power wire are convenient sites for the owl to perch with a good view, and the owl has an enough space for hunting (Abe *et al*. 1979; Oba 1996). When the owl catches a large insect, its tears it up and discards aside its hard parts, such as wings, wing sheaths, legs, and head, and eats the remaining soft part of the prey. The insect parts left under the road lamps provide evidence that the owl feeds on large insects (Taniguchi 1983; Tomita 1990).

Little is known about biology and the natural history of the brown hawk owl. Furthermore, it has been categorized as the second-class preserve species defined as a valuable and scarce bird in Taiwan (Yao 1995). This study was intended to determine the kinds, biomass, utilization rates, and seasonal changes of large insects consumed by the brown hawk owl.

Materials and Methods

Three areas in the peripheral hills of the Central Mountain Range in the central Taiwan were studied: Dar-Ken (12048E; 267415N), Lain-Hwa-Chi (12055E; 264825N), and Wu-Fang (12047E; 266150N) at elevations of 400m, 750m, and 450m, respectively. The areas were covered with second growth forests mixing with some natural and man-made forests. Brown hawk owls in the areas apparently belonged to the resident population, and of ten perched nearby by road lamps to prey on insects and other animals attracted by the light. The observation could be conducted all the year round.

In each of the three study areas, a digital camera was used to monitor and to choose proper road lamps for the study, and we located three road lamps at each study areas for following research. The food remains of two pairs of the owls were collected, respectively, in Dar-Ken and Lain-Hwa-Chi from November 1999 to October 2000, and of one pair in Wu-Fang from January 2001 to December 2001. The collection was conducted once every two weeks at the end of the owls' daily nocturnal feeding activity, about an hour before sunrise (Voous 1988). In the reconnaissance phase of this study, the tape recorded by the digital camera revealed that some of food remains were left by small diurnal birds that were also attracted by the light, so that, we eliminated food remains before owl's activity period to assure that the collected food remains for data analysis were left only by the owls. The food remains collected were dried at 50℃ in an oven, and sorted according to their attributes, such as head, chest, paired legs, wings and wing sheaths. According to the method of reverse, the attributes were used to re-establish individual insects, identified to species, and weighed to estimate the biomass by family and order.

In order to estimate biomass and utilization rate of different kinds of insects consumed by the brown hawk owl, insects aggregated under the road lamps were also collected by the light-sucking trap. They were classified to family, dried, weighed, and combined by order. The reverse biomass (B) and utilization rate (U) for each order was estimated according to the following formula:

$$B = N \times W$$

$$U = (B - b) \times 100 / B$$

where N is the number of large insect remains of an order of insects; W is a mid point of average complete individual weight of insect in the order; and b is weight of remains of each order.

The seasonal percent compositions of large insects consumed by the owl were compared among the insect orders: March to May for spring, June to August for summer, September to November for fall, and December to January for winter.

Results

Large insects

A total of 2,269 large insect were collected in the three areas during the study period, consisting of 192 species, 44 families, and 10 orders. Lepidoptera was the most dominant and had 91 species and 18 families, in which 39 species belonged to Sphingidae and Noctuidae. Coleoptera was the second dominant group with 9 families and 51 species, in which 34 species were Scarabaeidae and Cerambycidae. The third largest group was Odonata and Orthoptera, that had 4 families, 17 and 13 species, respectively. The other orders were rare, each 1 to 3 families and 1 to 6 species.

The largest number of insects collected was Coleoptera and Lepidoptera, that had 844 (37.2%) and 751 (33.1%), respectively. The second large group was Homoptera and Orthoptera, with 249 (11.0%) and 188 (8.3%). The third large group was Odonata and Mantodea with 82 (3.6%) and 74 (3.3%). Blattaria, Megaloptera, Neuroptera and Phasmida had a few numbers: 45, 29, 5, and 2, respectively (about 2.0% to 0.1%)(Table 1). Scarabeidae of Coleoptera was the family that had the largest number, 533 individuals, consumed by the owl during study period (23.5%). It was followed by Cicadiae, Noctuidae, and Sphingidae with 11.0%, 9.8% and 9.0%, respectively.

Total biomass

Total biomass of large insects consumed by the brown hawk owl was 1,281.7g at the three study area during the study period. Coleoptera had the largest biomass with 481.1g (37.5%). It was followed by Lepidoptera, Orthoptera and Homoptera with 262.9g (20.5%), 253.8g (19.8%), and 204.2g (15.9%), respectively. Mantodea, Odonata and Blattaria had low biomass of 31.8g (2.5%), 27.9g (2.2%), and 12.6g (1.0%), while Megaloptera had 6.4g

Table 1. Number, biomass, and utilization rate preyed by the brown hawk owl (percent in parentheses)

Insect category	Number of large insect remains	Average biomass	Reverse biomass (B)	Weight of total remains (b)	Weight of utilization	Utilization rate (%)
Coleoptera	844 (37.2)	0.57±0.21	481.08 (37.5)	129.89	351.19	73.0
Lepidoptera	751 (33.1)	0.35±0.13	262.85 (20.5)	17.35	245.50	93.4
Homoptera	249 (11.0)	0.82±0.25	204.18 (15.9)	17.55	186.63	91.4
Orthoptera	188 (8.3)	1.35±0.84	253.80 (19.8)	74.62	179.18	70.6
Odonata	82 (3.6)	0.34±0.20	27.88 (2.2)	0.67	27.21	97.6
Mantodea	74 (3.3)	0.43±0.19	31.82 (2.5)	5.09	26.73	84.0
Blattaria	45 (2.0)	0.28±0.10	12.60 (1.0)	1.76	10.84	86.0
Megaloptera	29 (1.3)	0.22±0.09	6.38 (0.5)	0.17	6.21	97.3
Neuroptera	5 (0.2)	0.10±0.05	0.50 (<0.1)	0.02	0.48	96.0
Phasmida	2 (0.1)	0.31±0.12	0.62 (<0.1)	0.01	0.61	98.4
Total	2269		1281.71	237.13	1044.58	81.5

(0.5%). Phasmida and Neuroptera had the lowest rates of 0.6g and 0.5g (less than 0.1% in total), respectively (Table 1).

Utilization rate

Utilization of large insects by the brown hawk owl was highest for Phasmida at 98.4%. It was followed by Odonata, Megaloptera, Neuroptera, Lepidoptera, and Homoptera with the rates of 97.6%, 97.3%, 96.0%, 93.4%, and 91.4%, respectively. These six orders of insects were considered as the highest group with the utilization rate higher than 90.0%. The second high group was Mantodea and Blattaria with the rates at 84.0% and 86.0%, respectively. Coleoptera and Orthoptera had the lowest rates of 73.0% and 70.6%. The total remains of large insects was 237.1g, and total biomass utilized was 1,044.6g, so that average utilization of large insects by the brown hawk owl was estimated to be 81.5% (Table 1).

Seasonal changes

The major insect groups consumed by the brown hawk owl were Lepidoptera, Coleoptera, Homoptera, and Orthoptera. Lepidoptera and Coleoptera were consumed all the year round and composed of 64.0% to 78.1% of the total biomass of insects consumed by the owl. The highest rate was found in fall and the lowest rate in winter. The second dominant group was Homoptera and Orthoptera, that made up a total of 23.8%; the former had 20% and the latter had 3.8%. In winter Orthoptera constituted 28.3% and Homoptera 0%, while in spring and fall, they was fairly similar at the rates of 8.9% and 6.3%, respectively, in spring, and 5.5% and 6.1% in fall. For the orders other than those mentioned above, their percentage composition in the biomass of insects consumed by the owl was low, about 10.4% for all the year round.

The biomass of large insects consumed by the brown hawk owl was estimated as 186.2g in spring, 511.2g in summer, 367.5g in fall and 216.8g in winter. In spring, summer, and fall, 91.8% to 93.7% were made up of Lepidoptera, Coleoptera, Homoptera and Orthoptera, while in winter, Lepidoptera, Coleoptera and Orthoptera consitituted 96.3% of biomass, of which 54.9% was from Orthoptera. The orders other than those mentioned above had low biomass composition (Figs. 1 and 2).

Discussion and Conclusions

The brown hawk owl in the peripheral hills in the central Taiwan preyed on large insects, primarily Lepidoptera, Coleoptera, Homoptera, and Orthoptera. These four orders of insects constituted 89.6% in number and 93.7% in biomass of insects consumed by the owl. Lepidoptera and Coleoptera occurred all the year round and thus, they showed no seasonal change. Also, they were highly abundant, so that they provided the basic food source for the owl. In contrast, Homoptera and Orthoptera occurred seasonally (summer and winter), and their occurrence depended on weather conditions. For instance, cicadas were abundant in summer, and thus the brown hawk owl consumed more cicadas than any other kinds of insects in this period. In winter most insects were scarce with the exception of Orthoptera. The grasshopper such as *Chondracris rosea* became mature in this season and provided large biomass for the owl's consumption. The brown hawk owl also preyed

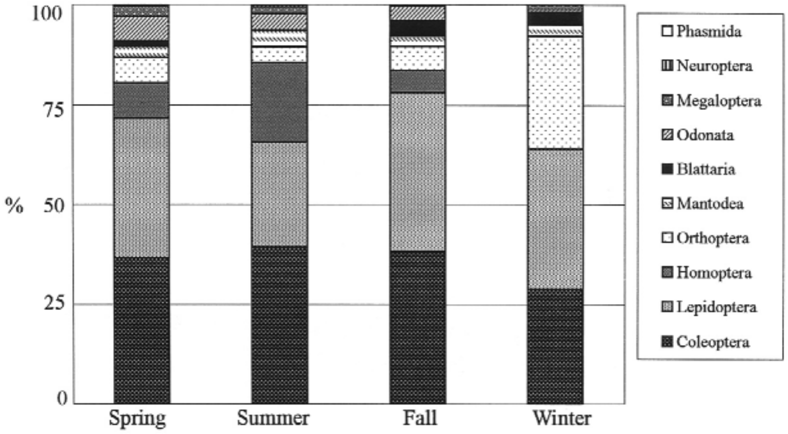

Fig. 1. Seasonal changes in the numbers of large insects consumed by the brown hawk owl.

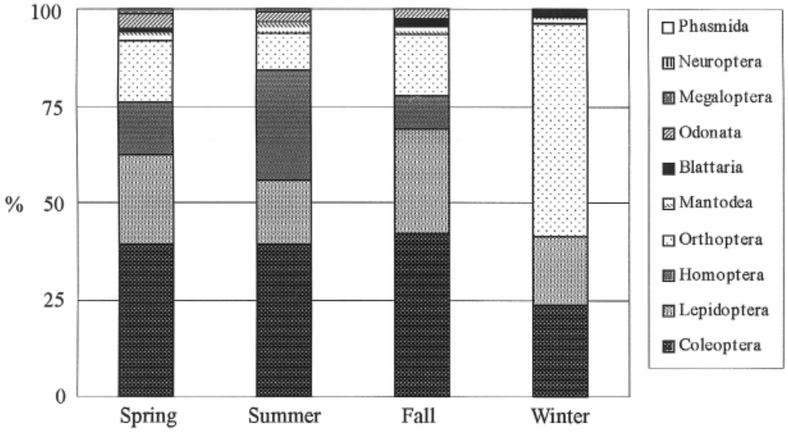

Fig. 2. Seasonal changes in the biomass of large insects consumed by the brown hawk owl.

on insects of Mantodea and Odonata, that supplied large biomass as food for the owl in spring and fall, but as compared to the above four groups, they were still the minor food sources for the owl.

The brown hawk owl consumed the soft parts of the insects, and discarded aside the hard parts, but with exception of some insects, of that entire bodies were swallowed by the owl. Although there were some remains, they were so little and so light that they were blown away, and could not recovered under the road lamps. Such case might occur for some insects of Lepidoptera, Neuroptera, Odonata, Blattaria, and Phasmida. Therefore, the biomass estimated by remains recovered might result in underestimation. In addition some insects have been known to be consumed by the owl, such as Pyralidae, Lymantriidae, Hesperiidae, Asilidae, and Tabanidae (Taniguchi 1983). However, they were not found in this study.

The consumption of Lepidoptera, Homoptera, Odonata, Phasmida, Megaloptera, and Neuroptera was higher than 91.4%. Only their wings were torn apart and discarded aside by the owl, that occupied a very small part of the insects' body weight, so that their utilization rates estimated were very high. In contrast to the above insects, for Mantodea and Blattaria the owl did not utilize their wings and legs, and sometimes also discarded their whole thorax, so that their utilization rate was calculated to be low at 84% and 86%, respectively . For all insects that the owl consumed, the utilization rate was the lowest for Coleoptera and Orthoptera, since the owl only consumed their abdomens, and discarded head, thorax, wing-sheath, wings, and legs of beetles and wings, jumping legs of grasshoppers. Their abdomens occupied a very small part of total body weight, so that the utilization rates of these insects were low. However, because their biomass was large, they offered more energy than other insects, and constituted a high composition of the owls' diet.

The results obtained in this study were fairly similar to those obtained in Japan with a single peak of the insect consumption in the summer. However, there was longer food consumption period from June to August in Taiwan, but only a month from late June to mid July in Japan (Taniguchi 1983). The seasonal changes in the insect consumption by the owl is caused by increasing food demand of fledges (Taniguchi 1983). Why did it last for just a month in Japan but several months in Taiwan? Possibly, since the owl is a summering bird in Japan, and stays in Japan only for five to seven months. It starts breeding in April, incubates eggs in May, and fledges hatch in early June. The fledging period lasts for a month, and then they migrate to the south in late August or early September. Therefore, young fledges must grow and learn hunting techniques as quickly as possible, before migrate south. It has a short fledging period as compared to that of Taiwan. In Taiwan the owl is a resident in the hill and mountain areas and fledges have no pressure to migrate, and their food resources are plentiful all the year round, so that the parents may have more time to raise the youngs, leading to a longer fledging period.

Ishizawa (1934) used the stomach content analysis to prove that the brown hawk owl eats small insects, such as nocturnal moths, cranefly, and stonefly. Food remains of these small insects are minimal or even absent, because most of them in the stomachs were intact. Many medium or small birds such as the large-billed crow (*Corvus macrorhynchos*), Formosan blue magpie (*Urocissa carerulea*), red-headed babbler (*Stachyris ruficeps*), grey-eyed nun babbler (*Alcippe morrisonia*), lesser scimitar babbler (*Pomatorhinus ruficollis*), Chinese bulbul (*Pycnonotus sinensis*), black-naped blue flycatcher (*Hypothymis azurea*), pied wagtail (*Motacilla alba*), black drongo (*Dicrurus macrocercus*), and Chinese white-eye (*Zosterops japonica*) also hunt small insects and leave remains like owls, though they hunt in different time of a day. Therefore, it is essential to use the stomach content analysis to obtain more precise data on small insects preyed by the brown hawk owl. Raptor diet was usually studied by the method of fecal analysis, that examines prey's remains in its feces. However, this method allows only for identification of large items of preys, often resulting in overestimation of large preys and underestimation of smaller ones (Redpath *et al*. 2001). This problem still remains for the food remain analysis, because small insects are often entirely consumed, such as case found for the brown hawk owl in this study.

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Seasonal Changes in Reproductive Hormones of Female Formosan Black Bears (*Ursus thibetanus formosanus*) in Captivity

圈養雌性台灣黑熊繁殖內分泌季節性變化之初探

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Abstract

Seasonal changes in serum reproductive hormones of three female Formosan black bears (*Ursus thibetanus formosanus*) in captivity were studied monthly from April 2001 to May 2003 at the Low Altitude Experimental Station of Endemic Species Research Institute. The LH concentration was significantly higher (ANOVA, $p < 0.05$) in spring than those in other three seasons, but no significant seasonal differences ($p > 0.05$) were found for the concentrations of FSH, prolactin, estradiol and progesterone. Also, there were significantly positive correlations in concentrations between FSH and progesterone, between LH and estradiol, between LH and progesterone, and between estradiol and progesterone. The female Formosan black bears seem to be capable for breeding all the year round, but spring is the major mating season. The results of this study provide important reproductive information useful for the preservation of the Formosan black bear.

摘要

本實驗爲從2001年4月起至2003年5月，針對季節性影響圈養在特有生物研究保育中心低海拔試驗站之三隻台灣黑熊繁殖內分泌所做的研究。結果發現四季血清中激濾泡素 (FSH)、泌乳素 (prolactin)、雌二醇 (estradiol)及助孕素 (progesterone) 濃度無季節性的差異 ($p > 0.05$)，但血清中排

卵素 (LH) 濃度在春季是最高且具有顯著差異 ($p < 0.05$)。此外，在雌性台灣黑熊的血清激濾泡素和助孕素、排卵素和雌二醇、排卵素和助孕素及雌二醇和助孕素間存有正相關關係。由結果可發現台灣黑熊爲全年均可繁殖，而春季爲主要的發情交配季節。本研究成果提供關於台灣黑熊重要的繁殖資訊，希望能作爲台灣黑熊保育的參考。

Key words : Formosan black bear, reproductive hormone, seasonality

關鍵詞：台灣黑熊、繁殖內分泌、季節性

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Introduction

The family Ursidae consists of two subfamilies: Ailurinae and Ursinae. The subfamily Ursinae has 4 genera and 7 species, of which brown bear (*Ursus arctos*), polar bear (*Ursus maritimus*), American black bear (*Ursus americanus*), and Asiatic black bear (*Ursus thibetanus*) belong to the genus *Ursus*. The Formosan black bear (*Ursus thibetanus formosanus*) is a subspecies of the Asiatic black bear (Wilson and Reeder 1993), and is the largest carnivore endemic to Taiwan. It is an omnivorous animal that lives widely in low to high elevations of 2,000m to 2,500m, and active in both day and night (Hwang *et al*. 2000). In recent years it is at the verge of nearly extinction, because of habitat destruction and human interference. According to the wildlife conservation law of Taiwan, in 1989 the Council of Agriculture of the Executive Yuan listed the Formosan black bear as an endangered species, that is prohibited for hunting, possessing, or killing. Because its population was extremely low and rarely seen, very few studies had been conducted, and seasonal changes in its reproductive hormones was lacking.

American black bear has hibernation and delayed implantation. It is a seasonal breeder, and its estrus is in May to July (Domico and Newman 1988; Foresman and Daniel 1983; Renfree and Calaby 1981; Tsubota *et al*. 1987; Tsubota *et al*. 1997). For Asiatic black bear it is suspected to be in heat and to mate in March to December (Domico and Newman 1988). In Taiwan the studies on the Formosan black bear were limited to a few observations on its distribution and activity in natural environments. In terms of breeding, no hibernation has been observed so far for this subspecies (Kenneth and Wendell 1989; Hwang *et al*. 2000), and it processes a peculiar reproductive status characterized by induced ovulation, delayed implantation for 5-6 months, and pseudo-pregnancy (Chang *et al*. 1994; Yang *et al*. 2003).

Concentrations of serum reproductive hormones, such as the follicle stimulating hormone (FSH), luteinizing hormone (LH), and prolactin, have been reported in female bears. FSH and LH surge coincidently with an acute increase at the peaks of urinary oestrone conjugate, behavioral oestrus, and urinary estradiol in female giant panda (*Ailuropoda melanoleuca*) (Monfort *et al*. 1989; Shi *et al*. 1991). The LH concentration is not significantly different between March and December in captive female American black bears housed at Bear Country of USA, but higher in November to December in free-ranging female bears (Tsubota *et al*. 1998). The LH concentration is low in January to April and higher in December in Japanese black bears (*Ursus thibetanus japonicus*) kept at the Akita, Japan (Sato *et al*. 2000). For female American black bears the estradiol concentration is highest in March prior to mating and in June during the mating season, and then, followed by a significant decrease in November and December (Tsubota *et al*. 1998). In captive female Japanese black bears, serum estradiol concentration is low in November and December, high in January, and varies in April to October (Sato *et al*. 2000). The prolactin concentration pattern is similar to those of estradiol, with elevated levels during the mating season in June, decreasing slightly in July, and low level in November to December in female American black bears (Tsubota *et al*. 1998). In free-ranging female American black bears, progesterone concentration increases gradually after mating to the peak in November to December (Tsubota *et al*. 1998). In captive female Japanese black bears, which include animals of both known and unknown reproductive status, serum progesterone concentration is low from April to July, higher after August and much higher in November and December, and then returns to low in March (Sato *et al*. 2000). Progesterone concentration is higher in March to June than non-mating season for non-pregnant giant pandas, and its estradiol concentration is higher during the spring mating season (Lindburg *et al*. 2001; Etsuo *et al*. 2003).

This study was intended to obtain basic information on reproductive hormones, FSH, LH, and prolactin, in captive female Formosan black bears, pertaining to their seasonal changes, relationships, and reproductive traits.

Materials and Methods

Animals studied

Three female Formosan black bears were used in this study. Each of them was paired with a male bear in the breeding season each year. Bear No.1 was from private donation and 9 years old, Bear No.2 was confiscated from a hunter and 8 years old, and Bear No.3 was obtained from a private amusement park and its age was unknown. No.1 was kept with her male partner in the enclosure from April to September 2001, but without expressing mating behavior. No.2 was mated on March 22-23, 2001, May 5-9, 2002, and April 15-18, 2003. It produced a cub in each of early November of 2001 and 2002. However, the cub produced in 2002 died two days after the birth. No.3 had an infection with serious inflammation on the back in 2001, and had no mating.

The bears studied were housed in covered outdoor enclosures with ambient light and temperature at the Low Altitude Experimental Station of Endemic Species Research Institute (120°56'52.47"E and 24°16'24.39"N) near Taichung. The breeding climate and latitude were fairly similar to those in their nature habitat. The proper diet was provided according to Yang *et al*. (2001). The times of estrus and mating were observed and recorded.

Sample collections and analyses

Blood samples were collected from the 3 female bears monthly from April 2001 to May 2003, except at the time of pregnancy, bearing, nursing, and healthy problems. All bears were anaesthetized with Zoletil 50 (10 mg/kg; Virbac Co. Ltd., Taipei, Taiwan) and then, blood samples were collected via jugular vein with the intravenous method. Blood samples were kept at room temperatures for 2 to 3 min for cooling, and then centrifuged at 3,000 rpm for 10 min to collect serum. The serum samples were frozen in ice cube and sent to Apex' Medical Laboratory in Taichung for analysis. FSH, LH, prolactin, estradiol, and progesterone concentrations were measured by an automatic immunoassay instruments (Axsym™ system; Abbott Laboratories, Taipei, Taiwan) with the enzyme-linked immunosorbent assay (ELISA). Sample, anti-hormone coated microparticles, hormone assay buffer, and line diluent (0.1M phosphate buffer) were combined in a well of the reaction vessel (RV). Alkaline phosphatase conjugate was added to the second well of the RV. After being incubated, the reaction mixture was washed to remove unbound materials. The substrate (4-methylumbelliferyl phosphate) was added, and the fluorescent product formed was measured by the ELISA optical assemble. The assays specifically quantified hormones with minimal cross-reactivity (0.24%) with other endogenous steroids. The assay sensitivity was 0.37 mIU/ml, 0.5 mIU/ml, 28 pg/ml, 0.6 ng/ml, and 30 pg/ml for the FSH, LH, estradiol, prolactin, and progesterone, respectively.

Statistical analyses

Data collected were grouped into 4 seasons: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February). Individual reproductive hormone concentrations for each season were calculated as mean±S.E., and compared among the four seasons by ANOVA and Duncan's New Multiple Rang tests. Relationships among the hormones in the serum were also analyzed by the correlation analysis.

Results

FSH concentrations were higher in winter (1.72±0.37 mIU/ml), and then, followed by autumn (1.62±0.3 mIU/ml), spring (1.45 mIU/ml), and summer (1.2±0.13 mIU/ml) (Table 1), while the LH concentrations were significantly higher ($p < 0.05$) in spring (4.3±3.3 mIU/ml) than those in summer (1.0 mIU/ml), autumn (1.01±0.01 mIU/ml) and winter (1.02±0.01 mIU/ml). The estradiol concentrations were higher in spring (1.76±0.76 ng/ml) than those in autumn (1.4±0.4 ng/ml), summer (1.36±0.23 ng/ml), and winter (1.15±0.11 ng/ml), but the differences were not statistically significant (p>0.05). The prolactin concentrations were higher in summer (2.85± 0.86 ng/ml) and then, followed by autumn (2.60 ± 0.85 ng/ml), winter (1.85±0.94 ng/ml), and spring (1.49 ng/ml). The progesterone concentrations were higher in spring (2.24± 0.83 ng/ml) and winter (2.24±1.32 ng/ml), highest in autumn (3.83±1.02 ng/ml), and lowest in summer (0.56±0.14 ng/ml). Significant positive correlations were found for the concentrations between FSH and progesterone (r = 0.76, p<0.05) and between LH and estradiol (r = 0.89, p<0.05), but not between LH and progesterone (r = 0.01, p>0.05) and between estradiol and progesterone (r = 0.06, p>0.05).

Discussion and Conclusions

This report first describes the seasonal changes in concentrations of serum FSH, LH, prolactin, progesterone and estradiol and their relationships for the Formosan black bear. FSH concentrations were highest in winter, lowest in summer, while estradiol concentrations were higher in spring (Table 1), suggesting that FSH raises follicular action and started the estrus cycle in spring. These phenomena are fairly similar to those of other species of Ursidae; the animals begin their reproductive cycle after hibernation (Howell-Skalla *et al*. 2000; Lundberg *et al*. 1976; Mead 1989; Tsubota *et al*. 1998).

Basal LH concentration in the American black bear does not have seasonal difference (Horan *et al*. 1993; Howell-Skalla *et al*. 2000), but the concentration was highest statistically in spring for the female Formosan black bear (Table 1). This indicates that ovulation of the Formosan black bear occurs in spring. This result was supported by Tsubota *et al*. (1998) who reported that the rise in serum LH concentration during the peri-implantation period suggests that LH may be luteotropic and concomitant with the higher serum progesterone concentration. The above demonstrates that there is a positive relationship between LH and progesterone concentrations.

Estradiol concentration of the Formosan black bears was high in all the year round without seasonal changes (Table 1), suggesting that it has a yearlong polyestrous cycle with a long reproductive capacity. Its reproductive season in Taiwan is similar to that of male American black bears in Virginia, while those in North Carolina in the lower latitude zone were earlier and longer (Garshelis and Hellgren 1994). The above may indicate that the Formosan black bears mate in spring, as that of the giant panda (Lindburg *et al*. 2001). The mating season of captive polar bears in Canadian Central Arctic and Manitoba is in spring and of the North American bears is in summer (Howell-Skalla *et al*. 2002; Renfree and Calaby 1981). Therefore, the breeding season is species specific in the family Ursidae.

For American black bears housed in the United States Department of Agriculture, their serum prolactin concentration is lowest in

Table 1. Seasonal changes in concentrations (mean±S.E., n=20) of reproductive hormones for the female Formosan black bears in captivity

Items	Spring	Summer	Autumn	Winter
FSH, mIU/ml	1.45±0.001	1.20 ± 0.13	1.62 ± 0.30	1.72 ± 0.37
LH, mIU/ml	4.30 ± 3.3^{a}	1.00 ± 0.001^{b}	1.01 ± 0.01^{b}	1.02 ± 0.01^{b}
Estradiol, ng/ml	1.76 ± 0.76	1.36 ± 0.23	1.40 ± 0.40	1.15 ± 0.11
Prolactin, ng/ml	1.49±0.001	2.85 ± 0.86	2.60 ± 0.85	1.85 ± 0.94
Progesterone, ng/ml	2.24 ± 0.83	0.56 ± 0.14	3.83 ± 1.02	2.24 ± 1.32

[a, b] The concentrations were significantly different (ANOVA, p<0.05) between the numbers with superscript a and superscript b.

autumn and winter when daylight is short, and then increases steadily during spring (Tsubota *et al*. 1995). This supports this study that the serum prolactin concentration in the Formosan black bears rose with increasing day length (spring to summer) and decreased with decreasing day length (autumn to winter)(Table 1). Furthermore, prolactin concentration plays an important role in seasonal testicular function and cyclical progesterone changes (Curlewis 1992). In contrast, increasing serum prolactin inhibits luteinic function and decreases serum prolactin after activating corpus luteum (Tsubota *et al*. 1998). The results of this study showed that the highest prolactin concentration was in summer at the time when the progesterone concentration was the lowest. The prolactin concentrations decreased in autumn and winter at the time of short daytime, allowing a subsequent blastocyst implantation (Tsubota *et al*. 1998).

Progesterone concentration was higher in spring (Table 1) for functional corpus luteum formation, and increased in autumn to winter, as the case found for the Hokkaido brown bear, Japanese black bear, American black bear in Rhode Island (Seager and Demorest 1986; Tsubota *et al*. 1987; Foresman and Daniel 1983), and giant panda without mating (Monfort *et al*. 1989; Shi *et al*. 1991). For Japanese black bears, progesterone concentration increases in November to February without mating (Sato *et al*. 2001), similar to that of Formosan black bears in this study. Progesterone concentration was low in summer after oestrus, similar to that reported for captive female American black bears (Tsubota *et al*. 1998). The surge of progesterone concentration in autumn is possible with embryo implantation (Foresman and Daniel 1983; Tsubota *et al*. 1987; Palmer *et al*. 1988; Hellgren *et al*. 1990). Therefore, the progesterone concentration in Formosan black bears changed as those of other animals with delayed implantation, increased slightly during the delayed implantation, and were higher during the embryo implantation, such as the cases found for American black bears and polar bears captured in Manitoba and Beaufort Sea, and Hokkaido brown bears (Foresman and Daniel 1983; Palmer *et al*. 1988; Tsubota *et al*. 1987).

In conclusions, there are seasonal changes in reproductive hormones in female Formosan black bears, and the changes in the LH concentrations are statistically significant. These findings provided the important information for the reproductive physiology and the management of the Formosan black bear.

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A Production of Four Successive Clutches of Eggs by a Female Grass Lizard (*Takydromus stejnegeri* van Denburgh) in Captivity

圈養中之蓬萊草蜥 （*Takydromus stejnegeri*） 連續四窩蛋的生產現象

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Abstract

A female grass lizard *Takydromus stejnegeri* van Denburgh was captured after mating in the field on 24 April 2003. It was immediately brought back to the laboratory and kept under observation. It produced four clutches of eggs from10 May to 22 June. The average time interval of the successive clutches was 14.75 days, and the average clutch size was 2.75 eggs. The production of the successive clutches without mating in captivity may be due to the sperm storage in the female reproductive tract. The fertilization ratio and hatching ratio were 100% for the first three clutches, but only 33.3% and none, respectively, for the fourth clutch. The clutch order was significantly positively correlated with egg width and also with egg weight. *T. stejnegeri* was an intermediate egg retainer, whose gestation (egg retention) period was at an average of 25% of the total embryonic development period.

摘　要

2003年4月24日於野外捕捉到一隻剛交配過的雌性蓬萊草蜥，隨即帶回實驗室飼養及觀察。被隔離的雌蜥於同年5月10日至6月22日間連續產下四窩蛋，此四窩蛋產出的間隔平均爲14.75天，每窩平均2.75個蛋。此圈養後無再次交配的連續性生產現象，表示該雌蜥可能具有精子儲存的能力。前三窩的受精率及孵化率均爲100%，而第四窩其值則分別降爲33%及0%。此四窩蛋的產出順序與蛋的寬度及重量呈現顯著性地正相關。蓬萊草蜥所產下的蛋屬於居中型的胚胎發育，

其胚胎保存在雌蜥體中的平均時間約占總成長時間的25%。

Key words: *Takydromus stejnegeri*, clutch, sperm storage

關鍵詞：蓬萊草蜥、窩數、精子儲存

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Introduction

Lizards of the genus *Takydromus* (Lacertidae) are small reptiles commonly found in grasslands and bush areas. Females produce two to several clutches of eggs during a single breeding season (Loveridge 1945; Fukada 1965; Huang 1998). For reptiles when gonadal activities of both sexes are not synchronous, sperm storage is evolved (Pough *et al.* 1998), so that the sperms remain viable and fertile in female reproductive tracts for many months (Frisch 1963; Cuellar 1996a). However, there was no information whether the *Takydromus* lizards that produce successive clutches of eggs have evolved with sperm storage capacity.

As embryonic development of a reptilian egg is initiated immediately after fertilization, and the egg must be retained within female reproductive tract for a certain period for shell deposition, a considerable embryonic development has been preceded at the time of its deposition. For most lizards, approximately 12 to 73% of the embryonic development have been completed within the female bodies when eggs are laid (Shine 1983; DeMarco 1993).

Takydromus stejnegeri van Denburgh, 1912 is a small, slender, long-tailed lizard endemic to Taiwan. It is commonly found in grass and bush environments. It is an oviparous animal and its eggs are found from March to August (Lin and Cheng 1990). Clutch sizes have been reported to be 2 to 4 eggs (Cheng 1987; Lin and Cheng 1990). This study used a mated female of *T. stejnegeri* in captivity to determine the clutch frequency, clutch interval, clutch size, egg size, egg weight, fertilization ratio, hatching ratio, and percentage of embryonic development at the time of egg deposition.

Materials and Methods

On April 24 2003, an adult female *T. stejnegeri* was captured in the field near Shitan, Maioli, Taiwan (Lat. 24°33'N and Long. 120°55'E, elevation 350m). Its back and abdomen had fresh marks of being bitten with bloodstains, and thus, it was confirmed to have just mated. It was immediately brought back to the laboratory of Endemic Species Research Institute in Chichi, Nantou (elevation 240m), 80 km from the captured site. The lizard was under observation from 24 April to 11 July 2003, the period corresponding fairly well with the breeding season of *T. stejnegeri* (Lin and Cheng 1990). It was kept in a 1x0.5x0.5m (length x width x height) terrarium, in that bricks, debris, woods, grasses and a water dish were placed to mimic its natural environments. Two carton shelters and a 20x10 cm container filled with moist soil and fallen leaves were placed in the terrarium as its resting and egg deposition sites. Once a day the lizard was fed with mealworms (larvae of *Tenebrio molitor*) until it stopped feeding, and the number of mealworms consumed was recorded.

The lizard was daily palpated to determine the approximate time of its ovulation. When eggs were observed in the terrarium, they were removed and incubated in a 20x10 cm container at ambient temperature. The time of ovulation, the gestation period, and the time of egg deposition of the lizard were recorded. The size and frequency of the clutches, color, size and weight of the eggs, the fertilization ratio, the incubation period, and the hatching ratio were also recorded. Each of the eggs was weighed to the nearest 0.001g, and its length and width were measured to the nearest 0.05 mm. Total embryonic development period was the number of days from the time of ovulation to the time of hatching. The gestation (egg retention) period was the number of days for eggs to have retained in uterus before deposition. Egg incubation period refered to the number of days from the time of deposition to the time of hatching. The percentage of embryonic development period at the time of deposition was measured by the proportion of the gestation period divided by total embryonic development period. Spearman's rank correlation analysis (Krebs 1999) was used to determine the relationships between clutch order and each of egg length, width and weight, and between the egg length and the egg width.

Results

The female lizard used in this study was 73 mm SVL. Its weight varied from 4.9g to 7.2g during the study period. It laid eggs of a clutch usually within a day in a den site with moist soil and fallen leaves. After deposition, it left the site and moved to foraging areas. It consumed 0 to 4 mealworms a day with an average of about two mealworms. About three days before each of the egg depositions, its appetite decreased and ate only one mealworm, but after the deposition its appetite immediately increased and ate 4 mealworms in the first feeding. Apparently, its appetite fluctuated greatly during the breeding season in correspondence with gestation and egg deposition. It shed its skin once in the middle of each of the gestation periods.

The color of fertilized eggs changed from white to gray in correspondence with the embryonic development. An infertile egg usually remained creamy white for weeks after deposition, and then gradually became yellowish white later instead of gray. The fertilized eggs were 10.49±0.37 mm (ranged between 10.00 mm to 11.30 mm) in length, 6.46±0.30 mm (6.00 mm to 7.10 mm) in width, and 0.236±0.019g (0.207g to 0.302g) in weight. The fertilization ratios and hatching ratios were 100% for the first three clutches. For the fourth clutch, only one egg of the three eggs was fertilized but its embryo died on 8 July 2003. The clutch order was significantly correlated with egg width ($r = 0.851$, df = 7, $p < 0.01$) and egg weight ($r = 0.714$, df = 7, $p < 0.05$). The egg length was not significantly correlated with egg width ($r = 0.055$, df = 7, $p > 0.05$) and clutch order ($r = -0.214$, df = 7, $p > 0.05$),

After each of the egg depositions, we could palpate the ova in the lizard at the second or third days, and thus, the second day after the egg deposition was assumed to be the time of beginning ovulation and fertilization. The gestation period was 16, 11, 12, and 20 days, respectively, for the four successive clutches. The egg incubation period was 38 days for the first clutch, 41 and 42 days for the two eggs of the second clutch, and 40 days for the third clutch. The percentages of embryonic development period at the time of deposition were 25%±4% with a range between 20% and 30%.

Discussion

In this study the *T. stejnegeri* female was in captivity alone after mating in the field, and successively laid four clutches of eggs from 24 April to 22 June. The discovery of the second, third and fourth clutches of this female lizard without mating under captivity could only be explained by the fact that female *T. stejnegeri* stored sperms that were viable and fertile for at least 41 days.

Sperm storage has been suggested to make females less dependent on multiple mating and to ensure multiple fertilizations of subsequent clutches in the absence of males (Conner and Crews 1980; Gist and Jones 1987). The capacity for prolonged sperm storage in female reproductive tract is highly developed in reptiles (Birkhead and Moller 1998), and has been reported in several lizard species, such as *Tarentola m. mauretanica* (Picariello *et al*. 1989), *Calotes versicolor* (Ruth Shantha Kumari *et al*. 1990), *Heteronotia bionei* (Whittier *et al*. 1994), and *Psammophilus dorsalis* (Srinivas *et al*. 1995).

On the other hands, seminal receptacles may have evolved in the female reproductive tracts to prevent sperms from being forced out of the oviduct by the first egg of a clutch (Birkhead and Moller 1998). Although seminal receptacles increase the survival of spermatozoa, the decrease in fertility in subsequent clutches is also an inevitable result; only 53% of the eggs in second clutch were fertile, and 0% in third clutch in *Uta stansburiana* (Cuellar 1966b), and 84% to 62% for three subsequent clutches in *Chamaeleo hoehnelii* (Lin 1982). In this study the female *T. stejnegeri* in captivity had 100% fertility for the first three clutches but only 33.3% for the fourth (last) clutch. The decrease in sperm fertility during the storage period in the female tracts (seminal receptacles) might be due to increase in sperm senility, mortality and/or passive loss.

According to the time of mating and the duration of gonadal activity, reptiles exhibit three general types of reproductive cycles: associate cycle, dissociated cycle, and continuous cycle (Pough *et al*. 1998). For the associated cycle, gonadal activities of both sexes increase almost synchronously before mating, and then they regress out with their breeding seasons. There is no sperm storage by female. For the dissociated cycle, the breeding season is short, and the time for mating does not correspond well with the time of the female gonadal activity. The species with the dissociate cycle would evolve the storage of sperms (Pough *et al*. 1998). For the continuous cycle, gonadal activity of both sexes is sustained throughout most of a year in tropical habitats, so that no sperm storage is evolved.

In this study, the reproductive cycle of *T. stejnegeri* is likely to be the dissociated cycle. The breeding season of female *T. stejnegeri* is from March to August (Lin and Cheng 1990). The spermatogenesis occurs all the year around except for September and October (Cheng and Lin 1977; Lin and Cheng 1990). Although gonadal activities of both sexes regress synchronously, the spermatogenesis increases in November earlier than the timing of female gonadal activity. The earlier spermatogenesis might evolve to benefit male-male competition for mating, and each female perhaps mates only once.

In nature lizards are subjected to conflicting energy demands for reproduction, escaping predators, and foraging activities. In this study the female *T. stejnegeri* in captivity produced four clutches and 2.75 eggs per clutch, perhaps resulted from the absence of predator and the substantial availability of food. In lacertid lizards the first clutch size and egg size are determined mainly by energy reserves stored, but those in its successive clutches were determined by their subsequent energy intakes (Brana *et al*. 1991). In this study the female *T. stejnegeri* in captivity was provided with sufficient food supplies, so that it produced larger and heavier eggs for the latter clutches.

DeMarco (1993) proposed that sceloporine lizards may be divided into brief egg retainer, intermediate egg retainer, or extreme egg retainer, according to gestation (egg retention) period relative to the total embryonic development period at the averages of 12.7%, 29.8%, and 73.7%, respectively. In this study the gestation period relative to the total embryonic development period was averaged at 25%. Accordingly, *T. stejnegeri* may be considered as an intermediate egg retainer.

The results obtained in this study were based on the observation of a single female *T. stejnegeri* in captivity, and further studies are required particularly in the field to shed light on the reproductive pattern of this species.

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台灣南部地區的鳥種組成與海拔分布

Avian Species Composition and Distribution along Elevation Gradient in the Southern Taiwan

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摘　要

本研究自1997年8月至2000年12月，在台灣南部地區的118個調查區中，共記錄到鳥類16目55科256種。若加上近年的文獻資料，本地區共有16目59科319種鳥類的紀錄，其中包括台灣特有種15種及特有亞種67種，而屬於保育類的鳥類有78種。部分鳥種被記錄的調查區數少，在本研究所記錄的256種鳥類中，有106種被記錄的調查區數少於6個。依照本研究所劃分的7個海拔類別，我們分析其中140種具留鳥遷移屬性的鳥種，發現其物種豐富度隨著海拔梯度變化而呈現峰形分布的改變趨勢，如果同時將其它緯度遷移候鳥納入分析，則會減緩其峰形分布的改變趨勢，但兩者都是以1,500-1,999m海拔類別記錄到最高的鳥種數。各海拔類別間的鳥種組成則以500-999m與1,000-1,499m及1,500-1,999m與2,000-2,500m這兩組海拔類別間具有較高的相似性。台灣南部地區鳥種豐富度與海拔梯度間呈現峰形分布，可能與人為干擾、初級生產力、歷史地質事件及生物性競爭等因素有關，而在探討物種豐富度的分布時必須注意到調查努力量及分析類群本身的差異對結果所可能造成的影響。

Abstract

An inventory survey of avifauna in the southern Taiwan was conducted in August 1997 to December 2000. A total of 256 species were recorded at 118 sites, of which 106 species were found only at less than 6 sites. When the species that had been reported in literature were also taken into account, there were a total of 319 species in 16 orders and 59 families with 15 endemic species, 67 endemic subspecies, and 78 protected species in the southern Taiwan. The species richness was highest at 1,500-1,999m in elevations, while the similarity coefficient were highest between 500-999m and 1,000-1,499m, and also between 1,500-1,999m and 2,000-2,500m. There was a hump-shaped relationship between the species richness and the elevation gradient, possibly due to human disturbance, primary productivity, historical vicariance, and biotic competition. Sampling effort and functional groups varieties, such as foraging guilds or migrant status, should be considered in the examination of avian diversity and distribution.

關鍵詞：物種豐富度、分布、海拔、峰形、努力量

Key words: species richness, distribution, elevation, hump-shaped, effort

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緒　言

生物多樣性是指各類不同生態系及棲地中的物種組成、數量及其變異性，甚至包含它們所可能衍生的各種生態作用(林及趙 1998)。生物資源調查是瞭解生物圈內動、植物組成現況的最佳方法，也是維護生物資源多樣性的基礎工作。在生物多樣性的諸多特性中，物種豐富度(species richness)及特有性(endemism)是兩個普遍受到關注的關鍵特性(Caldecott *et al*. 1996)。其中，物種豐富度更常被用來評估生態保育工作(Magurran 1988)或是作爲生物多樣性熱點(hotspots)的選擇依據(呂 1999; Pressey *et al*. 1993)。物種豐富度的分布也一直是生態學和生物地理學的研究焦點(Spellerberg 1996)，其與海拔梯度(elevation gradient)變化之間的關係，更是近年來許多研究探討的焦點(Rahbek 1995; Blake and Loiselle 2000; Ding 2001)。

由於高海拔區域的面積比率較低且具有較大的地理隔離(isolation)效應，加上植被結構單純(MacArthur 1972)、無脊椎動物量低及生物性競爭(Terborgh 1971; Janes 1994; Blake and Loiselle 2000)等等因素，傳統上認爲物種豐富度會隨著海拔上升而逐漸降低(MacArthur 1972; Stevens 1992)。但近年來的一些研究發現，物種豐富度會隨著海拔上升而呈現峰形(hump-shaped)或先呈水平而後降

低(horizontal, then decreasing)的分布，而不僅是單純的下降改變(Colwell and Hurtt 1994; Rahbek 1995; Lomolino 2001; Brown 2001)。Rahbek(1995)整理90個不同類別生物的研究發現，在所有的結果中峰形分布趨勢占有較高的比例。較常被探討可能導致這種物種豐富度隨海拔梯度而呈現峰形分布的因素有：(1)因逢機性所產生的結果(Colwell and Hurtt 1994)；(2)中海拔區域的降雨量及初級生產力(primary productivity)高(McCoy 1990; Md. Nor 2001)；(3)從中海拔至高海拔是種化(speciation)速度最快的區域(Terborgh 1977; Heaney 2001)。但不同的分析類群，例如不同的生態功能群(guilds)或不同遷移屬性(migrant status)生物類群也可能發現其物種豐富度呈現不同的海拔梯度改變趨勢(Blake and Loiselle 2000)。

台灣是一個多山的島嶼，海拔100m以上的地區約占全島面積的2/3。高聳的中央山脈南北縱貫在台灣的中央，其最高峰的玉山海拔高達3,997m(林及周 1974)。此外，台灣的地勢陡峭，許多地區在短短的距離內便形成極大的海拔落差(陳 1993)。海拔梯度的變化，會直接造成氣溫及降水量等環境因子的改變，進而影響植被及動物的分布(Terborgh 1971; Su 1984)。已有許多報告指出鳥種豐富度會隨著海拔高度上升而變化(Orians 1969; MacArthur 1972)；近年來，也有一些研究探討台灣海拔梯度變異與鳥種豐富度之間的關係(翟 1977；林 1989；丁 1993；顏 1997；聶 1999；Ding 2001)，但這些研究大都是以繁殖留鳥爲主要的探討對象，同時較少考量到調查努力量對結果所可能造成的影響(許 2001)。因此，本研究藉由行政院農業委員會特有生物研究保育中心在台灣南部地區的鳥類相調查資料，在考量鳥類遷移屬性與調查努力量的狀況，來探討該地區的鳥種組成及鳥種豐富度與海拔梯度變化之間的關係。

材料與方法

一、鳥類調查方法

爲瞭解台灣南部地區的鳥種組成及海拔分布，本研究自1997年8月至1998年7月於嘉義、1998年8月至1999年7月於高雄及1999年7月至2000年12月於屏東等縣市進行鳥類相的調查。各縣市鳥類調查區的設計主要是利用橫麥卡脫投影方格系統將調查範圍劃分成數量不等的2x2 km^{2}的面積方格，再以方格來進行調查區的選取。調查區的選取是先將各方格依其絕對地理海拔高度劃分成海拔未達100m、100-999m、1,000-2,000m及超過2,000m等4個子區域，在參考4個海拔子區域的方格數量及棲地型態下來分配選取調查區。每個縣市在權衡人力、物力及時間的情況下，以設立30個調查區，每個調查區每季進行1次調查爲原則，唯鄰近沿海的調查區因有較多遷移性候鳥的棲息而每月進行1次調查。此外，爲獲取各縣市更詳確的鳥類相資料，對部分不易到達或在特定需求下增加的不固定調查區，則分別於調查期間進行1-2次不等的調查。總計本研究自1997年8月至2000年12月共於嘉義、高雄及屏東等縣市行政區域中設置了118個調查區(圖1；附錄I)，其中11個調查區每個月至少調查1次，82個調查區每季至少調查1次，其它25個調查區則於調查期間分別進行1-2次不等的調查。

鳥類的調查是採用與穿越線法相近似的道路沿線調查法(road sampling, Bookhout 1996)，即於調查區選擇一條固定之調查路線，沿著調查路線以每小時約1.5 km的速度緩步前進，每次調查以2小時劃分成4個時段來記錄，總紀錄路線的長度約爲3 km。唯受到調查環境及天候的影響，本研究在石卓、十字路、來吉及南橫145K等4個調查區僅進行1小時約1.5 km路線長度的觀察紀錄，而東石橋及鹽港則是以1小時約1.5 km的路線長度來

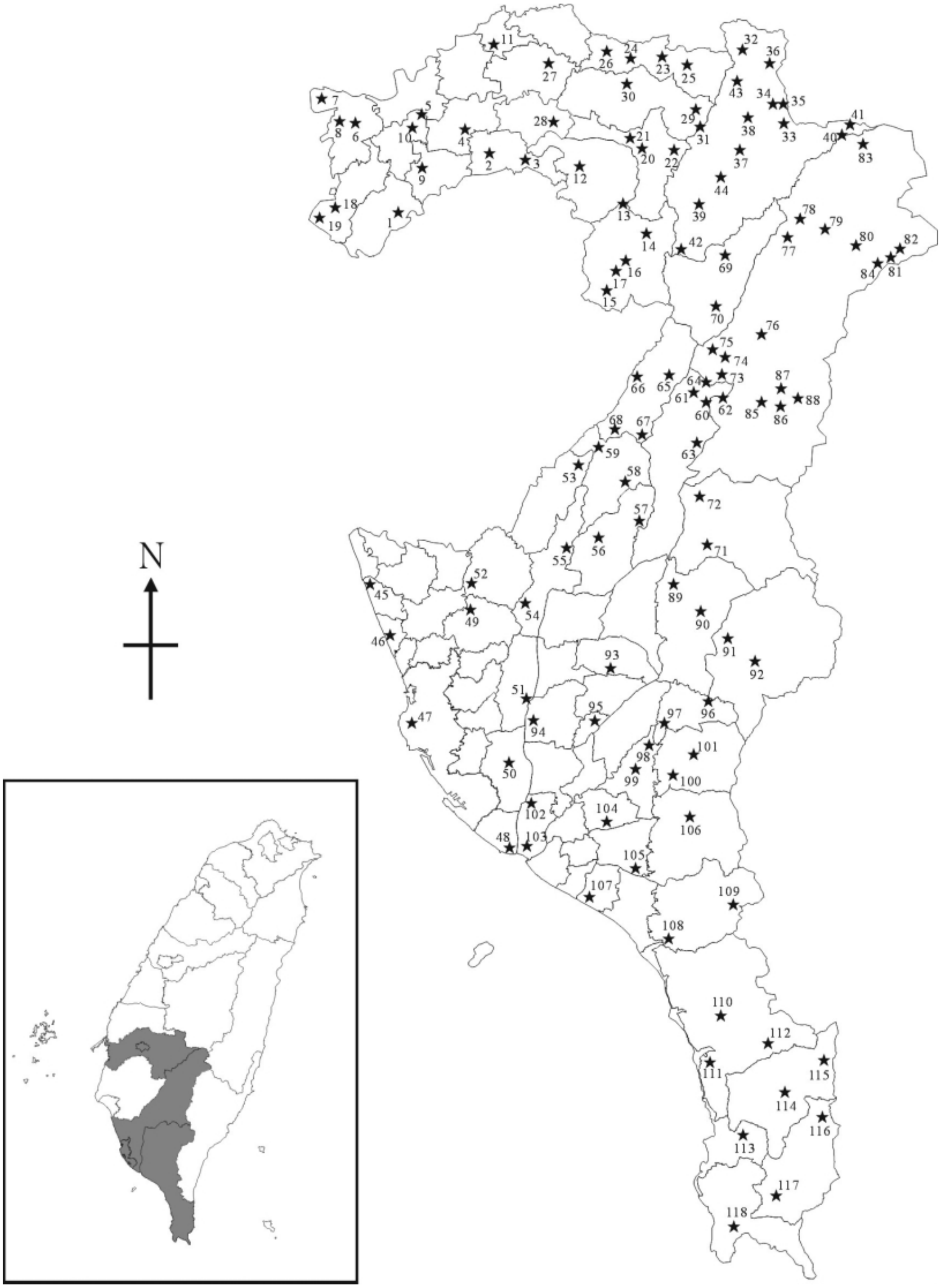

圖1. 本研究之鳥類調查區分布圖。

Fig. 1. Bird survey sites (stars with number) in Chiayi, Kaushong, and Pingtong counties in the southern Taiwan. The numbers 1-118 are the site codes in appendix I.

進行重複調查。調查時於視野開闊或鳥種出現較頻繁的地點做較長時間的停留觀察，以雙筒或單筒望遠鏡沿途記錄調查路線兩側所見、所聽的鳥種、數量、出現地點、時間及行爲等資料。

二、資料分析

本研究分別蒐集近20年來在嘉義縣市境內進行調查的鳥類資源調查報告12篇(陳 1981；林及李 1982；陳 1983；陳 1987；張 1988；沙 1988，1989a，1989b，1990；丁 1993；林 1997；黃 1997)、在高雄縣市境內進行調查的鳥類資源調查報告12篇(林及李 1982；王 1986；陳 1987；何 1988；呂等 1989；黃 1991a；周 1991；張 1993；高及張 1993；徐等 1994；湯 1995；裴及孫 1999)及在屏東縣市境內進行調查的鳥類資源調查報告20篇(王 1985；王等 1989；陳等 1990；黃 1991b；涂 1992；賴 1992；周 1993；楊 1993；蔡 1994；裴等 1995；劉 1996；方 1996a，1996b，1997；裴及孫 1997；方 1998，2000a，2000b；蘇 2000)，以彙整這三個縣市區域內所調查記錄的鳥類相資料。同時依據Howard and Moore (1991)的分類系統及中華民國野鳥學會(1995)的台灣鳥類名錄來界定本研究所彙整鳥類的分類地位。

爲探討不同遷移屬性對鳥種豐富度與海拔分布的影響，本研究參照王等(1991)及中華民國野鳥學會(1995)所定義各鳥種的遷移屬性(附錄II)。在本文中除對所有調查發現的鳥種進行分析之外，同時也就留鳥遷移屬性的鳥種單獨進行分析。另一方面，本研究將118個調查區，除海拔未達100m的沿海濕地與平原農耕地之調查區另外劃分成一個類別外，其它則以500m的海拔變化當作劃分的基準，而將所有的調查區劃分成<100m、100-499m、500-999m、1,000-1,499m、1,500-1,999m、2,000-2,500m及>2,500m等7個絕對地理海拔高度類別(elevation ranges)。但受到高海拔區域的面積比率低且調查區較不易到達的影響，使本研究在高海拔區域所設置的總調查區數及總調查時數比低海拔區域少(表1)。

爲比較各海拔類別間所調查記錄的鳥種組成相似性(similarity)，我們首先將各海拔類

表1. 本研究所劃分七個海拔類別的調查區數、調查時數及所記錄的鳥種數

Table 1. Number of survey sites, survey hours, and species richness of birds at seven elevation ranges in the southern Taiwan

Elevation ranges (m)	Number of survey sites	Survey hours	Total species			Resident species		
			Orders	Families	Species	Orders	Families	Species
0-99	31	367	16	45	176	15	37	74
100-499	36	286	13	42	138	13	39	95
500-999	22	153	10	34	100	9	30	81
1000-1499	10	57	10	33	96	9	29	81
1500-1999	6	41	10	30	93	8	27	82
2000-2500	8	49	8	28	84	7	25	72
>2500	5	17	6	20	48	5	19	46
Total	118	970	16	55	256	15	47	140

別內所有調查區的鳥種資料合併，再利用Jaccard Index (JI, Ludwig and Reynolds 1988)來計算各海拔類別間鳥種組成的相似性係數(similarity coefficient)，其係數值介於0到1之間，計算公式如下：

$$JI = a / (a + b + c)$$

其中，a表同時在兩個海拔類別均有出現紀錄的種類數；b及c則分別表示僅在單一海拔類別中出現的種類數。

此外，爲去除不同海拔類別調查區數及調查時數之努力量不一致的影響，本研究再以總調查時數超過8小時之93個調查區的資料，來計算7個海拔類別單一調查區所能發現的平均鳥種數並分析其海拔的改變趨勢。由於調查物種數與努力量之間會呈現非線性增長的物種累積曲線(species accumulation curve)，而半對數(semilogarithm)則可提供作爲物種累積曲線的預測模式(Dawson 1981)。因此，在計算7個海拔類別單一調查區所能發現的平均鳥種數之前，本研究即先利用半對數來轉換計算14個調查時數超過8小時之調查區(附錄I)在8小時調查努力量之下的鳥種豐富度，以降低不同調查努力量所造成的影響。其計算公式如下：

$$S_n = S_1 + a \log n \text{；} \quad a = (S_t - S_1) / \log t$$

其中S_n表在n個努力量之下所能發現的物種豐富度；S_1表平均單一努力量之下所能發現的物種豐富度；a表S_n隨努力量而改變的增加係數；S_t表在t個努力量之下所能發現的物種豐富度。

結果

自1997年8月至2000年12月，於台灣南部地區所進行的118個調查區中，共記錄到鳥類16目55科256種，加上其它文獻資料則共記錄有16目59科319種(附錄II)。其中，嘉義縣市記錄有15目54科213種，加上文獻資料則爲15目55科245種；高雄縣市記錄有15目51科198種，加上文獻資料則爲16目55科259種；屏東縣市則記錄有16目55科190種，加上文獻資料則爲16目55科248種。在所有記錄的319種鳥類中，台灣15種特有種鳥類均含括其中，而台灣的69種特有亞種鳥類中，僅環頸雉(*Phasianus colchicus*)及草鴞(*Tyto capensis*)未曾有發現的紀錄。列入台灣保育類的鳥種共有78種，其中瀕臨絕種保育類12種；珍貴稀有保育類43種；其他應予保育類23種。比較往年文獻資料與本研究之調查結果發現，以往在嘉義、高雄及屏東等地區曾有紀錄的鳥類中，有63種鳥類未在本調查中發現。但是包括黑鸛(*Ciconia nigna*)、白肩雕(*Aquila heliaca*)、董雞(*Gallicrex cinerea*)、灰腳秧雞(*Rallina eurizonoides*)、紅胸鴴(*Charadrius veredus*)、劍鴴(*Charadrius placidus*)、跳鴴(*Vanellus cinereus*)、小杓鷸(*Numenius minutus*)、灰瓣足鷸(*Phalaropus fulicarius*)、黑嘴鷗(*Larus saundersi*)、灰沙燕(*Riparia riparia*)、黑翅山椒鳥(*Coracina melaschistos*)、灰叢鴝(*Saxicola ferrea*)、褐色柳鶯(*Phylloscopus fuscatus*)、灰椋鳥(*Sturnus cineraceus*)、絲光椋鳥(*Sturnus sericeus*)、臘嘴雀(*Coccothraustes coccothraustes*)、聖䴉(*Threskiornis aethiopicus*)、白腰鵲鴝(*Copsychus malabaricus*)、爪哇雀(*Padda oryzivora*)、紅梅花雀(*Amandava amandava*)、橙頰梅花雀(*Estrilda melpoda*)及黑領椋鳥(*Sturnus nigricollis*)等23種鳥類，則是本研究所新記錄到的鳥種(附錄II)。

本研究在118個調查區的總調查時數爲970小時。各調查區的調查時數分別介於1至24小時不等，其所記錄的鳥種數則介於15到99種之間(附錄I)。所有記錄之256種鳥類在各調查區的發現頻度，以綠繡眼(*Zosterops japonica*)在95個調查區中有紀錄最高，其次是洋燕(*Hirundo tahitica*)在92個調查區中有紀

錄。但有44種的鳥類僅在單一調查區有紀錄，而調查區記錄在6個(約占調查區總數的5%)以下的鳥類有106種，約占所有記錄鳥種的41%(附錄II)。

依照所劃分的7個海拔類別來彙整調查資料發現，合併各海拔類別所有調查區的紀錄鳥種，以<100m海拔類別共記錄有176種爲最多，然後隨著海拔升高，所記錄到的鳥種數逐漸減少，至>2,500m海拔類別僅記錄有48種爲最少(表1)。但如果僅就本研究所發現具備留鳥遷移屬性的140種鳥類(附錄II)來進行計算，則可發現各海拔類別中仍以>2,500m海拔類別僅記錄有46種留鳥爲最少，但以100-499m海拔類別共記錄有95種留鳥爲最多，而500-999m、1,000-1,499m及1,500-1,999m等3個海拔類別則都大約記錄有80種留鳥(表1)。

爲了在相同調查努力量下來進行比較，我們計算各海拔類別單一調查區在8 小時調查努力量下所平均記錄的鳥種數。結果發現不論是以全部鳥種或是僅以留鳥來進行計算，其所記錄到的平均鳥種數均隨著海拔上升而呈峰形分布，而且均以1,500-1,999m海拔類別所記錄的鳥種數爲最高(圖2)。但以全部鳥種來進行計算時，各個海拔類別單一調查區所發現的平均鳥種數大約介於39至47種之間，各海拔類別間的差距較不明顯。其中，<100m海拔類別因記錄到較多鸛形目、雁形目及鴴形目的候鳥，而比100-499m海拔類別具有稍高的鳥種數。

另一方面，我們比較各海拔類別間鳥種組成的相似性係數發現，無論是以全部鳥種或僅以留鳥來進行分析，其相似性均隨著海拔的差距變大而降低，而且兩者均以500-999m與1,000-1,499m及1,500-1,999m與2,000-

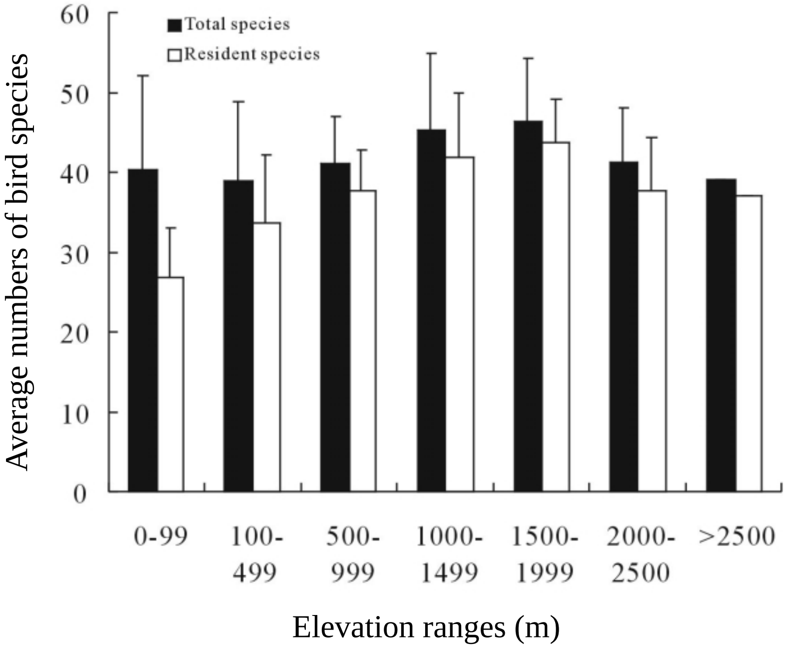

圖2. 本研究七個海拔類別之單一調查區所發現的平均鳥種數。

Fig. 2. Average numbers of bird species at seven elevation ranges in the southern Taiwan.

2,500m這兩組海拔類別間具有較高的相似性(表2)。當海拔類別序列差異超過兩級以上，其相似性係數則皆小於0.5(表2)，亦即海拔高度差別超過1,000m以上，其物種組成的相似度較低。此外，本研究所記錄的256種鳥類中，各鳥種所記錄之最高與最低調查區間的海拔分布幅度(相對地理海拔高度)有146種(57%)小於1,000m。其中所記錄的140種留鳥，則有49種(35%)的海拔分布幅度小於1,000m(表3)。

討 論

台灣南部地區所彙整記錄的319種鳥類中，過去文獻有紀錄而未在本研究中發現的63種鳥類及本研究所新記錄的23種鳥類，大部分都屬於數量較爲稀少或僅分布在特定棲地的鳥種。本研究所記錄的256種鳥類，也有106種的被記錄調查區數少於6個(約占總調查區數的5%)，顯示台灣南部地區的鳥種組成中，數量稀少或棲息在特定環境的鳥種占有相當高的比例。另外，本研究記錄有外來種鳥類19種，其中高雄地區便記錄有16種，這些外來種大部分都棲息在低海拔都會區及農耕地附近，這對台灣低海拔原生鳥種的生態可能造成某種程度的影響(劉 2000)。

本研究顯示台灣南部地區的鳥種豐富度有隨著海拔升高而逐漸減少的現象(表1)。但如果僅以具備留鳥遷移屬性的鳥種來進行計算，則不存在這種海拔梯度與鳥種豐富度之間的反相關係(inverse relationship)，這可能與台灣大部分的緯度遷移候鳥(latitudinal migrants)主要棲息在中、低海拔有關。Blake and Loiselle (2000)在Costa Rica發現大型鳥種、緯度遷移鳥種及海拔遷移(elevation migrants)鳥種隨著海拔梯度變化而呈現不同物種豐富度的改變趨勢。因此，在探討鳥種豐富度與海拔梯度變化之間的關係時，需要注意到鳥類不同遷移屬性或生態功能群對分析結果所可能造成的影響。

另一方面，由於本研究各海拔類別的調查區數及調查時數皆隨著海拔升高而遞減(表1)，這種調查區域及調查努力量的差異，也可能導致海拔梯度與鳥種豐富度之間趨勢探討的偏差(許等 2001；Wiens 1981)。各調查區所能發現鳥種數可能受到該調查區的棲息鳥

表2. 本研究所有記錄鳥種(對角線上方)與具留鳥遷移屬性鳥種(對角線下方)在七個海拔類別間的Jaccard相似性係數

Table 2. Jaccard similarity indices of total species (above diagonal) and resident species (below diagonal) of birds among seven elevation ranges in the southern Taiwan

Elevation ranges (m)	<100	100-499	500-999	1000-1499	1500-1999	2000-2500	>2500
<100		0.47	0.27	0.22	0.14	0.13	0.04
100-499	0.63		0.58	0.50	0.35	0.32	0.13
500-999	0.41	0.69		0.70	0.50	0.47	0.21
1000-1499	0.32	0.60	0.76		0.62	0.58	0.27
1500-1999	0.21	0.42	0.55	0.66		0.69	0.41
2000-2500	0.17	0.37	0.49	0.58	0.77		0.47
>2500	0.06	0.16	0.23	0.31	0.45	0.51	

表3. 本研究所有記錄鳥種及留鳥在各種海拔分布幅度的發現頻度

Table3. Frequence distribution of elevation amplitudes of total species and resident species of birds in southern Taiwan

Elevation amplitudes (m)*	Total species	Resident species
0-200	106	22
201-400	19	10
401-600	4	3
601-800	6	6
801-1000	11	8
1001-1200	9	7
1201-1400	11	9
1401-1600	9	8
1601-1800	21	17
1801-2000	5	5
2001-2200	14	13
2201-2400	21	14
2401-2600	6	5
2601-2800	3	2
2801-3000	7	7
3001-3200	4	4

*註：表相對地理海拔高度 (relative geographic elevation).

種數、調查方法、調查範圍大小及調查努力量等因素的影響(謝 1986；尤 1997；許及賴 2000；許 2001；Ekman 1981; Scott and Ramsey 1981; Bennetts *et al*. 1999)。故本研究進一步比較各海拔類別單一調查區，在8小時調查努力量之下所能記錄的平均鳥種數。結果發現具留鳥遷移屬性的鳥種豐富度會隨著海拔上升而呈現明顯峰形分布的變化趨勢，但在加入緯度遷移候鳥而以全部鳥種來進行分析時，則可發現峰形分布的變化趨勢較爲平緩，但兩者均是以1,500-1,999m海拔類別記錄到最高的鳥種數(圖2)。這種峰形分布與上述反相關係變化趨勢的差異，除了受到不同調查努力量的影響，是否會受到不同地景(landscape)分析尺度的影響(Wiens 1981; Ding 2001)，則有待進一步的分析探討。

台灣南部地區鳥種豐富度隨著海拔梯度而呈現峰形分布可能受到下列幾個因素的影響：第一、Ding(2001)發現台灣的人爲開發情況，隨著海拔上升而遞減。Blair(1996)則發現，歐美人爲開發區的鳥種豐富度會降低，但部分種類的族群量則會上升。低海拔區域的人爲開發可能減少或改變鳥類的棲息環境，使其棲息的鳥種數降低，而這種影響愈往低海拔愈爲顯著(翟 1977)。第二、台灣中海拔區域具有最高的初級生產力(Ding

2001)。較高的初級生產力會使物種的族群量增高且降低物種滅絕的機會，因而增高該區域的物種豐富度(Wright 1983)，有許多研究報告即指出初級生產力與一些植物或動物類群間的物種豐富度呈線性遞增的關係(Currie and Paquin 1987; Currie 1991; Brown and Lomolino 1998; Gaston 2000)。第三、台灣歷史地質事件(historical vicariance)的影響。台灣在上新世(Pliocene)後期約三百萬年前始與大陸分離(蕭等 1993)，而後在更新世(Pleistocene)到第四紀期間，也曾多次因冰河期海平面下降及造山運動所形成的陸橋與亞洲大陸、菲律賓及琉球群島相連(林 1963，1966)。每一次冰河期海平面下降，台灣海峽大部分區域形成乾地，許多生物便可藉由陸橋由亞洲大陸東部播遷到台灣。Kano(1940)在台灣的雪山山脈以脊椎動物爲對象進行了動、植物的分布調查，指出台灣的脊椎動物主要包含兩個不同地理區系來源的物種；目前棲息分布在低海拔的物種大都屬於東洋區系(Oriental Region)的物種，棲息分布在高海拔的物種則大都屬於古北區系(Palaearctic Region)的物種(顏 1989；Kuroda 1952)。林(1985)認爲海拔1,500至2,000m這個範圍，很可能是台灣高、低海拔哺乳類動物分布的交接帶。這種不同來源物種棲息在台灣的海拔差異，也可能導致中海拔交接區域具有較高的鳥種豐富度。第四、生物性競爭的影響。由於台灣大部分的緯度遷移候鳥都棲息在低海拔區域，雖然他們只在特定季節占據所棲息的區域，但對於經年棲息於台灣低海拔的留鳥也可能因爲競爭排斥而降低其所棲息的鳥種數(Terborgh 1971; Diamond 1973)。

此外，各海拔類別的鳥種相似性隨著海拔的差距變大而降低，主要是因爲大部分鳥類均具有一定的海拔分布幅度，海拔差距越大其鳥種的相似性自然越低。翟(1977)觀察台灣124種留鳥的海拔分布幅度，發現有38種(31%)小於1,000m，本研究的結果亦相近似。Terborgh(1971)於祕魯安底斯山區(Andes)記錄207種鳥類，其中有163種(79%)的海拔分布幅度落在100-1,000m之間，僅有3種超過2,000m。本研究發現500-999m與1,000-1,499m、1,500-1,999m與2,000-2,500m這兩組海拔類別間具有較高的相似性，可能與一些同時新加入的鳥種有關。翟(1977)發現在海拔1,000與2,200m兩處位置附近，分別有14種與9種數量衆多的顯要鳥種同時出現。因此，翟(1977)推測台灣的鳥種組成在海拔1,000及2,000m附近發生較爲顯著的組成轉換。海拔1,500-2,000m這個區域，可能因爲處於鳥種組成轉換的交接帶，加上台灣鳥類的海拔垂直遷移、初級生產力較高及人爲干擾較低等等因素，導致該區域擁有較高的鳥種豐富度。

綜合觀之，台灣南部地區的鳥種組成相當豐富，但族群數量少或棲息在特定環境的鳥種則占有相當高的比例，且調查努力量的差異會對物種豐富度與海拔梯度變化之課題探討產生影響。在考量調查努力量的情況下，台灣南部地區留鳥的鳥種豐富度會隨著海拔上升而呈峰形分布的改變趨勢，這與近年來一些以台灣繁殖留鳥爲探討對象的研究結果相類似(翟 1977；林 1989；丁 1993；顏 1997；聶 1999；Ding 2001)。當我們將緯度遷移鳥種納入分析時，則會減緩這種峰形分布的改變趨勢，顯示在探討鳥種豐富度與海拔梯度變化之間的關係時，必須要考量到不同分析類群所可能造成的差異(Blake and Loiselle 2000)。值得注意的是本研究及以往的研究大都未考慮到海拔遷移鳥種對相關研究所可能造成的影響，而台灣的留鳥在不同的季節間進行海拔垂直遷移是相當普遍的現象(翟1977)。因此，若能僅以留鳥較爲穩定棲息的繁殖季節調查資料來進行分析，對於相關課題的探討應有明顯的助益。

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附錄I. 本研究各調查區之位置、海拔、所發現的鳥種數及主要棲地類型

Appendix I. Bird richness at the survey sites with locations, elevations, and habitat types in the southern Taiwan

							鳥種數		主要棲地類型
編號	縣市	鄉鎮	調查區名稱	海拔(m)	東經	北緯	全部	留鳥	
1	嘉義	義竹鄉	☆ 角帶圍(8)	20	120°15'-16'	23°21'-22'	38	29	溪流、農耕地
2	嘉義	水上鄉	※ 大掘尾(4)	50	120°22'-23'	23°26'-27'	19	16	農耕地
3	嘉義	水上鄉	☆ 外溪洲(8)	30	120°26'-27'	23°26'-27'	42	32	溪流、農耕地
4	嘉義	太保市	※ 老碑(4)	40	120°20'-21'	23°28'-29'	21	18	埤塘、農耕地
5	嘉義	六腳鄉	☆ 蒜頭橋(8)	30	120°16'-17'	23°29'-30'	30	22	溪流、農耕地
6	嘉義	東石鄉	㊣ 東石橋(12)	20	120°10'-11'	23°27'-28'	66	33	溪流、魚塭、農耕地
7	嘉義	東石鄉	㊣ 海埔墾殖場(24)	10	120°08'-09'	23°27'-28'	99	39	海濱溼地、魚塭
8	嘉義	東石鄉	㊣ 鹽港(11)	5	120°08'-09'	23°28'-29'	43	26	海濱溼地、魚塭
9	嘉義	鹿草鄉	☆ 農業改良場(8)	40	120°16'-17'	23°25'-26'	31	22	農耕地、果園
10	嘉義	朴子市	☆ 雙溪口(8)	40	120°15'-16'	23°29'-30'	30	23	溪流、農耕地
11	嘉義	溪口鄉	☆ 崙尾(8)	20	120°22'-23'	23°35'-36'	35	27	溪流、農耕地
12	嘉義	中埔鄉	☆ 中埔橋(8)	195	120°30'-31'	23°25'-26'	60	51	溪流、檳榔園、竹林
13	嘉義	中埔鄉	☆ 分水嶺(10)	915	120°34'-35'	23°22'-23'	56	49	闊葉林、竹林、檳榔園
14	嘉義	大埔鄉	☆ 沙崙橋(8)	300	120°36'-37'	23°20'-21'	40	39	溪流、檳榔園、竹林、闊葉林
15	嘉義	大埔鄉	☆ 嘉義農場(8)	310	120°32'-33'	23°14'-15'	38	32	水庫、果園、竹林、闊葉林
16	嘉義	大埔鄉	☆ 大埔(8)	335	120°35'-36'	23°18'-19'	40	38	水庫、農耕地、闊葉林
17	嘉義	大埔鄉	※ 掬月半島(2)	310	120°34'-35'	23°17'-18'	45	42	水庫、果園、竹林、闊葉林
18	嘉義	布袋鎮	㊣ 布袋鹽田(24)	5	120°09'-10'	23°21'-22'	60	24	海濱溼地、魚塭
19	嘉義	布袋鎮	㊣ 好美寮(24)	10	120°07'-08'	23°20'-21'	66	31	海濱溼地、魚塭、防風林
20	嘉義	番路鄉	☆ 社口(8)	270	120°35'-36'	23°26'-27'	30	29	檳榔園、竹林、闊葉林
21	嘉義	番路鄉	☆ 半天岩(8)	435	120°35'-36'	23°27'-28'	47	39	檳榔園、竹林、闊葉林
22	嘉義	番路鄉	※ 籠頭(2)	1325	120°40'-41'	23°26'-27'	23	21	茶園、竹林、闊葉林
23	嘉義	梅山鄉	☆ 梅山大峽谷(8)	510	120°38'-39'	23°34'-35'	42	38	溪流、竹林、闊葉林
24	嘉義	梅山鄉	☆ 太平(8)	980	120°36'-37'	23°33'-34'	34	33	檳榔園、竹林、闊葉林
25	嘉義	梅山鄉	☆ 瑞里(8)	1070	120°39'-40'	23°32'-33'	43	40	檳榔園、竹林、闊葉林
26	嘉義	梅山鄉	☆ 梅山(8)	150	120°33'-34'	23°34'-35'	26	24	檳榔園、農耕地、竹林
27	嘉義	民雄鄉	☆ 中正大學(8)	130	120°38'-39'	23°34'-35'	28	25	檳榔園、農耕地、竹林
28	嘉義	嘉義市	☆ 蘭潭水庫(8)	110	120°28'-29'	23°28'-29'	32	29	水庫、竹林、闊葉林
29	嘉義	竹崎鄉	☆ 奮起湖(8)	1385	120°41'-42'	23°30'-31'	46	43	檳榔園、竹林、闊葉林
30	嘉義	竹崎鄉	☆ 科底(8)	660	120°35'-36'	23°32'-33'	36	33	檳榔園、竹林、闊葉林
31	嘉義	竹崎鄉	※ 石卓(1)	1335	120°41'-42'	23°28'-29'	17	17	檳榔園、竹林、闊葉林
32	嘉義	阿里山鄉	☆ 豐山(8)	750	120°44'-45'	23°34'-35'	51	45	溪流、竹林、闊葉林
33	嘉義	阿里山鄉	☆ 自忠(8)	2300	120°48'-49'	23°29'-30'	44	40	闊葉林、人工針葉林
34	嘉義	阿里山鄉	☆ 沼平公園(8)	2250	120°48'-49'	23°31'-32'	41	34	闊葉林、人工針葉林
35	嘉義	阿里山鄉	※ 祝山(2)	2500	120°49'-50'	23°30'-31'	17	17	闊葉林、人工針葉林
36	嘉義	阿里山鄉	※ 眠月(4)	2318	120°48'-49'	23°33'-34'	18	17	闊葉林、人工針葉林
37	嘉義	阿里山鄉	☆ 達邦(8)	950	120°44'-45'	23°27'-28'	44	41	闊葉林、竹林、果園
38	嘉義	阿里山鄉	※ 十字路(1)	1610	120°44'-45'	23°29'-30'	29	27	闊葉林、竹林、茶園
39	嘉義	阿里山鄉	☆ 達娜伊谷(10)	480	120°40'-41'	23°23'-24'	57	53	闊葉林、竹林
40	嘉義	阿里山鄉	※ 楠溪林道(3)	2300	120°53'-54'	23°27'-28'	29	28	闊葉林、人工針葉林

附錄I. 本研究各調查區之位置、海拔、所發現的鳥種數及主要棲地類型(續)

Appendix I. Bird richness at the survey sites with locations, elevations, and habitat types in the southern Taiwan (continued)

							鳥種數		
編號	縣市	鄉鎮	調查區名稱	海拔(m)	東經	北緯	全部	留鳥	主要棲地類型
41	嘉義	阿里山鄉	※ 塔塔加(4)	2670	120°53'-54'	23°28'-29'	28	28	闊葉林、針葉林
42	嘉義	阿里山鄉	※ 茶山(2)	625	120°40'-41'	23°20'-21'	30	28	闊葉林、竹林、人工針葉林
43	嘉義	阿里山鄉	※ 來吉(1)	880	120°44'-45'	23°31'-32'	15	15	闊葉林、竹林、人工針葉林
44	嘉義	阿里山鄉	※ 里佳(2)	1230	120°42'-43'	23°24'-25'	24	23	闊葉林、竹林、檳榔園
45	高雄	永安鄉	㊣ 鳥投林(24)	10	120°11'-12'	22°50'-51'	63	33	木麻黃林、鹽灘
46	高雄	彌陀鄉	☆ 六塊厝(8)	10	120°13'-14'	22°46'-47'	36	24	農耕地、闊葉林、竹林
47	高雄	高雄市	㊣ 壽山(24)	200	120°15'-16'	22°38'-39'	32	27	闊葉林、竹林
48	高雄	林園鄉	㊣ 高屏溪口(24)	10	120°23'-24'	22°29'-30'	54	35	溪流、農耕地
49	高雄	燕巢鄉	☆ 阿公店(8)	100	120°21'-22'	22°48'-49'	29	23	水庫、農耕地、闊葉林
50	高雄	大寮鄉	☆ 拷潭(8)	50	120°22'-23'	22°34'-35'	47	29	農耕地
51	高雄	大樹鄉	☆ 大樹橋(8)	100	120°26'-27'	22°40'-41'	48	31	溪流、農耕地
52	高雄	田寮鄉	☆ 大岡山(8)	200	120°20'-21'	22°50'-51'	23	22	農耕地、竹林、闊葉林
53	高雄	內門鄉	☆ 金瓜寮(8)	400	120°30'-31'	23°01'-02'	41	35	農耕地、闊葉林、竹林
54	高雄	旗山鎮	☆ 中寮(8)	300	120°25'-26'	22°49'-50'	27	25	農耕地、闊葉林、竹林
55	高雄	旗山鎮	※ 旗尾橋(2)	40	120°28'-29'	22°53'-54'	39	32	溪流、農耕地
56	高雄	美濃鎮	☆ 美濃湖(8)	100	120°32'-33'	22°54'-55'	35	25	人工湖、農耕地、竹林
57	高雄	美濃鎮	☆ 黃蝶翠谷(8)	300	120°35'-36'	22°56'-57'	47	44	溪流、農耕地、闊葉林、竹林
58	高雄	杉林鄉	☆ 獅子山(8)	400	120°33'-34'	22°59'-60'	43	36	闊葉林、竹林
59	高雄	杉林鄉	☆ 八張犂(10)	200	120°31'-32'	23°02'-03'	43	36	農耕地
60	高雄	六龜鄉	☆ 月仙(8)	600	120°40'-41'	23°01'-02'	39	33	農耕地、闊葉林、竹林
61	高雄	六龜鄉	☆ 寶來(8)	350	120°40'-41'	23°06'-07'	38	35	果園、闊葉林、竹林
62	高雄	六龜鄉	※ 石洞溫泉(2)	510	120°42'-43'	23°06'-07'	25	25	果園、闊葉林、竹林
63	高雄	六龜鄉	※ 三合橋(2)	230	120°38'-39'	22°57'-58'	33	29	果園、闊葉林、竹林
64	高雄	六龜鄉	※ 七坑溫泉(2)	820	120°41'-42'	23°05'-06'	21	21	果園、闊葉林、竹林
65	高雄	甲仙鄉	☆ 五指寮(8)	1000	120°39'-40'	23°07'-08'	39	37	闊葉林、竹林、人工針葉林
66	高雄	甲仙鄉	☆ 贏橋(8)	350	120°35'-36'	23°07'-08'	56	48	溪流、果園、竹林、闊葉林
67	高雄	甲仙鄉	☆ 三山國王廟(8)	500	120°36'-37'	23°04'-05'	35	32	溪流、竹林、闊葉林
68	高雄	甲仙鄉	※ 四德大橋(2)	250	120°34'-35'	23°05'-06'	23	22	溪流、農耕地
69	高雄	三民鄉	☆ 民生二村(8)	300	120°42'-43'	23°16'-17'	51	46	溪流、農耕地、竹林、闊葉林
70	高雄	三民鄉	☆ 天使瀑布(8)	740	120°41'-42'	23°13'-14'	45	44	闊葉林、竹林
71	高雄	茂林鄉	☆ 多納林道(8)	650	120°42'-43'	22°54'-55'	37	36	闊葉林、竹林
72	高雄	茂林鄉	☆ 鳳崗林道(8)	800	120°40'-41'	22°58'-59'	39	37	闊葉林、竹林
73	高雄	桃源鄉	※ 綠茂橋(2)	405	120°41'-42'	23°07'-08'	22	22	闊葉林、果園、竹林
74	高雄	桃源鄉	☆ 高中林道4K(8)	800	120°42'-43'	23°08'-09'	38	35	果園、闊葉林、竹林
75	高雄	桃源鄉	※ 高中林道8K(4)	1150	120°41'-42'	23°09'-10'	37	35	果園、闊葉林、竹林
76	高雄	桃源鄉	☆ 少年溪溫泉(8)	640	120°45'-46'	23°10'-11'	50	46	溪流、農耕地、竹林、闊葉林
77	高雄	桃源鄉	☆ 梅蘭林道5K(8)	1070	120°48'-49'	23°17'-18'	54	50	闊葉林、人工針葉林、農耕地
78	高雄	桃源鄉	※ 梅蘭林道18K(2)	1800	120°48'-49'	23°19'-20'	39	37	闊葉林、人工針葉林
79	高雄	桃源鄉	☆ 禮觀(8)	1645	120°50'-51'	23°17'-18'	58	51	闊葉林、人工針葉林
80	高雄	桃源鄉	☆ 關山越古道(8)	2040	120°53'-54'	23°17'-18'	48	46	針闊混合林、人工針葉林

附錄I. 本研究各調查區之位置、海拔、所發現的鳥種數及主要棲地類型(續)

Appendix I. Bird richness at the survey sites with locations, elevations, and habitat types in the southern Taiwan (continued)

編號	縣市	鄉鎮	調查區名稱	海拔(m)	東經	北緯	鳥種數		主要棲地類型
							全部	留鳥	
81	高雄	桃源鄉	※ 塔關山(2)	3100	120°56'-57'	23°16'-17'	25	25	闊葉林、針葉林、箭竹林
82	高雄	桃源鄉	☆ 啞口林道(8)	2700	120°57'-58'	23°17'-18'	39	37	闊葉林、針葉林
83	高雄	桃源鄉	※ 楠溪15-18K(2)	2000	120°53'-54'	23°25'-26'	29	28	針闊混合林
84	高雄	桃源鄉	※ 南橫145K(1)	2600	120°57'-58'	23°16'-17'	20	19	針闊混合林
85	高雄	桃源鄉	☆ 石山林道A段(14)	1600	120°45'-46'	23°04'-05'	52	52	闊葉林、人工針葉林
86	高雄	桃源鄉	☆ 石山林道B段(8)	1800	120°47'-48'	23°04'-05'	41	40	闊葉林、人工針葉林
87	高雄	桃源鄉	☆ 石山林道C段(12)	2300	120°47'-48'	23°05'-06'	37	35	闊葉林、造林地、人工針葉林
88	高雄	桃源鄉	※ 溪南鬼湖(4)	2300	120°48'-49'	23°05'-06'	25	25	闊葉林
89	屏東	三地門鄉	☆ 海神瀑布(8)	250	120°37'-38'	22°49'-50'	42	39	果園、闊葉林、竹林
90	屏東	三地門鄉	☆ 大社(8)	500	120°41'-42'	22°48'-49'	34	32	溪流、農耕地、闊葉林、竹林
91	屏東	霧臺鄉	☆ 佳暮(8)	500	120°43'-44'	22°46'-47'	39	36	溪流、農耕地、闊葉林、竹林
92	屏東	霧臺鄉	☆ 阿禮(8)	1300	120°44'-45'	22°43'-44'	58	51	果園、闊葉林、竹林
93	屏東	鹽埔鄉	☆ 台糖農場(8)	30	120°32'-33'	22°43'-44'	43	27	農耕地、果園
94	屏東	屏東市	☆ 糖廠畜牧場(8)	20	120°26'-27'	22°39'-40'	24	18	農耕地、果園
95	屏東	麟洛鄉	☆ 新田(8)	100	120°32'-33'	22°40'-41'	23	19	農耕地、果園、闊葉林
96	屏東	瑪家鄉	☆ 好茶(8)	700	120°39'-40'	22°42'-43'	46	43	農耕地、果園、闊葉林
97	屏東	瑪家鄉	☆ 笠頂山(8)	550	120°37'-38'	22°39'-40'	42	35	果園、闊葉林、竹林
98	屏東	萬巒鄉	☆ 穎達農場(8)	80	120°36'-37'	22°38'-39'	52	43	果園、闊葉林
99	屏東	萬巒鄉	☆ 五溝水(8)	50	120°35'-36'	22°35'-36'	33	29	農耕地、果園
100	屏東	泰武鄉	☆ 泰武(8)	750	120°40'-41'	22°36'-37'	37	31	農耕地、果園、闊葉林
101	屏東	泰武鄉	☆ 北大武登山口(8)	1500	120°42'-43'	22°37'-38'	42	39	闊葉林
102	屏東	新園鄉	☆ 田洋堤防(8)	10	120°27'-28'	22°33'-34'	41	25	溪流、農耕地
103	屏東	新園鄉	㊣ 新園堤(24)	10	120°25'-26'	22°29'-30'	51	37	溪流、農耕地
104	屏東	潮洲鎮	☆ 永興寮(8)	50	120°33'-34'	22°31'-32'	30	24	農耕地、果園
105	屏東	新埤鄉	☆ 餉潭(8)	50	120°36'-37'	22°28'-29'	39	35	溪流、農耕地
106	屏東	來義鄉	☆ 來義(8)	200	120°41'-42'	22°31'-32'	43	38	溪流、果園、闊葉林
107	屏東	佳冬鄉	㊣ 鹽豐(24)	10	120°31'-32'	22°24'-25'	49	28	魚塭、沿海溼地
108	屏東	春日鄉	☆ 古華草山橋(8)	100	120°38'-39'	22°21'-22'	48	38	溪流、果園、闊葉林
109	屏東	春日鄉	☆ 大漢林道23K(8)	1400	120°44'-45'	22°24'-25'	32	30	闊葉林、人工針葉林
110	屏東	獅子鄉	☆ 枋野(8)	150	120°42'-43'	22°16'-17'	45	38	溪流、果園、闊葉林
111	屏東	獅子鄉	☆ 楓林(8)	50	120°42'-43'	22°12'-13'	45	38	果園、闊葉林、竹林
112	屏東	獅子鄉	☆ 雙流(8)	200	120°47'-48'	22°13'-14'	25	22	果園、竹林、闊葉林
113	屏東	車城鄉	☆ 四重溪(8)	100	120°44'-45'	22°05'-06'	40	32	果園、闊葉林、竹林
114	屏東	牡丹鄉	☆ 鐵線橋(8)	350	120°48'-49'	22°09'-10'	42	34	溪流、果園、闊葉林
115	屏東	牡丹鄉	☆ 牡丹灣(8)	10	120°52'-53'	22°11'-12'	29	23	溪流、農耕地
116	屏東	滿州鄉	☆ 中港(8)	10	120°52'-53'	22°06'-07'	15	11	溪流、農耕地
117	屏東	滿州鄉	☆ 七孔瀑布(8)	100	120°48'-49'	22°01'-02'	41	33	果園、闊葉林、竹林
118	屏東	恆春鎮	㊣ 龍鑾潭(24)	20	120°43'-44'	21°59'-60'	81	38	人工湖泊、農耕地、果園

註1：㊣表該調查區每月至少進行一次調查；☆表該調查區每一季至少進行一次調查；※表不固定調查區。

註2：調查區名稱後括弧內之數字表其調查時數。

附錄II. 本研究所有鳥種之學名、記錄縣市、記錄調查區數及其遷移屬性

Appendix II. A checklist of birds with migratory status, counties of records, and numbers of recorded sites in the southern Taiwan

目 名	科 名	中 文 名	學 名	記錄縣市※			記錄調查區數	遷移屬性⊕
				嘉義	高雄	屏東		
鸊鷉目	鸊鷉科	冠鸊鷉	*Podiceps cristatus*			(*)		W
		黑頸鸊鷉	*Podiceps nigricollis*		(*)			W
		小鸊鷉	*Podiceps ruficollis*	*	*	*	13	R
鵜形目	熱帶鳥科	紅尾熱帶鳥	*Phaethon rubricauda*			(*)		V
	鸕鷀科	鸕鷀	*Phalacrocorax carbo*	*	*	*	7	W
		丹氏鸕鷀	*Phalacrocorax capillatus*		(*)			V
	軍艦鳥科	白斑軍艦鳥	*Fregata ariel*		(*)			S
		軍艦鳥	*Fregata minor*		(*)			V
鸛形目	鷺科	蒼鷺	*Ardea cinerea*	*	*	*	18	W
		紫鷺	*Ardea purpurea*	*		*	2	W
		池鷺	*Ardeola bacchus*		*	(*)	1	W
		大麻鷺	*Botaurus stellaris*			*	1	W
		黃頭鷺	*Bubulcus ibis*	*	*	*	39	S W
		綠簑鷺	*Butorides striatus*	*	*	*	11	R W
		大白鷺	*Egretta alba*	*	*	*	15	W
		唐白鷺	*Egretta eulophotes*		(*)			W
		小白鷺	*Egretta garzetta*	*	*	*	70	R
		中白鷺	*Egretta intermedia*	*	*	*	18	W
		岩鷺	*Egretta sacra*		*	*	2	R
		黑冠麻鷺	*Gorsachius melanolophus*	*	*	*	13	R
		栗小鷺	*Ixobrychus cinnamomeus*	*	*	*	18	R
		黃小鷺	*Ixobrychus sinensis*	*	*	*	9	R
		夜鷺	*Nycticorax nycticorax*	*	*	*	23	R
	鸛科	黑鸛	*Ciconia nigna*	*			1	T
	䴉科	黑面琵鷺	*Platalea minor*	*	*	(*)	2	W
雁形目	雁鴨科	鴛鴦	*Aix galericulata*		(*)			R W
		尖尾鴨	*Anas acuta*	*	*	*	3	W
		琵嘴鴨	*Anas clypeata*	*	(*)	*	3	W
		小水鴨	*Anas crecca*	*	*	*	13	W
		羅文鴨	*Anas falcata*		(*)	*	1	W
		赤頸鴨	*Anas penelope*	*	(*)	*	2	W
		綠頭鴨	*Anas platyrhynchos*	*	(*)	*	4	W
		花嘴鴨	*Anas poecilorhyncha*	*	*	*	5	W R
		白眉鴨	*Anas querquedula*	*	(*)	*	4	T W
		白額雁	*Anser albifrons*			(*)		V
		小白額雁	*Anser erythropus*			(*)		V
		赤膀鴨	*Anas strpera*		(*)	*	1	W
		青頭潛雁	*Aythya baeri*			(*)		W
		紅頭潛雁	*Aythya ferina*	*	(*)	*	2	W
		鳳頭潛鴨	*Aythya fuligula*		(*)	*	1	W
		斑背潛鴨	*Aythya marila*		(*)	*	1	W

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Appendix II. A checklist of birds with migratory status, counties of records, and numbers of recorded sites in the southern Taiwan (continued)

目 名	科 名	中 文 名	學 名	記錄縣市※			記錄調查區數	遷移屬性⊕
				嘉義	高雄	屏東		
		川秋沙	*Mergus merganser*			(*)		V
		唐秋沙	*Mergus squamatus*			(*)		V
		花鳧	*Tadorna tadorna*			(*)		W
隼形目	鷲鷹科	北雀鷹	*Accipiter nisus*	(*)		*	1	W
		松雀鷹	*Accipiter virgatus*	*	*	*	19	R
		赤腹鷹	*Accipiter soloensis*	*	*	*	7	T
		鳳頭蒼鷹	*Accipiter trivirgatus*	*	*	*	30	R
		花雕	*Aquila ckanga*	(*)	*		1	T
		白肩雕	*Aquila heliaca*		*		1	V
		灰面鵟鷹	*Butastur indicus*	*	(*)	*	6	T W
		鵟	*Buteo buteo*	*		(*)	2	W
		毛足鵟	*Buteo lagopus*		(*)	(*)		W
		澤鵟	*Circus spilonotus*	*	(*)	*	4	W
		灰澤鵟	*Circus cyaneus*	(*)		(*)		W
		林雕	*Ictinaetus malayensis*	*	*	*	6	R
		黑鳶	*Milvus migrans*	*	*	*	11	R
		蜂鷹	*Pernis ptilorhynchus*	*	*	*	5	W T
		大冠鷲	*Spilornis cheela*	*	*	*	59	R
		熊鷹	*Spizaetus nipalensis*	(*)	*	(*)	1	R
	鶚科	魚鷹	*Pandion haliaetus*	*	*	*	7	W
	隼科	遊隼	*Falco peregrinus*	*		(*)	1	W R
		紅隼	*Falco tinnunculus*	*	*	*	18	W
雞形目	雉科	台灣山鷓鴣	*Arborophila crudigularis*	*	*	*	24	R
		竹雞	*Bambusicola thoracica*	*	*	*	67	R
		小鵪鶉	*Coturnix chinensis*	(*)				R
		藍腹鷴	*Lophura swinhoii*	*	*	*	10	R
		黑長尾雉	*Syrmaticus mikado*	*	*	*	4	R
鶴形目	三趾鶉科	棕三趾鶉	*Turnix suscitator*	*	*	*	14	R
	秧雞科	白腹秧雞	*Amaurornis phoenicurus*	*	*	*	29	R
		白冠雞	*Fulica atra*	*	*	*	3	W
		董雞	*Gallicrex cinerea*			*	1	S R
		紅冠水雞	*Gallinula chloropus*	*	*	*	36	R
		緋秧雞	*Porzana fusca*	*	*	*	10	R
		灰腳秧雞	*Rallina eurizonoides*			*	1	T R
		秧雞	*Rallus aquaticus*	(*)		(*)		W R
		灰胸秧雞	*Rallus striatus*	*		(*)	2	R
鴴形目	水雉科	水雉	*Hydrophasianus chirurgus*		(*)	(*)		R S
	彩鷸科	彩鷸	*Rostratula benghalensis*	*	*	*	8	S R
	反嘴鷸科	高蹺鴴	*Himantopus himantopus*	*	*	*	7	S W
		反嘴鴴	*Recurvirostra avosetta*		(*)			W
	燕鴴科	燕鴴	*Glareola maldivarus*	*	(*)	*	6	S W

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Appendix II. A checklist of birds with migratory status, counties of records, and numbers of recorded sites in the southern Taiwan (continued)

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				嘉義	高雄	屏東		
	鴴科	東方環頸鴴	*Charadrius alexandrinus*	*	*	*	12	W S R
		紅胸鴴	*Charadrius veredus*	*			1	V
		小環頸鴴	*Charadrius dubius*	*	*	*	28	W S R
		環頸鴴	*Charadrius hiaticula*		(*)	*	2	V
		鐵嘴鴴	*Charadrius leschenaultii*	*	(*)	*	3	T
		蒙古沙鴴	*Charadrius mongolus*	*	*		6	T W
		劍鴴	*Charadrius placidus*		*		1	V
		跳鴴	*Vanellus cinereus*			*	1	T
		金斑鴴	*Pluvialis dominica*	*	*	*	12	W
		灰斑鴴	*Pluvialis squatarola*	*	*		3	W
		小辮鴴	*Vanellus vanellus*	*		*	2	W
	鷸科	翻石鷸	*Arenaria interpres*	*	*	(*)	5	T W
		尖尾濱鷸	*Calidris acuminata*	*	*	*	7	T
		黑腹濱鷸	*Calidris alpina*	*	*	*	9	W
		彎嘴濱鷸	*Calidris ferruginea*	*	*		5	T
		紅胸濱鷸	*Calidris ruficollis*	*	*	*	8	T W
		長趾濱鷸	*Calidris subminuta*	*	*	*	5	W
		丹氏濱鷸	*Calidris temmincki*		*	(*)	1	W
		大濱鷸	*Calidris tenuirostris*		(*)			T
		三趾濱鷸	*Colidris alba*			(*)		W
		田鷸	*Gallinago gallinago*	*	*	*	11	W
		寬嘴鷸	*Limicola falcinellus*	(*)	(*)			T
		斑尾鷸	*Limosa lapponica*	*	(*)		1	T
		黑尾鷸	*Limosa limosa*	*	*		5	T
		大杓鷸	*Numenius arquata*	*	(*)		2	T W
		小杓鷸	*Numenius minutus*	*			2	T
		中杓鷸	*Numenius phaeopus*	*	*	*	7	T W
		流蘇鷸	*Philomachus pugnax*	(*)	*		1	T
		山鷸	*Scolopax rusticola*		(*)	*	2	W
		黃足鷸	*Heteroscelus brevipes*	*	*	*	3	T
		鶴鷸	*Tringa erythropus*	(*)	(*)			W
		鷹斑鷸	*Tringa glareola*	*	*	*	15	W
		磯鷸	*Actitis hypoleucos*	*	*	*	32	W R
		青足鷸	*Tringa nebularia*	*	*	*	11	W
		白腰草鷸	*Tringa ochropus*	*	*	*	9	W
		小青足鷸	*Tringa stagnatilis*	*	*	*	10	W T
		赤足鷸	*Tringa totanus*	*	(*)		5	T W
		反嘴鷸	*Xenus cinereus*	*	*		3	T
		灰瓣足鷸	*Phalaropus fulicarius*	*			1	V
		紅領瓣足鷸	*Phalaropus lobatus*	*	(*)	(*)	3	T
	鷗科	黑脊鷗	*Larus argentatus*	*			1	W

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				嘉義	高雄	屏東		
		燕鷗	*Sterna hirundo*		(*)	*	1	T
		黑尾鷗	*Larus crassirostris*	(*)	(*)	*	1	W
		紅嘴鷗	*Larus ridibundus*	*	(*)	(*)	5	W
		黑嘴鷗	*Larus saundersi*	*			4	W
		小燕鷗	*Sterna albifrons*	*	*	(*)	6	S W R
		黑腹燕鷗	*Chlidonias hybrida*	*	*	*	10	W T
		白翅黑燕鷗	*Chlidonias leucopterus*	*	(*)	*	7	T
		蒼燕鷗	*Sterna sumatrana*		(*)			S T
		裏海燕鷗	*Hydroprogne caspia*	*			1	W
鴿形目	鳩鴿科	翠翼鳩	*Chalcophaps indica*	*	*	*	26	R
		灰林鴿	*Columba pulchricollis*	*	*	*	7	R
		斑頸鳩	*Streptopelia chinensis*	*	*	*	65	R
		金背鳩	*Streptopelia orientalis*	*	*	*	30	R
		紅鳩	*Streptopelia tranquebarica*	*	*	*	55	R
		紅頭綠鳩	*Treron formosae*			(*)		R
		綠鳩	*Treron sieboldii*	*	*	*	28	R
鵑形目	杜鵑科	番鵑	*Centropus bengalensis*	*	*	*	33	R
		大杜鵑	*Cuculus canorus*	(*)		*	1	V
		小杜鵑	*Cuculus poliocephalus*		(*)			T
		中杜鵑	*Cuculus saturatus*	*	*	*	20	S
		鷹鵑	*Cuculus sparverioides*	*	*	*	10	S
鴞形目	鴟鴞科	鵂鶹	*Glaucidium brodiei*	*	*	*	10	R
		黃魚鴞	*Ketupa flavipes*	(*)		(*)		R
		褐鷹鴞	*Ninox scutulata*	(*)	(*)	(*)		R T
		領角鴞	*Otus bakkamoena*	*	*	*	6	R
		角鴞	*Otus scops*			(*)		T
		黃嘴角鴞	*Otus spilocephalus*	*	*	*	9	R
		灰林鴞	*Strix aluco*	(*)	*	*	3	R
		褐林鴞	*Strix leptogrammica*	*	(*)		1	R
夜鷹目	夜鷹科	台灣夜鷹	*Caprimulgus affinis*	(*)		*	1	R
雨燕目	雨燕科	小雨燕	*Apus affinis*	*	*	*	84	R
		叉尾雨燕	*Apus pacificus*	*	(*)	*	4	S R
		針尾雨燕	*Hirundapus caudacuta*	(*)	*	(*)	4	S
佛法僧目	翡翠科	翠鳥	*Alcedo atthis*	*	*	*	41	R
		赤翡翠	*Halcyon coromanda*	(*)		(*)		T
	戴勝科	戴勝	*Upupa epops*		(*)			T
鴷形目	鬚鴷科	五色鳥	*Megalaima oorti*	*	*	*	68	R
	啄木鳥科	小啄木	*Picoides canicapillus*	*	*	*	46	R
		大赤啄木	*Picoides leucotos*	*	*	*	10	R
		綠啄木	*Picus canus*	*	*	*	7	R
雀形目	八色鳥科	八色鳥	*Pitta brachyura*	*		(*)	2	S

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Appendix II. A checklist of birds with migratory status, counties of records, and numbers of recorded sites in the southern Taiwan (continued)

目名	科名	中文名	學名	記錄縣市※			記錄調查區數	遷移屬性⊕
				嘉義	高雄	屏東		
	雲雀科	小雲雀	*Alauda gulgula*	*	*	*	19	R
	燕科	毛腳燕	*Delichon urbica*	*	*	*	28	R
		家燕	*Hirundo rustica*	*	*	*	50	S W R
		赤腰燕	*Hirundo striolata*	*	*	*	75	R
		洋燕	*Hirundo tahitica*	*	*	*	92	R
		棕沙燕	*Riparia paludicola*	*	*	*	37	R
		灰沙燕	*Riparia riparia*			*	1	T
	山椒鳥科	黑翅山椒鳥	*Coracina melaschistos*		*		1	V
		花翅山椒鳥	*Coracina novaehollandiae*	(*)	*	(*)	3	R
		灰山椒鳥	*Pericrocotus divaricatus*	(*)		*	1	T
		灰喉山椒鳥	*Pericrocotus solaris*	*	*	*	41	R
	卷尾科	小卷尾	*Dicrurus aeneus*	*	*	*	56	R
		大卷尾	*Dicrurus macrocercus*	*	*	*	56	R
	黃鸝科	黃鸝	*Oriolus chinensis*	*	(*)	*	3	R T
		朱鸝	*Oriolus trailli*	*	*	*	14	R
	鴉科	巨嘴鴉	*Corvus macrorhynchos*	*	*	*	52	R
		樹鵲	*Dendrocitta formosae*	*	*	*	69	R
		松鴉	*Garrulus glanderius*	*	*	*	14	R
		星鴉	*Nucifraga caryocatactes*	*	*	(*)	7	R
		喜鵲	*Pica pica*	*	*	*	6	R
		台灣藍鵲	*Urocissa caerulea*	*	*	*	12	R
	鸚嘴科	黃羽鸚嘴	*Paradoxornis nipalensis*	*	*	(*)	4	R
		粉紅鸚嘴	*Paradoxornis webbianus*	*	*	*	23	R
	長尾山雀科	紅頭山雀	*Aegithalos concinnus*	*	*	*	25	R
	山雀科	煤山雀	*Parus ater*	*	*	(*)	13	R
		黃山雀	*Parus holsti*	*	*	*	15	R
		青背山雀	*Parus monticolus*	*	*	*	33	R
		赤腹山雀	*parus varius*	*	(*)		1	R
	鳾科	茶腹鳾	*Sitta europaea*	*	*	*	10	R
	畫眉科	紋翼畫眉	*Actinodura morrisoniana*	*	*	(*)	11	R
		頭烏線	*Alcippe brunnea*	*	*	*	60	R
		灰頭花翼	*Alcippe cinereiceps*	*	*	(*)	9	R
		繡眼畫眉	*Alcippe morrisonia*	*	*	*	79	R
		白喉噪眉	*Garrulax albogularis*	(*)	*	(*)	2	R
		畫眉	*Garrulax canorus*	*	*	*	35	R
		台灣噪眉	*Garrulax morrisoniana*	*	*	*	15	R
		棕噪眉	*Garrulax poecilorhynchus*	*	*	*	13	R
		白耳畫眉	*Heterophasia auricularis*	*	*	*	47	R
		黃胸藪眉	*Liocichla steeri*	*	*	*	33	R
		小鷦眉	*Pnoepyga pusilla*	*	*	*	16	R
		大彎嘴	*Pomatorhinus erythrogenys*	*	*	*	62	R

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Appendix II. A checklist of birds with migratory status, counties of records, and numbers of recorded sites in the southern Taiwan (continued)

目名	科名	中文名	學名	記錄縣市※			記錄調查區數	遷移屬性⊕
				嘉義	高雄	屏東		
		小彎嘴	*Pomatorhinus ruficollis*	*	*	*	78	R
		山紅頭	*Stachyris ruficeps*	*	*	*	81	R
		冠羽畫眉	*Yuhina brunneiceps*	*	*	*	41	R
		綠畫眉	*Stachyris zantholeuca*	*	*	*	41	R
	鵯科	棕耳鵯	*Hypsipetes amaurotis*			(*)		R
		紅嘴黑鵯	*Hypsipetes madagascariensis*	*	*	*	66	R
		白頭翁	*Pycnonotus sinensis*	*	*	*	85	R
		烏頭翁	*Pycnonotus taiwanus*			*	10	R
		白環鸚嘴鵯	*Spizixos semitorques*	*	*	*	60	R
	河烏科	河烏	*Cinclus pallasii*	*	*	*	8	R
	鷦鷯科	鷦鷯	*Troglodytes troglodytes*	*	*	(*)	2	R
	鶇科	小翼鶇	*Brachypteryx montana*	*	*	*	13	R
		小剪尾	*Enicurus scouleri*		*	*	4	R
		野鴝	*Erithacus calliope*	*	*	*	9	W
		藍磯鶇	*Monticola solitaria*	*	*	*	51	W R
		台灣紫嘯鶇	*Myiophoneus insularis*	*	*	*	26	R
		白尾鴝	*Myomela leucura*	*	*	*	34	R
		黃尾鴝	*Phoenicurus auroreus*	*	*	*	19	W
		鉛色水鶇	*Rhyacornis fuliginosus*	*	*	*	28	R
		灰叢鴝	*Saxicola ferrea*	*			1	V
		黑喉鴝	*Saxicola torquata*	(*)				W
		藍尾鴝	*Erithacus cyanurus*	*	*	(*)	3	W
		白眉林鴝	*Erithacus indicus*	*	*	(*)	6	R
		栗背林鴝	*Erithacus johnstoniae*	*	*	(*)	15	R
		赤腹鶇	*Turdus chrysolaus*	*	*	*	25	W
		虎鶇	*Zoothera dauma*	*	*	*	8	W R
		黑鶇	*Turdus merula*			(*)		T
		斑點鶇	*Turdus naumanni*	(*)	*	*	4	W
		白眉鶇	*Turdus obscurus*	*	*	(*)	3	W T
		白腹鶇	*Turdus pallidus*	*	*	*	14	W
		白頭鶇	*Turdus poliocephalus*	*	*	(*)	4	R
	鶯科	棕面鶯	*Abroscopus albogularis*	*	*	*	47	R
		大葦鶯	*Acrocephalus arundinaceus*	*	*	*	15	W
		雙眉葦鶯	*Acrocephalus bistrigiceps*		(*)			W
		台灣叢樹鶯	*Bradypterus alishanensis*	*	*	*	13	R
		深山鶯	*Cettia acanthizoides*	*	*	(*)	11	R
		短翅樹鶯	*Cettia diphone*	*	*	*	26	W
		短尾鶯	*Urosphena squameiceps*		(*)			T W
		小鶯	*Cettia fortipes*	*	*	*	18	R
		黃頭扇尾鶯	*Cisticola exilis*	*	*	*	9	R
		棕扇尾鶯	*Cisticola juncidis*	*	*	*	21	R

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Appendix II. A checklist of birds with migratory status, counties of records, and numbers of recorded sites in the southern Taiwan (continued)

				記錄縣市※			記錄調查區數	
目 名	科 名	中 文 名	學 名	嘉義	高雄	屏東		遷移屬性⊕
		蒼眉蝗鶯	*Locustella fasciolata*	(*)				V
		茅斑蝗鶯	*Locustella lanceolata*	(*)				T
		極北柳鶯	*Phylloscopus borealis*	*	*	*	23	W
		褐色柳鶯	*Phylloscopus fuscatus*	*			1	V
		黃眉柳鶯	*Phylloscopus inornatus*	*	*	*	17	W
		黃腰柳鶯	*Phylloscopus proregullus*		(*)			T
		斑紋鷦鶯	*Prinia criniger*	*	*	*	22	R
		灰頭鷦鶯	*Prinia flaviventris*	*	*	*	55	R
		褐頭鷦鶯	*Prinia subflava*	*	*	*	80	R
		火冠戴菊	*Regulus goodfellowi*	*	*	(*)	8	R
	王鶲科	黑枕藍鶲	*Hypothymis azurea*	*	*	*	77	R
		授帶鳥	*Terpsiphone atrocaudata*		(*)			S T R
	鶲科	白腹琉璃	*Ficedula cyanomelana*	(*)		(*)		T
		黃胸青鶲	*Ficedula hyperythra*	*	*	*	11	R
		白眉黃鶲	*Ficedula mugimaki*		(*)			W
		黃眉黃鶲	*Ficedula narcissina*			(*)		T
		紅尾鶲	*Muscicapa ferruginea*	*	*	*	7	S R
		灰斑鶲	*Muscicapa griseisticta*		(*)	(*)		T
		寬嘴鶲	*Muscicapa latirostris*	(*)	(*)			T
		黃腹琉璃	*Niltava vivida*	*	*	*	26	R
	岩鷚科	岩鷚	*Prunella collaris*	*	*		3	R
	鶺鴒科	赤喉鷚	*Anthus cervinus*	(*)	(*)	*	1	W
		樹鷚	*Anthus hodgsoni*	*	*	*	13	W
		大花鷚	*Anthus novaeseelandiae*	(*)	(*)	*	1	W
		小水鷚	*Anthus spinoletta*			(*)		W
		山鶺鴒	*Dendronanthus indicus*			(*)		V
		白鶺鴒	*Motacilla alba*	*	*	*	54	W R
		灰鶺鴒	*Motacilla cinerea*	*	*	*	58	W R
		黃鶺鴒	*Motacilla flava*	*	*	*	37	W
	伯勞科	紅尾伯勞	*Lanius cristatus*	*	*	*	71	T W
		棕背伯勞	*Lanius schach*	*	*	*	22	R
	八哥科	八哥	*Acridotheres cristatellu*	*	*	*	22	R
		灰椋鳥	*Sturnus cineraceus*			*	1	W
		灰背椋鳥	*Sturnus sinensis*		*	*	3	W
		絲光椋鳥	*Sturnus sericeus*		*		2	W
		歐洲椋鳥	*Sturnus vulgaris*	(*)				W
	啄花鳥科	綠啄花鳥	*Dicaeum concolor*	*	*	(*)	3	R
		紅胸啄花鳥	*Dicaeum ignipectus*	*	*	*	20	R
	繡眼科	綠繡眼	*Zosterops japonica*	*	*	*	95	R
	梅花雀科	斑文鳥	*Lonchura punctulata*	*	*	*	61	R
		白腰文鳥	*Lonchura striata*	*	*	*	47	R

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Appendix II. A checklist of birds with migratory status, counties of records, and numbers of recorded sites in the southern Taiwan (continued)

目名	科名	中文名	學名	記錄縣市※			記錄調查區數	遷移屬性⊕
				嘉義	高雄	屏東		
		黑頭文鳥	*Lonchura malacca*		*		1	R
	文鳥科	麻雀	*Passer montanus*	*	*	*	78	R
		山麻雀	*Passer rutilans*	*	*	*	7	R
	雀科	酒紅朱雀	*Carpodacus vinaceus*	*	*	(*)	10	R
		臘嘴雀	*Coccothraustes coccothraustes*		*		1	V
		花雀	*Fringilla montifringilla*	(*)				T W
		灰鷽	*Pyrrhula erythaca*	*	*		8	R
		褐鷽	*Pyrrhula nipalensis*	*	*	*	3	R
	鵐科	黃喉鵐	*Emberiza elegans*			(*)		W
		小鵐	*Emberiza pusilla*			(*)		T
		黑臉鵐	*Emberiza spodocephala*	*	*	*	17	W
		野鵐	*Emberiza sulphurata*			(*)		W T
		冠鵐	*Melophus lathami*	(*)				V
	籠中逸鳥	聖䴉	*Threskiornis aethiopicus*	*			3	E
		家鴿	*Columba livia*	*	*	*	9	E
		紅耳鵯	*Pycnonotus jocosus*		(*)			E
		白腰鵲鴝	*Copsychus malabaricus*	*			1	E
		大陸畫眉	*Garrulax canorus*		(*)			E
		銀耳相思鳥	*Leiothrix argentauris*		(*)			E
		爪哇雀	*Padda oryzivora*		*		1	E
		紅梅花雀	*Amandava amandava*		*		1	E
		橙頰梅花雀	*Estrilda melpoda*		*		1	E
		輝椋鳥	*Aplonis panayensis*		(*)			E
		九官	*Gracula religiosa*		(*)			E
		白尾八哥	*Acridotheres javanicus*	*	*	*	18	E
		家八哥	*Acridotheres tristis*	*	*	*	9	E
		斑椋鳥	*Sturnus contra*	(*)				E
		黑領椋鳥	*Sturnus nigricollis*	*	*		2	E
		紅領綠鸚鵡	*Psittacula krameri*	*	(*)		1	E
		虎皮鸚鵡	*Melopsittacus undulatus*		(*)			E
		巴丹鸚鵡	*Cacatua alba*		(*)			E
		戈芬氏鳳頭鸚鵡	*Cacatua goffini*		(*)			E
		目數		15		15	16	16
		科數		54		51	55	55
		種數		213		198	190	256
		目數（含文獻記錄）		15		16	16	16
		科數（含文獻記錄）		55		55	55	59
		種數（含文獻記錄）		245		259	248	319

※註：*表於該縣市有實際之觀察紀錄；(*)表僅有文獻紀錄。

⊕註：遷移屬性係參考王等人(1991)及中華民國野鳥學會(1995)的定義，各種最多列述三個類別。
其中：R表留鳥；W表冬候鳥；S表夏候鳥；T表過境鳥；V表迷鳥；E表外來種。

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探討光潤金線蛭(*Whitmania laevis*)捕食有口蓋淡水螺類之偏好

Foraging Preference of the Leech *Whitmania laevis* on Two Operculated Freshwater Snails

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摘　要

光潤金線蛭(*Whitmania laevis*)是台灣平原緩流水域中以淡水螺類爲主食之肉食性水蛭。本實驗旨在探討光潤金線蛭對共域的兩種具口蓋淡水螺類－福壽螺(*Pomacea canaliculata*)與網蜷(*Thiara tuberculata*)的捕食能力及偏好，並且嘗試了解產生捕食偏好之原因。實驗結果顯示體長7 cm以上、體重介於0.5-0.7g之光潤金線蛭均明顯偏好取食殼口長 5 mm以下的網蜷及福壽螺個體。當同時提供光潤金線蛭最適合捕食尺寸一殼口長2.7至3.7 mm的網蜷與福壽螺時，則光潤金線蛭對網蜷有明顯的取食偏好。實驗發現螺類的味道並非造成偏好之因素，反之若將福壽螺殼口蓋破壞，則光潤金線蛭捕食福壽螺的偏好便顯著上升且高於共存的網蜷。因此推論殼口蓋密合度爲造成光潤金線蛭捕食偏好之重要因子。根據實驗結果推論光潤金線蛭捕食偏好應可以最適捕食理論(optimal foraging theory)來解釋，亦即不同螺類口蓋密合度之差異影響光潤金線蛭捕食所需付出能量，連帶的使捕食經濟效益改變而使光潤金線蛭產生對口蓋密合度較差的螺類之捕食偏好。

Abstract

This study investigated feeding preference of the carnivorous leech *Whitmania laevis* on two operculated freshwater snails, *Pomacea canaliculata* and *Thiara tuberculata*, inhabiting in the same aquatic environment. Adult leeches longer than 7 cm with weights between 0.5 and 0.7g significantly preferred to feed on both species of the snails with aperture length less than 5 mm. When the snails with apertures of 2.7 to 3.7 mm long were provided, the leeches preferred to feed on *T. tuberculata* than *P. canaliculata*. This is attributable to the fact that the body of the latter prey was better sealed with operculum than that of the former prey. When the upper corner of *P. canaliculata* operculum was artificially removed, the feeding preference distinctly shifted from *T. tuberculata* to *P. canaliculata*, suggesting that the snail operculum affected the feeding preference. The feeding preference was independent of the snail body odor. The foraging preference of *W. laevis* may be explainable by "optimal foraging theory," i.e. the degree of opercular tightness of the snails affects the energy cost and foraging efficiency of the leech.

關鍵詞：光潤金線蛭、網蜷、福壽螺、捕食偏好

Key words: *Whitmania laevis*, *Thiara tuberculata*, *Pomacea canaliculata*, foraging preference

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緒言

蛭類(leech)的分類地位屬於環節動物門(Annelida)環帶綱(Clitellata)蛭亞綱(Hirudinea)。在海水或淡水、陸上潮濕的草澤地、林下底層，乃至土壤中都能發現其蹤跡(Pechenik 2000)。一般將在水中生活的種類稱爲水蛭，而行陸棲生活的種類則俗稱螞蟥。在大多數人的印象裡，蛭類多以吸血爲生，然而蛭類並非均以血液爲食。整體而言，所有的蛭類均爲肉食性，不少種類會捕食小型動物，或以死亡的動物軀體爲食；部分的蛭類則行暫時或永久性的體外寄生，以寄主體液包括血液爲食。

在蛭類各項研究課題中研究最透徹的，莫過於其唾腺分泌物所含的抗凝血能力，相關的研究成果甚至已開發成藥品作爲臨床應用治療(Salzet 2001)。另外，在神經及行爲科學相關領域中，蛭類因其單純的神經系統，研究詳盡的神經功能，及簡單而容易觀察定義的行爲模式等優點，成爲該領域中重要的實驗對象(Anholt 1986; Brönmark and Malmqvist 1986; Karrer and Sahley 1988; Brodfuehrer *et al*. 1995; Davies *et al*. 1996; Simon and Barnes 1996; Lewis and Kristan 1998; Cang and Otto Friesen 2000)。在生態領域方面，蛭類在自然界中多扮演較基層之消費者，不但其族群消長變動與許多生態系統基層的動物有相當密切的關係，其對化學物質的敏感度也被用來監測環境是否受到污染破壞(Davies *et al*. 1995; Wicklum *et al*. 1997)。

台灣的蛭類研究始於1910年代日本人Oka與Takahashi等人的採集調查與分類報告(Cited by Wu 1979)，當時有多位日本學者發表許多台灣地區新種與新紀錄種水蛭，也爲台灣地區的蛭類研究奠定基礎。但台灣光復後，蛭類的研究便停滯不前，除了1960年間美國海軍因越南戰爭駐紮台灣，爲了防止作戰時水

蛭攻擊美國士兵所做的相關研究外(Keegan and Weaver 1964; Keegan *et al*. 1964)，就只有吳錫圭教授整理相關文獻與標本後所發表的兩篇報告(Wu 1979, 1981)。在台灣登山或溯溪很容易遭到水蛭或螞蟥的攻擊，亦顯示台灣擁有豐富的水蛭資源，然而台灣的水蛭研究不但相當缺乏基礎的種類分布和生態資料，更遑論以水蛭爲實驗物種進行藥物開發或深入之相關研究。

筆者偶然在台大農場溝渠中發現有大型水蛭族群生活其中，經查閱文獻，鑑定出該種水蛭爲光潤金線蛭(*Whitmania laevis*)，並得知其爲捕食淡水螺類之肉食性水蛭(楊 1996)，由於有多種淡水螺類與光潤金線蛭共棲於同一水域中，因此本實驗主要目的想要瞭解光潤金線蛭捕食各種螺類的能力是否具有差異？是否偏好捕食其中某些螺類？如果對特定螺類具有捕食偏好，那麼產生偏好的可能原因又是什麼？前人的研究提到肉食性水蛭多依靠嗅覺尋找獵物(Simon and Barnes 1996)，是否因光潤金線蛭對螺類的氣味喜好程度有別，而導致捕食的偏好？故本實驗中選定福壽螺(*Pomacea canaliculata*)與網蜷(*Thiara tuberculata*)兩種螺作爲淡水螺類的兩代表物種，除了因爲此兩種螺的數量最多又容易取得之外，更由於兩種螺類在生態上的差異：網蜷爲台灣原生種之淡水螺，而福壽螺則是近二十年才被引進台灣的外來種，並已造成農業上巨大的損失(李 1997)。以此二種淡水螺類爲實驗物種，將可同時探討本土與外來淡水螺種受天敵壓力的差異。

在前人研究螺類之相關文獻中，多以螺重或殼長作爲測量尺寸之形質(Khalid *et al*. 2001; Michael *et al*. 2001)，然而實驗中所選用的網蜷其螺塔尖端常因磨擦而缺損，導致相近體型的網蜷其螺塔高度變動極大，易造成主要來自測量形質上的誤差，而在邱(2002)研究田螺的報告中曾測量殼口長與殼寬/殼長間的對應關係，並且提出兩者之間的確存在顯著的相關曲線，同樣的，本實驗中兩種螺類的殼口長與螺重經研究後亦發現兩者呈顯著相關(賴及陳 2003)，故本實驗選擇螺的殼口長取代螺塔高爲測量之主要形質。

材料與方法

一、 光潤金線蛭的採集與飼養

自2001年8月起至2002年3月間，從台大農場溝渠中採集到體長7 cm以上光潤金線蛭成體(圖1)6隻，每隻個體採集後在室內環境馴養二星期即參與實驗，在此期間平均每隻光潤金線蛭每星期餵食3-5隻包含網蜷、福壽螺、田螺屬螺類(*Cipangopaludina* sp.)等共域之淡水螺種。在進行實驗之前將光潤金線蛭從水中取出，拭乾體外水分後秤取每一隻個體的體重，選取體重介於0.5-0.7g的個體進行實驗。

二、 網蜷與福壽螺的採集與飼養

自2001年8月起至2002年5月間，從野外採集殼口長7 mm以下的網蜷與福壽螺(圖2a，2b)，分別飼養在盛有曝氣一天以上之除氯自來水的塑膠盒中，餵以空心菜等植物性食物並且視情況換水以維持水質清潔。

三、探討光潤金線蛭最適合捕食之網蜷或福壽螺的尺寸

將光潤金線蛭分別單獨飼養在長23 cm、寬15 cm、高7 cm的乳白色半透明塑膠加蓋容器中，保持25℃、12小時光週期變化。將網蜷或福壽螺依殼口長分成1-3 mm、3-5 mm、5-7 mm等3級大小供光潤金線蛭捕食。實驗爲期7天，隨時保持每隻光潤金線蛭與9隻螺共存，即3種尺寸的網蜷或福壽螺各3隻以供捕食，每12小時記錄被捕食後殘留的螺殼之殼口長，並計算3種不同大小的網蜷或福壽螺被

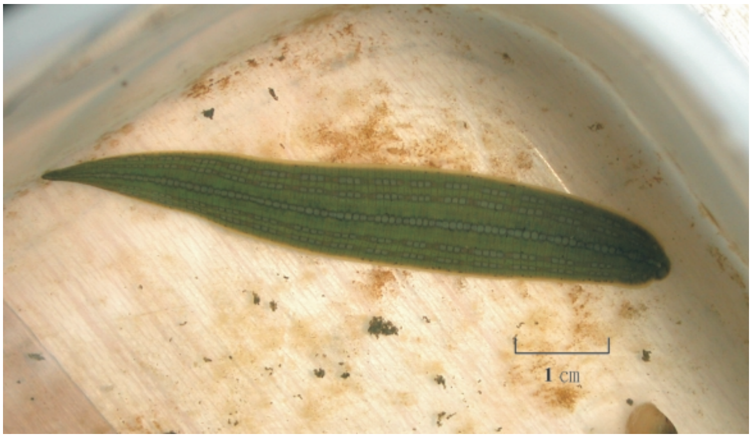

圖1. 光潤金線蛭。

Fig. 1. *Whitmania laevis.*

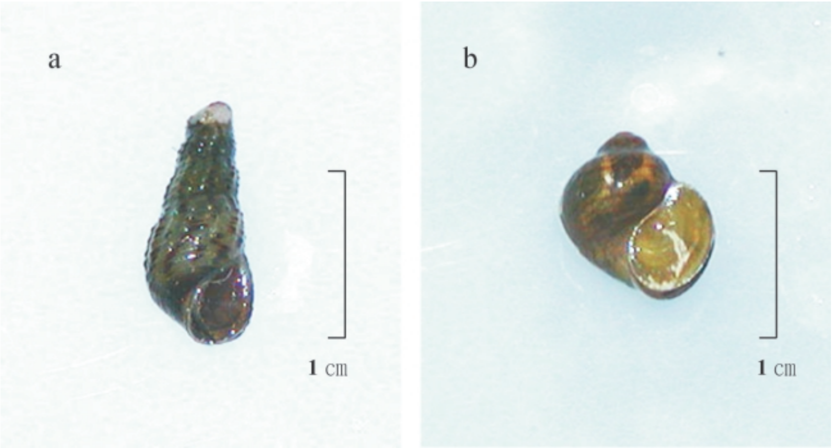

圖2. a. 網蜷；b. 福壽螺。

Fig. 2. a. *Thiara tuberculata*； b. *Pomacea canaliculata*.

捕食之個數，記錄完畢再依照被捕食螺類個體之等級大小加以補充，以維持每一隻光潤金線蛭隨時均有3隻3種大小等級的螺供其捕食選擇。實驗所得數據採ANOVA統計分析，並以Duncan檢定法測試3種不同尺寸範圍之網蜷或福壽螺被光潤金線蛭捕食的數量是否具有顯著差異。另外，爲精確求出適合光潤金線蛭捕食之網蜷或福壽螺尺寸，分別將被捕食之網蜷或福壽螺殼口長數值以Sturges氏資料處理法分組計算每組平均數量，以找出最適合光潤金線蛭捕食之網蜷或福壽螺尺寸範圍(沈 2001)。

四、探討光潤金線蛭捕食螺類之偏好

依照前一實驗結果，隨時提供每隻光潤金線蛭最適合捕食的尺寸之網蜷與福壽螺各5隻。實驗記錄僅計算每隻實驗個體捕食網蜷與福壽螺之數量，其他均與前一實驗相同。數據處理以Paired T-test檢定分析。

五、探討光潤金線蛭偏好捕食網蜷的因素

(一)口蓋密合度之影響

將所有進行實驗的光潤金線蛭依照亂數表隨機分爲兩組，每隻光潤金線蛭均提供最適合捕食的尺寸之網蜷與福壽螺各4隻，但其中一組所提供的福壽螺不經任何處理，具完整殼口蓋；另一組提供的福壽螺口蓋則以解剖剪刀剪除殼口蓋尖端部分。由於該部分口蓋與螺體游離的面積較大，只要拉住口蓋將解剖剪刀從口蓋尖端向中央稍微移動，便可以剪去口蓋的尖端部分而幾乎不傷害到螺的肉體，同時造成口蓋缺損導致閉合時無法完全蓋住殼口(圖3)。實驗方式與記錄如同探討捕食偏好之實驗。數據分析採卡方檢定法測試兩組之間福壽螺與網蜷分別被捕食數量，以及兩組內分別被光潤金線蛭捕食的網蜷與福壽螺之數量是否有顯著差異，以瞭解殼口蓋的密合度是否會影響光潤金線蛭的捕食偏好。

(二)氣味的偏好

將光潤金線蛭放在長23 cm、寬15 cm、高7 cm的保麗龍盒中，內面鋪上一層保鮮膜，並且在兩側之短邊底部接上直徑2 cm、長25 cm可拆卸之透明塑膠管與直角轉接管，裝置內盛800 ml曝氣除氯水(圖4)。起初先封住兩端透明塑膠管通向保麗龍盒的開口以確保實驗的光潤金線蛭個體僅能在中央的保麗龍盒中活動。待其在盒中安靜且無企圖進入任一側透明塑膠管之顧忌後，將以紗網包起內含相同數量，且爲最適合光潤金線蛭捕食之尺寸之網蜷或福壽螺的網袋，依亂數表(左或右)隨機且同時放入左右兩端之直角轉接管中，並浸入水面下，然後開啓保麗龍盒中通向兩側透明塑膠管之開口。當實驗個體在10分鐘內碰觸到任一包有螺個體的紗網包即結束實驗，若10分鐘內沒有碰觸到任一端的紗

圖3. 口蓋具缺損之福壽螺(係以解剖剪將口蓋上緣即箭頭處切除)。

Fig. 3. The golden apple snail (*Pomacea canaliculata*) with the upper portion of operculum (arrow) removed.

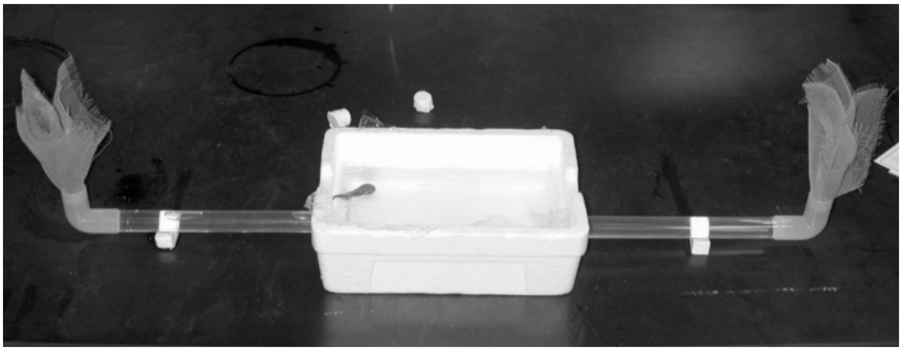

圖4. 氣味偏好實驗裝置。

Fig. 4. Experimental design for the odor preference test of snails. Testing snails inside the screen bags were put in the L-shape tubes at two terminals.

網包則終止該次實驗並且不列入紀錄。每隻光潤金線蛭每天僅進行一次實驗以避免學習行爲的產生。爲避免前一實驗個體留下的分泌物影響下一實驗個體的實驗，每次實驗後倒去盒內之水，拔去透明塑膠管，清洗保麗龍盒並換上新的盒內保鮮膜與兩側的透明塑膠管。空白實驗如同上述步驟，但隨機選擇其中一側的內有螺個體之紗網包不放入。實驗記錄每次光潤金線蛭起始位置較爲接近的螺種、選擇所需時間與選擇之螺種，實驗所得數據以卡方檢定法測試。

結　果

一、 成熟光潤金線蛭最適合捕食之網蜷或福壽螺的尺寸

以ANOVA分析三種不同尺寸等級大小之網蜷或福壽螺被光潤金線蛭(n=6)捕食的數量，發現此三種尺寸的網蜷或福壽螺被捕食的數量均具有顯著差異(p<0.01)，經Duncan測驗法檢定後得知：不論是網蜷或是福壽螺，光潤金線蛭均傾向捕食殼口長5 mm以下的個體(表1)。爲瞭解光潤金線蛭偏好捕食之網蜷與福壽螺的精確尺寸，將所有被捕食網蜷或福壽螺之殼口長資料以Sturges氏資料處理法分組後，發現網蜷殼口長2.5-3.25 mm、福壽螺殼口長2.72-3.58 mm爲光潤金線蛭捕食數量最多的尺寸範圍(圖5、圖6)。爲方便往後實驗的進行與測量，選取殼口長介於2.7-3.7 mm間之網蜷與福壽螺以進行後續光潤金線蛭之捕食螺類偏好實驗。

二、 光潤金線蛭偏好捕食之螺類

當同時提供光潤金線蛭(n=6)最適合捕食的尺寸(殼口長2.7-3.7 mm)之網蜷與福壽螺各5隻時，實驗結果顯示平均每日每隻光潤金線蛭捕食網蜷的數量爲1.43±0.57隻，遠高於捕食福壽螺的數量0.57±0.27隻，以T-test檢定得知當光潤金線蛭與同爲最適捕食尺寸之網蜷和福壽螺共存時，其捕食選擇明顯偏好網蜷(p<0.01)。

三、 光潤金線蛭偏好捕食網蜷的因素

(一)口蓋密合度的影響

實驗結果顯示，若同時提供同爲最適合捕食尺寸之網蜷與殼口蓋缺損的福壽螺，則

表1.不同尺寸的網蜷及福壽螺被光潤金線蛭捕食的數量

Table 1. Numbers of *Thiara tuberculata* and *Pomacea canaliculata* (mean±S.D.) with three different aperture lengths (1-3, 3-5 and 5-7 mm) preyed by *Whitmania laevis*

Snails	Aperture lengths of the snails		
	1-3 mm	3-5 mm	5-7 mm
Thiara tuberculata	0.8±0.06	0.6±0.06	0.09±0.03[1/]
Pomacea canaliculata	0.63±0.05	1.0±0.12	0.17±0.04[1/]

[1/] Significantly difference from the other two aperture lengths at significant level of 1% (ANOVA, *p*<0.01).

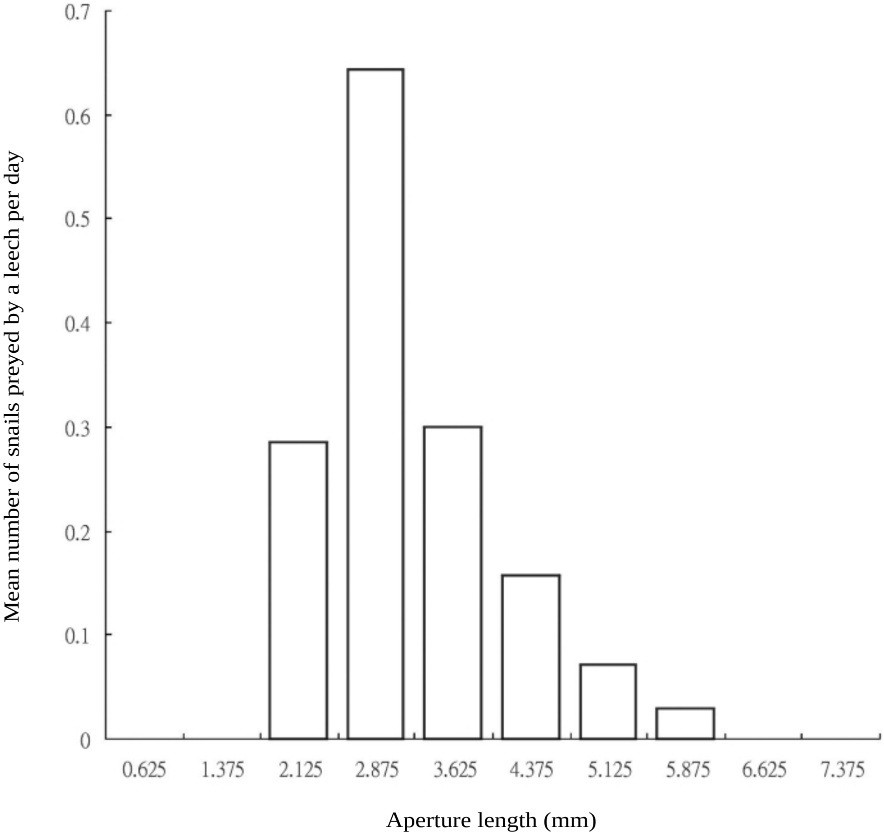

圖5. 光潤金線蛭捕食不同大小網蜷之數量分布。

Fig. 5. An aperture length frequency distribution of *Thiara tuberculata* preyed by *Whitmania laevis.*

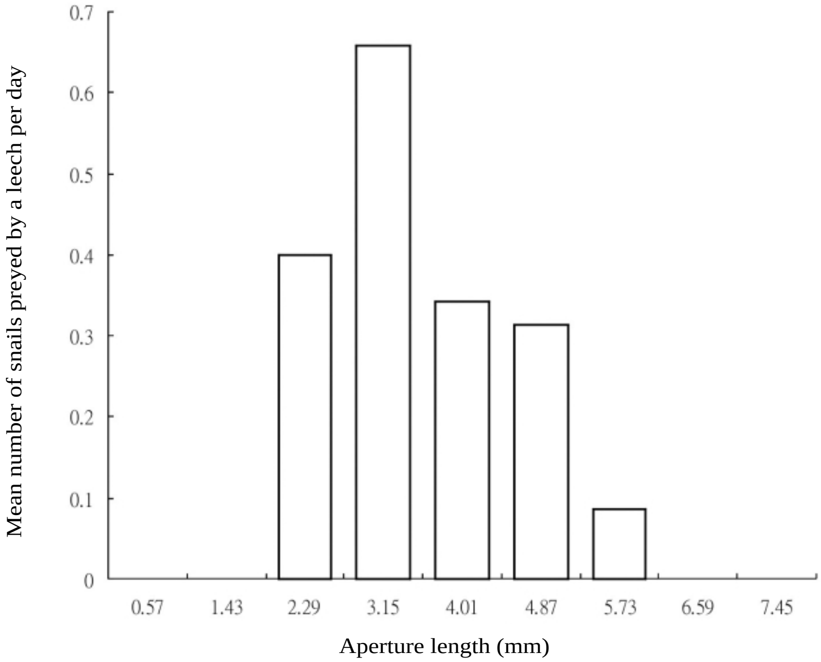

圖6. 光潤金線蛭捕食不同大小福壽螺之數量分布。

Fig. 6. An aperture length frequency distribution of *Pomacea canaliculata* preyed by *Whitmania laevis*.

光潤金線蛭(n=3)捕食福壽螺的數量顯著較網蜷爲高(p<0.01)；反之，若同時提供同爲最適合捕食尺寸之網蜷與殼口蓋完整的福壽螺，結果則與前述之實驗二相同，即光潤金線蛭(n=3)依然偏好捕食網蜷(p<0.05)。另外，將兩組不同處理之實驗數據作同種螺類被捕食數量統計檢定，得知兩不同條件之福壽螺被光潤金線蛭捕食的數量具有顯著差異(p<0.01)，而網蜷被捕食數量則沒有差異(圖7)。

(二)螺種氣味之影響

由空白實驗結果發現光潤金線蛭(n=6)的確能夠以嗅覺作爲線索找到獵物個體(p<0.01)，但氣味偏好實驗之結果顯示光潤金線蛭對網蜷或福壽螺的氣味並不具任何偏好。

討論

光潤金線蛭爲捕食淡水螺類之肉食性水蛭，由本實驗觀察得知光潤金線蛭的捕食行爲是採將頭部從螺的殼口處深入螺殼中攻擊內臟並且逕行呑食。由於光潤金線蛭無法對螺殼造成物理上的破壞，只能由殼口侵入殼中，但所捕食的螺類具有殼口蓋保護，對光潤金線蛭捕食會造成一定程度的阻礙。Sommer等人(1999)曾提到捕食者與獵物體型上的互動，會導致捕食者進行捕食行爲時，偏好挑選與其體型相對應的某一尺寸範圍的獵物，獵物體型過大或過小均不利於捕食行爲的進行，甚至會因爲獵物體型過大使得捕食者拒絕捕食。而依據最適捕食理論(optimal foraging theory)的解釋，認爲雖然體型較大的獵物能夠提供較多的能量報酬，但是捕食獵

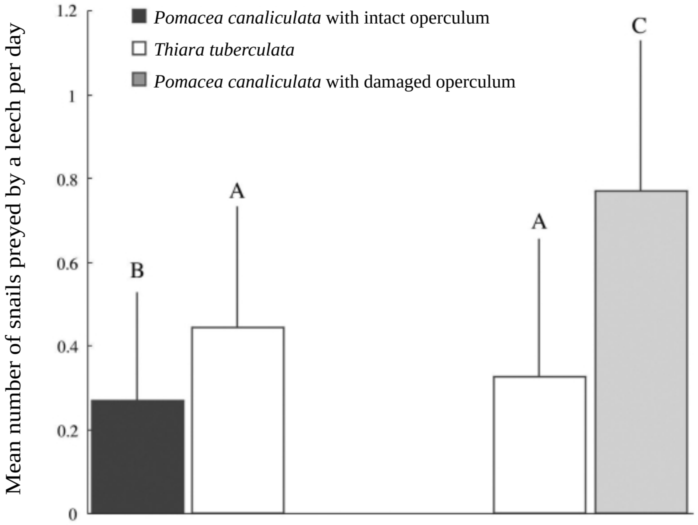

圖7. 光潤金線蛭對同時提供之網蜷及完整或缺損口蓋福壽螺的捕食偏好。直條上方之字母表Duncan檢定之結果。

Fig. 7. The foraging preference of *Whitmania laevis* on two simultaneously presented snails, *Thiara tuberculata* and *Pomacea canaliculata* with an intact or damaged operculum. The letters above the bars mean the result of the Duncan test.

物之能量耗損亦隨獵物體型增大而升高，所能獲得的淨能量反而小於捕捉較小的獵物之所得，因此捕食者偏好獵捕某一尺寸範圍的獵物(Sommer *et al*. 1999)。本實驗結果發現光潤金線蛭成體所捕食的網蜷與福壽螺均傾向偏好殼口長5 mm以下的個體，又兩種螺類被光潤金線蛭捕食的數量皆以殼口長3 mm左右爲最多，且兩種螺類被捕食之各尺寸數量分布曲線圖形亦相近。由於尺寸小的螺其殼口過小，光潤金線蛭頭部不易鑽入捕食，而大的螺殼口雖較大，但相對口蓋的閉合力量也較大，因此當光潤金線蛭欲捕食較大的螺，雖可獲得較多的食物，但也必須付出較大的力氣，以能量觀點未必划算。所以我們推論光潤金線蛭偏好捕食殼口長3 mm左右的螺，此一現象應與最適捕食理論有所關連。

當相等數量的網蜷與福壽螺共存，且兩者均爲最適合光潤金線蛭捕食之尺寸(殼口長2.7-3.7 mm)時，光潤金線蛭對網蜷的確具有明顯的捕食偏好。由觀察發現，因收起殼口蓋後網蜷的殼口蓋無法完全將殼口密合，在殼口內緣會有裸露的螺體；而福壽螺的口蓋則可以在螺體收入殼中之後完全與殼口密合。因此殼口蓋密合度的差異應會造成光潤金線蛭對不同種螺類的捕食難易度之差異，進而對捕食偏好造成影響。實驗結果明顯支持此一推論：即在福壽螺與網蜷共存的狀況下，若共存的福壽螺殼口蓋具有缺損，光潤金線蛭的捕食偏好明顯改變爲傾向捕食福壽螺，若福壽螺殼口蓋依然完整，則捕食偏好亦維持傾向網蜷。

另一方面，氣味偏好實驗的結果顯示，光潤金線蛭對於兩種螺類的氣味並沒有顯著的偏好，且亦不傾向選擇實驗開始時距離較

近的該側螺種。在餵食時常觀察到光潤金線蛭雖然表現出類似Simon and Barnes(1996)提到之嗅聞行爲，但單憑嗅覺似乎無法精確定位獵物的位置，且在接近獵物的過程中亦表現嘗試捕食路徑上的各種螺類空殼之行爲。因此猜測光潤金線蛭在覓食時無法以嗅覺精確找尋獵物，必須依賴與獵物個體之接觸才能正確感知獵物的位置。此一現象與同爲肉食性水蛭之*Nephelopsis obscura*比較，該種水蛭同樣以嗅覺偵測獵物，但亦必須至接觸獵物後才能確認獵物位置與種類(Anholt 1986)之情形實有相似之處。這可能是因爲光潤金線蛭其生活環境中共域的獵物數量通常較爲豐富，而獵物活動力又低於光潤金線蛭本身的活動能力，故僅需以嗅覺大略定位獵物方向後便開始搜尋獵物，而毋須精確定位獵物個體的位置，因此發展出來自己的捕食方式；又光潤金線蛭所表現出來的行爲亦可能採取以氣味確定環境中獵物的存在之後，選擇最佳路徑以增加與獵物接觸之機會的搜尋模式，唯上述討論均必須進一步實驗方能加以確定。

由本研究一系列的實驗顯示，光潤金線蛭捕食共存水域中的螺類並沒有先天上的偏好，極可能是採被動嗅聞獵物發出的氣味，再跟隨氣味散發的方向搜尋並捕捉接觸到的獵物，或是逢機的與附近發出氣味的獵物接觸。由於不同種類的獵物散發的氣味並不影響其選擇偏好，因此唯有在與不同獵物個體接觸後，光潤金線蛭捕食該個體的經濟效益或捕食困難度才是決定捕食與否之關鍵。在本次實驗中也的確觀察到符合的結果：光潤金線蛭接觸獵物開始進行捕食行爲後，若在過程中發現獵物體型不適合捕食或是捕食該個體經濟效益並不大，則放棄捕食該個體獵物並且離開，以繼續尋找適合的獵物。因此當網蜷與福壽螺共存時，基於網蜷的殼口蓋不能完全封閉殼口，即使將殼口蓋縮回亦難逃捕食，使得光潤金線蛭捕食網蜷成功的機會較大，較少發生放棄捕食網蜷而轉移至其他目標之情形(私人觀察)；相較之下福壽螺在緊閉殼口蓋之後，光潤金線蛭勢必得耗費更多的能量才能突破殼口蓋的防護攻擊螺體，捕食的困難度相較於網蜷爲高，若環境中有其他捕食機會可選擇，光潤金線蛭可能便會嘗試轉移捕食目標而放棄福壽螺。或許在此二情形的交互影響之下，導致同爲光潤金線蛭偏好捕食的尺寸之網蜷與福壽螺共存時，光潤金線蛭明顯的偏好捕食網蜷，而較不捕食福壽螺。

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以電腦模擬取樣探討比特立希法與方區法在森林調查上之比較研究

A Comparison of Bitterlich and Quadrate Sampling Methods for the Forest Inventory Using Computer Simulation

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摘　要

本研究主要以北東眼山天然闊葉樹林型大面積全面調查所得之實測資料，應用電腦模擬取樣技術，針對方區法及比特立希法分別以變異度法、信賴區間法及適合度測驗等三種方法進行比較，以供日後植群調查之參考。

在變異度法及信賴區間法之比較上，顯示相同的取樣面積下，方區法推估優勢度所需設置之理論樣區數明顯多於推估密度之所需，而比特立希法在取樣上之準確性，受角度尺之比例是否適當所影響。在本研究中，當角度尺比例小於1：40，則產生低估，且低估之情形隨著角度尺之比例愈小更加明顯。藉由適合度測驗發現，比特立希法較小比例角度尺對優勢度之低估，主要來自於對較大直徑級林木產生低估所致；而對密度之低估，則主要係來自於對較小直徑級林木產生低估所致。

Abstract

The quadrate sampling method and the Bitterlich sampling method were compared by computer simulation, using the tree census data obtained from the broad-leaved forest at Mt. North Tungyen. Based on variability and confident interval, for the quadrate method the number of sampling plots required for estimating dominance was much higher than that for density. For the Bitterlich method the sampling accuracy was affected by appropriateness of angle gauge; underestimation of both dominance and density was resulted when the angles were smaller than 1:40 and the underestimation increased with the decrease in angle. Based on the result of fitness test, the underestimation of dominance was mainly caused by bigger diameter classes of trees, while the underestimation of density was by smaller diameter classes.

關鍵詞：比特立希法、方區法、森林調查、電腦模擬取樣

Key words: Bitterlich method, quadrate method, forest inventory, computer simulation sampling

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緒 言

森林爲人類最重要再生資源之一，爲提供正確之資訊，以供經營決策之依據，必須對森林之組成、蓄積量之變化加以調查。然而由於森林面積廣闊，加上台灣地處亞熱帶，植群類型繁多、結構複雜，同時因受時間、人力、經費之限制，並無法全面調查，而必須藉由取樣調查以獲取所需之資料。然而因所設樣區之數量、面積，以及形狀等均會影響取樣費用、時間與取樣之準確性。因此，如何在有限之經費與時間下，迅速地獲得正確的森林資源資料，實爲林業工作人員所迫切需要解決之問題。

早期森林學者在植被調查上多採用樣區法(plot sampling method)，即設置某種形狀、面積及數目之樣區加以調查，此亦被稱爲面積法(area method)(Cottam *et al*. 1953)。然樣區法之實行，必須於林分內圍設樣區邊界，並實際量測邊界長度，此一步驟在下層灌木繁多之林下，常費去許多時間。在調查上，圍設樣區所費時間常不亞於實際調查植被之時間，且面積樣區有邊界效應(marginal effect)，即位於邊界線上樣木之取捨問題(劉及蘇 1989)，故許多學者乃積極去探討不用面積法，而同樣能正確獲得森林資源資料的調查方法之可行性(Grosenbaugh 1952; 陳及蔡 1980)。

比特立希法(Bitterlich variable radius method)係由奧人Walter Bitterlich於1948年根據角度、距離與面積比例之幾何原理所設計，經由美國南方林業試驗場Grosenbaugh(1952)加以修正並推廣應用，初時稱爲無樣區調查法(plotless method)。此法具有省時、省工、設備簡便等多重優點，但在台灣實際應用上並不普遍，探究其原因，或因地形、植群型態等限制因子不易克服，或爲對於此調查方法之生疏，而主觀認爲固定樣區法較爲可靠，而加以排斥。

然而，當Grosenbaugh於美國提出無樣區取樣之後，許多林業調查人員開始對樣區法及比特立希法進行比較，在不考慮花費因子時，大多就不同之樣區設置及林分結構，來比較兩種方法在推估密度、斷面積、材積之

準確度(Sukwong *et al*. 1971; Matern 1972)，所得之結果亦大多指出樣區法欲得到與比特立希法相同之準確度，則樣木必定多於比特立希法，亦即比特立希法較具有效性，且認爲樣區法對於推估有關株數之介量有較高之準確度，而比特立希法對於推估斷面積有關之介量有較高之準確度(Wensel and John 1969)；即樣區法對密度的推估較具無偏性，而比特立希法對優勢度之推估較具無偏性。

以往有關此兩種不同取樣方法之比較研究中，甚少涉及植群調查中樹種組成及重要值推估之準確性，而比特立希法在台灣闊葉樹林調查上之實用性、最佳斷面積指數及樣點數等之相關研究更罕被涉獵。

台灣之森林多分布於崇山峻嶺，面積遼闊，除小面積或特殊目的採用全部調查外，一般殆採用取樣調查，因此何種取樣調查方法能取得較具代表性之植群介量，實有加以評估之必要；同時目前在生態調查上所使用之方法殆衍自歐美等地區，其植群構造遠較地處熱帶與亞熱帶之交的台灣爲單純，因此這些調查方法的實用性亦有重新加以檢視之必要。本研究之目的即是藉由大面積全面調查所得之實測資料，應用電腦模擬取樣技術，針對樣區法中最常被應用的方區法與比特立希法做多方面之比較，並以原始植群資料爲標準，評估兩種取樣方法之準確性，以供日後植群調查之參考。

研究區域環境及植物社會概述

本研究區位於霧社正北方6 km之北東眼山區(東經121°07'，北緯24°05')，隸屬南投縣仁愛鄉行政區。北東眼山山頂地勢平坦，海拔高約2,050m，爲惠蓀林場內東峰溪集水區東側稜線的最高點。本研究之樣區設置於山頂附近之天然闊葉林，平均坡度爲10°。

依桑士偉氏氣候分類，可將本區歸爲AB$_2$區，爲暖溫重濕型氣候(陳 1957)。此區北方有蘇澳到豐原東西走向之雪山山脈的阻擋，不受東北季風之影響，而在南部有玉山山脈及阿里山山脈的阻擋，又免除西南季風之影響，故環境較穩定，冬季略爲乾旱(林等 1968)。

本研究區內，喬木層以卡氏櫧(*Castanopsis carlesii*)最占優勢，其它還有苦扁桃葉石櫟(*Lithocarpus amygdalifolius*)、豬腳楠(*Machilus thunbergii*)等；灌木層以紫珠葉泡花樹(*Meliosma callicarpaefolia*)、深山野牡丹(*Barthea barthei*)占優勢；地被層以華中瘤足蕨(*Plagiogyria euphlebia*)及倒葉瘤足蕨(*Plagiogyria dunnii*)占優勢。1.9044 ha樣區內共記錄到49種、4,028株木本植物，胸高斷面積爲79.82 m^2/ha，植株密度爲2,115 株/ha，平均胸徑21.9 cm，最大之胸徑爲248 cm(樹種爲卡氏櫧)。此研究區之植物社會屬於演替後期之植物社會。

研究方法

一、野外植群調查

本研究主要目的在評估方區法與比特立希法於植群取樣中，對密度與優勢度推估之準確性，並探討此兩種方法應用於台灣闊葉樹林取樣調查時之實用性及比特立希法之最佳斷面積指數，因此植群取樣工作必須以不同面積之樣區法以及不同斷面積指數之比特立希法，對同一處植群進行重複取樣。唯若如此進行，則不但將使得調查工作繁瑣、無效率，更容易造成調查資料的人爲誤差而造成錯誤的結論，Lindsey *et al*. (1958)曾指出藉由林木位置圖進行電腦模擬取樣，可使取樣得以正確、一致，避免樹種鑑定的不一致，更重要的是它可提供符合統計要求之足夠樣本數。因此本研究採用繪製調查區域林木位置圖，以進行電腦模擬取樣。

在比特立希法的使用上，坡度將使得原本在水平距離應被計入之立木被忽略，因此若要克服此一坡度的限制，則角度尺之比例必須乘上cos θ (θ 爲林地坡度)。台灣之森林多位於坡度變化急劇之地形，若同時考慮坡度校正的問題，將使得研究主題變大，資料的分析更複雜，且人爲誤差之機率更大。本研究主要之目的在評估兩種方法對植群取樣之準確度，因此野外調查區域選擇一處坡度較緩、廣大且較符合均質條件的植物社會，以避免坡度效應之產生。

在台灣之闊葉樹原始林欲取得如此研究地點是有些困難，而最終選擇北東眼山山頂地勢平坦處(平均坡度10°)設置138m x 138m之植群調查區，外圍之訂定是利用羅盤儀定出四邊，在此大樣區內植物調查以維管束植物爲限，凡直徑超過1 cm之木本植物記錄其樹種、胸徑及相對直角座標值，以便製作林木相對位置圖供電腦模擬取樣使用。野外調查於1997年2月進行。

二、電腦模擬取樣

無論在方區法或比特立希法之實際應用時，皆有發生邊界效應之可能，而本研究之電腦模擬取樣，樣區(樣點)位置之選取採逢機選擇，爲避免樣區(樣點)設置位置太接近原始調查林分之邊界造成接近邊界區之林木入選機率較預期小，在整個大樣區之植物社會爲均質之前提下，此模擬程式將整個1.9044 ha之大樣區，以"球形樣區"之觀念進行取樣。所謂"球形樣區"即是在取樣樣區之邊界超出整個1.9044 ha大樣區之範圍時，將超出右邊界(左邊界)之取樣部分，取樣自左邊界(右邊界)內部之植群，而超出上邊界(下邊界)之取樣部分，取樣自下邊界(上邊界)內部之植群，如此不但能使整個1.9044 ha內之植群資料能充分地被取樣利用，且能避免邊界效應影響兩種方法於取樣時之準確性。球形觀念樣區完成後，即以各種邊長的方形樣區以及各種斷面積指數的比特立希法進行取樣。在本研究中，樣區法共設置19種樣區面積，樣區邊長自4m至40m每級增加2m；而比特立希法之角度尺比例亦選擇19種，比例由1：10到1：100，分母每次增加5。

(一)方區法之模擬取樣

於球形觀念樣區中，逢機選擇方形樣區之中心點，依中心點直角座標(x_1, y_1)，逐一檢視各林木之直角座標(x_2, y_2)，若方區法之邊長訂爲am，則當$|x_1 - x_2| \leqq \frac{a}{2}$ m且$|y_1 - y_2| \leqq \frac{a}{2}$ m時，則此林木入選爲a^2m^2面積方區法之樣木。依各種取樣樣區數分別計算各樹種之密度及優勢度。計算如下：

密度(density) = 某樹種株樹之總和 ／所調查之總樣區數

優勢度(dominance) = 某樹種胸高斷面積之總和／所調查之總樣區數

相對密度(relative density) =(某樹種之密度／所有樹種密度之總和) x100%

相對優勢度(relative dominance) = (某樹種之優勢度／所有樹種優勢度之總和) x100%

(二)比特立希法之模擬取樣

此方法樣點位置之選取，亦是自球形觀念樣區中逢機選擇一中心點，再依中心點之直角座標(x_1, y_1)，逐一檢視各林木之直角座標值(x_2, y_2)，若比特立希角度尺之比例爲1：a，某胸徑爲Am之立木距離中心點Bm，則當$\frac{A}{B} \geqq \frac{1}{a}$ 時，此立木入選爲1：a角度尺之樣木，而B之計算由公式 $\sqrt{(x_1-x_2)^2+(y_1-y_2)^2}$ 而得。依各種取樣樣點個數分別計算各樹種之密度及優勢度。計算公式如下：

優勢度(dominance) = (於所有樣點中該樹種入選之株樹／總樣點數)x BAF值

各種比例(1：a)角度尺BAF值=($\frac{1}{4 \times a^2}$) x10000m^2(每公頃之斷面積)

密度(density)= 某樹種之優勢度／於所有樣點中該樹種入選爲樣木之平均胸徑斷面積

相對密度(relative density) = (某樹種之密度／所有樹種密度之總和)x100%

相對優勢度(relative dominance) = (某樹種之優勢度／所有樹種優勢度之總和)x100%

三、分析方法

(一)變異度法

將19種樣區面積之方區法及19種角度尺比例之比特立希法，各取樣50次求取密度與優勢度之平均值及變方，而後利用平均數之標準偏差(standard error of mean, $\sigma／\sqrt{n}$)與平均數(mean, M)之比值，即變異度(variability, V)= $\frac{\sigma／\sqrt{n}}{M}$，以此關係式尋求符合某一精確度的理論樣區數(n)。

欲求某一精確度所需之樣區數，則令變異度之值等於某一主觀決定之變異度，在介量平均數及其變方已知下，即可求出各種不同樣區面積及角度尺比例所應設置之理論樣區數。本研究訂定變異度爲0.1，也就是欲尋求各樣區面積對調查地區植物之密度及優勢度兩介量達到變異度小於0.1的精確度時，該樣區面積或角度尺比例級應設置之理論樣區數。

(二)信賴區間法

由於 $P\left(x-\frac{t_{(n-1,\ 1-\alpha)}S_x}{\sqrt{n}}<\mu<x+\frac{t_{(n-1,\ 1-\alpha)}S_x}{\sqrt{n}}\right)=1-\alpha$

μ 爲母體平均值

x爲樣本平均值

n爲取樣個數

S_x爲樣本標準偏差

1-α爲顯著水準

$t_{(n-1,\ 1-\alpha)}$爲在自由度n-1及顯著水準1-α下之Student's t值

因此信賴區間一半的寬度爲 $w=\frac{t_{(n-1,\ 1-\alpha)}S_x}{\sqrt{n}}$

而$E(w^2)= t^2_{(n-1,\ 1-\alpha)}\frac{V(a)}{n}$ 。

此處$E(w^2)$爲信賴區間一半寬度平方之期望值。

而$V(a)$爲樣區面積爲a時取樣所得之變方。

有了信賴區間寬度、各樣區面積級取樣之變方及樣區個數之關係後，再以該面積級取樣50次所得之變方，作爲變方之理論值，並以1.9044 ha大樣區內每木調查之結果爲母體平均值之理論值，在本研究中以母體平均值之20％作爲信賴區間一半之寬度，如此就只剩下n及$t^2_{(n-1,\ 1-\alpha)}$兩個變數，而此兩變數之關係爲$t_{(n-1,\ 0.95)}=1.96+3.22(n-1)^{-1.07}$ (O'regan and Richard 1973)，因此樣區數(n)之求算可以先以任一數值代入$t_{(n-1,\ 0.95)}$中，若所求得之n不符合其關係式，則再以n值代入 $t_{(n-1,\ 0.95)}$中，如此輾轉求算直到此兩變數相符，則可求出不同樣區面積下，對於密度、優勢度進行推估時，欲獲得母體平均值20%之準確度，所需設置之樣區數(n)。

在比特立希法中，角度尺比例值與樣點數之關係，亦是以相同的理論求得，其中$V(a)$以1：a之角度尺取樣50次所得之變方作爲理論值。因此，不同角度尺比例下，對於密度、優勢度進行推估時，在一定的準確度下，其理論樣點數(n)亦可算出。

(三)適合度測驗

將1.9044 ha原始調查林分內之植物組成每5 cm劃爲一直徑級，除去無林木分布之直徑級，共計37個直徑級，按照直徑級分別統計各直徑級內之密度與優勢度組成，再藉由各種取樣面積級之方區法及不同角度尺比例的比特立希法所獲得之各直徑級之密度、優勢度組成推估值，與原始調查林分中各直徑級之介量進行適合度測驗，用以判斷各種取樣處理對調查林分直徑級分布推估之準確度，並可從中探討此兩種取樣方法對各直徑

級樣木之選取與樣區面積(角度尺比例)間之關係。

結果與討論

一、變異度法

方區法各種取樣面積及比特立希法各種角度尺比例所獲得之密度、優勢度兩植物介量平均數與其變方，以及此兩種植物介量欲達到變異度小於0.1時之最少理論樣區數如表1、表2。

從表1中可觀察到方區法於相同之樣區面積時，欲使密度及優勢度兩介量推估值之變異度達到小於0.1之標準，則推估優勢度所需設置之樣區數幾乎爲推估密度時所需樣區數的6倍，並且由兩介量取樣所得之平均數，亦可以明顯看出，即使樣區面積僅有16 m^2，其對密度之推估值與原始調查林分之密度值亦僅有5％之誤差。由此數據可以知道方區法用於密度之推估，實爲一既準確又有效率的調查方法，但是在斷面積之推估上，必須當樣區面積大於144 m^2才能有較準確的推估值。在同一精確度之要求下，密度所需設置的樣區數小於優勢度所需者，此結果與許(1995)之研究結果吻合。探究其原因，乃是由於此部分理論樣區數之求算，是基於樣本變異係數之大小來決定應該設置多少個樣區，而方區法由於取樣機率與樣木出現之頻度成正比(probability proportional to frequency，P.P.F.取樣)，並不受樣木胸高斷面積大小所影響，因此所取得之樣木胸高斷面積變異係數較大可想而知；密度由於僅有計算株數，因此變異係數明顯較優勢度爲小，而所需設置之樣區數亦較推估優勢度時所需之樣區數爲少。

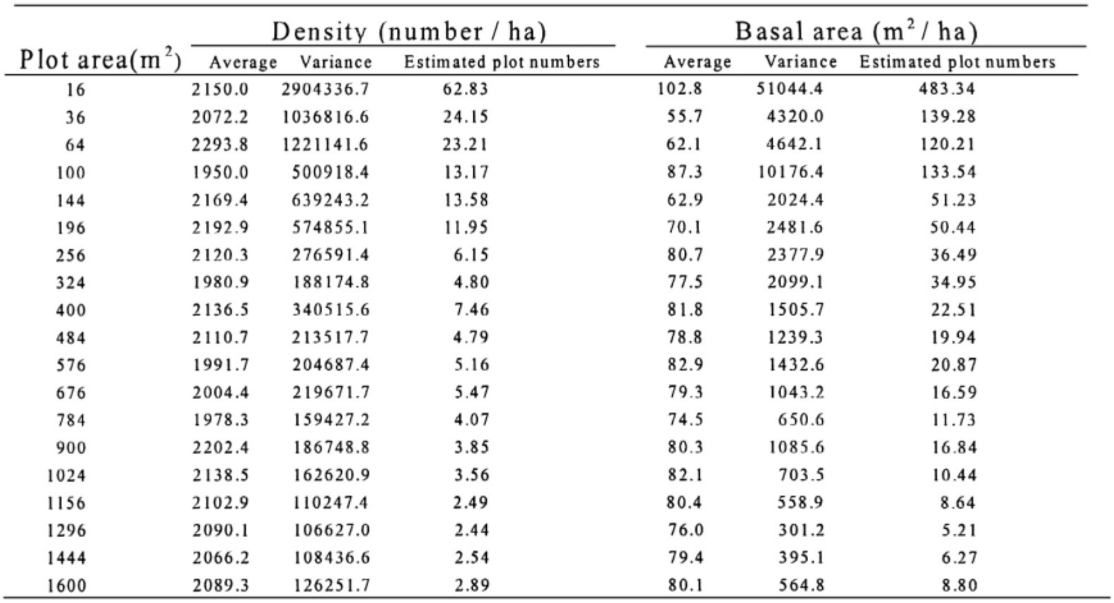
比較表1、表2，我們可以看見比特立希法對密度推估值之變異度雖明顯比方區法小得許多，然而由表2中卻可發現比特立希法所獲得之密度值與原始調查林分之實際值差異甚大，約造成了95%的低估，這種低估的情形，實乃歸因於比特立希法密度之求算方法，因爲比特立希法密度之求算乃由斷面積間接求得(參照比特立希法密度求算公式)，而比特立希法原本就是一種樣木入選機率與樣木胸徑大小成正比之取樣方法(probability proportional to size，P.P.S.取樣)，入選之樣木幾乎都是胸徑較大之林木，且調查林分中直徑分布多集中於16 cm以下之小徑木，由這些胸徑較大樣木之胸高斷面積來反推立木之株數，因此造成低估密度。此法推估密度的變異數會明顯小於方區法的原因有二，除了是因爲比特立希法斷面積之求算爲平均入選樣木株數乘上角度尺之斷面積指數，因此變異數原本就較方區法來得小，致使由斷面積求算而得之密度值變異數亦較小外，另外一個原因亦如上所述，用來反推密度之入選樣木爲變異數不大之大徑木平均值。因此，在此處若僅由變異度之標準來判斷，而忽略了此法對密度推估值的偏誤，恐怕就會錯誤地以爲如表2所列之樣點數就足以有效地推估林分之密度，卻忽略了此處理論樣區數之求算爲$(n)=\frac{\sigma^2}{(vM)^2}$ (參照第83頁，樣區數之求算)，而由於比特立希法如前面所述之原因致使平均數之變異數(σ^2)較方區法爲小，因此即使求算出之平均數(M)明顯低估，得到之理論樣區數也不會與方區法有明顯的差異，然而此處所求得之理論樣區數並不具實質上之意義。

在斷面積的推估方面，於表2中可看見隨著角度尺的比例變小，比特立希法對斷面積推估值的變異數亦隨之降低，然而低估的現象卻也更加顯著。

如前所述，比特立希法因取樣原理的不同，致使求算優勢度平均數之變異數本來就較方區法爲小，而此處樣區數之決定乃是基於平均數之可靠性或精確度可視其變異數之大小而評估之，然而由此法所求算出之優勢度平均數呈現隨角度尺比例縮小而遞減，顯

表1. 各面積級方區法求得之密度與斷面積及其理論樣區數

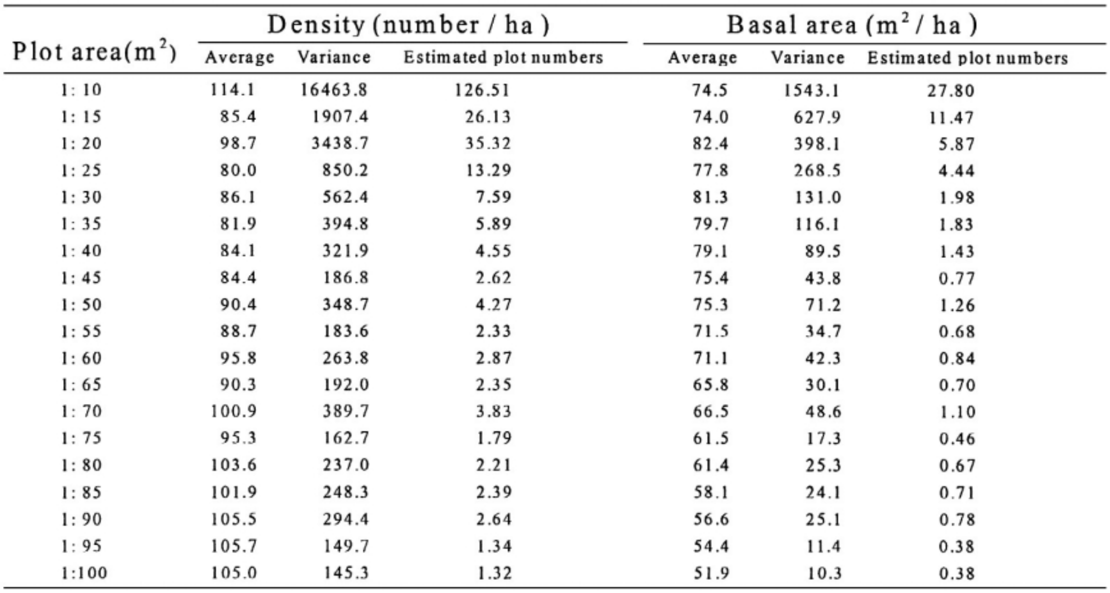
Table 1. Densities, basal areas, and plot numbers estimated at different plots of Mt. North Tungyen broad-leaved forest by computer simulation with the quadrate sampling method



Plot area(m^2)	Density (number / ha)			Basal area (m^2 / ha)		
	Average	Variance	Estimated plot numbers	Average	Variance	Estimated plot numbers
16	2150.0	2904336.7	62.83	102.8	51044.4	483.34
36	2072.2	1036816.6	24.15	55.7	4320.0	139.28
64	2293.8	1221141.6	23.21	62.1	4642.1	120.21
100	1950.0	500918.4	13.17	87.3	10176.4	133.54
144	2169.4	639243.2	13.58	62.9	2024.4	51.23
196	2192.9	574855.1	11.95	70.1	2481.6	50.44
256	2120.3	276591.4	6.15	80.7	2377.9	36.49
324	1980.9	188174.8	4.80	77.5	2099.1	34.95
400	2136.5	340515.6	7.46	81.8	1505.7	22.51
484	2110.7	213517.7	4.79	78.8	1239.3	19.94
576	1991.7	204687.4	5.16	82.9	1432.6	20.87
676	2004.4	219671.7	5.47	79.3	1043.2	16.59
784	1978.3	159427.2	4.07	74.5	650.6	11.73
900	2202.4	186748.8	3.85	80.3	1085.6	16.84
1024	2138.5	162620.9	3.56	82.1	703.5	10.44
1156	2102.9	110247.4	2.49	80.4	558.9	8.64
1296	2090.1	106627.0	2.44	76.0	301.2	5.21
1444	2066.2	108436.6	2.54	79.4	395.1	6.27
1600	2089.3	126251.7	2.89	80.1	564.8	8.80

表2. 比特立希法各種比例角度尺求得之密度與斷面積及其理論樣點數

Table 2. Densities, basal areas, and plot numbers estimated at different plots of Mt. North Tungyen broad-leaved forest by computer simulation with the Bitterlich sampling method



Plot area(m^2)	Density (number / ha)			Basal area (m^2 / ha)		
	Average	Variance	Estimated plot numbers	Average	Variance	Estimated plot numbers
1: 10	114.1	16463.8	126.51	74.5	1543.1	27.80
1: 15	85.4	1907.4	26.13	74.0	627.9	11.47
1: 20	98.7	3438.7	35.32	82.4	398.1	5.87
1: 25	80.0	850.2	13.29	77.8	268.5	4.44
1: 30	86.1	562.4	7.59	81.3	131.0	1.98
1: 35	81.9	394.8	5.89	79.7	116.1	1.83
1: 40	84.1	321.9	4.55	79.1	89.5	1.43
1: 45	84.4	186.8	2.62	75.4	43.8	0.77
1: 50	90.4	348.7	4.27	75.3	71.2	1.26
1: 55	88.7	183.6	2.33	71.5	34.7	0.68
1: 60	95.8	263.8	2.87	71.1	42.3	0.84
1: 65	90.3	192.0	2.35	65.8	30.1	0.70
1: 70	100.9	389.7	3.83	66.5	48.6	1.10
1: 75	95.3	162.7	1.79	61.5	17.3	0.46
1: 80	103.6	237.0	2.21	61.4	25.3	0.67
1: 85	101.9	248.3	2.39	58.1	24.1	0.71
1: 90	105.5	294.4	2.64	56.6	25.1	0.78
1: 95	105.7	149.7	1.34	54.4	11.4	0.38
1:100	105.0	145.3	1.32	51.9	10.3	0.38

然並非每一種比例的角度尺所求得之優勢度平均數皆具代表性，因此由變異度之標準來求算比特立希法之理論樣區數僅能代表這些樣區數已經能使取樣所得之變異度小於0.1，但無法表示所得到之介量平均數是否準確。然而，若是在適當的角度尺比例之前提下，由表2中可以明顯看出比特立希法用於調查單位面積內之胸高斷面積和，實爲一有效率之調查方法(1：30至1：40之角度尺於1.9044 ha內所需設置之樣點數不到二個)，但是在實際之野外調查時，究竟何種角度尺方爲“適當”？Sukwong等人(1971)認爲角度尺比例之選擇，受調查林分之林木空間分布、直徑級分布、密度組成等之綜合影響。由於本研究之研究區域僅分布於北東眼山之闊葉樹林型，因此文中僅針對此研究區域之植群狀況提出討論。

在使用比特立希法時，角度尺比例之選擇如前所述，實際上受到調查林分之林木空間分布、直徑級組成等所影響，此乃由於比特立希法之取樣原理，是將調查林分內林木之胸高斷面積依角度尺之比例等比例擴大，再以這些擴大之虛圓去推估單位面積內與此相同大小之虛圓究竟應有多少個，而獲得單位面積內之胸高斷面積和。因此，使用不同比例之角度尺，產生之擴大虛圓大小不同，而各直徑級林木之擴大虛圓亦不同，再加上林木於空間分布上之歧異性，這些因子之綜合影響，致使並非各種比例之角度尺皆能適用於不同直徑級大小之林木，而唯有當某直徑級林木依特定比例之角度尺所擴大之虛圓方能符合其實際之空間分布，亦始能獲得最準確之推估值。

在此處我們僅能初步認爲比特立希法用於北東眼山闊葉樹林型之斷面積推估，角度尺比例不宜超過1：40，否則會有低估的現象。各種比例角度尺欲得到變異度小於0.1之標準所需樣區數列於表2中。

由於僅藉由變異度之標準來判斷理論樣區數會有以上的情況發生，因此以下理論樣區數之求算，將以介量平均數之眞値(即原始調查林分每木調查所得之値)做爲評估之標準。

二、信賴區間法

利用方區法之各種取樣面積以及比特立希法各種角度尺比例，所獲得之密度與優勢度兩植物介量之平均數與其變異數，以及推估此兩種植物介量欲達到以眞値(即爲原始調查林分每木調查所得之植物介量)的20％爲信賴區間一半之精密水準，所需設置之理論樣區數列於表3及表4。

從表3中，可觀察到方區法於相同之樣區面積時，欲使密度及優勢度兩介量推估値達到相同之精密水準，則推估優勢度所需設置之樣區數明顯多於推估密度所需設置之樣區數，這與以變異度0.1爲標準求算最適樣區數所得之結果大致上相同(表1)。

而在表4中，我們可以看見比特立希法對密度之推估値欲達到此一精密水準，所需設置的樣區數幾乎都不到一個，然而由t値表中可以發現表4中推估密度所需設置的樣區數(n)與理論t値，並不符合。此乃因爲t分布的使用必須樣本之平均數爲常態分布，而由於比特立希法密度之求算實際上是由入選樣木平均斷面積推算而得，斷面積之推算又是由平均入選樣木株數乘上角度尺之斷面積指數而得，因此所得到之密度平均數實爲一經過多次平均後趨中性甚高之平均値，並不符合常態分布。

因此藉由此法求算比特立希法推估密度所需之理論樣區數，並不符合統計上之立論，所得到之結果亦不具任何意義。

而於表4中亦可發現比特立希法斷面積推估値之變異數明顯小於方區法(表3)，其原因如前所述；然而，若是在適當的角度尺比例

表3. 方區法利用信賴區間20%求取樣區數結果一覽表

Table 3. Densities, basal areas, and plot numbers estimated at 20% confident levels at different plots of Mt. North Tungyen broad-leaved forest by computer simulation with the quadrate sampling method

	Density (number / ha)				Basal area (m^2 / ha)			
Plot area(m^2)	Average	Variance	t-value	Plot numbers	Average	Variance	t-value	Plot numbers
16	2075	3721938.7	1.99	82.31	60	17511.1	1.97	266.17
36	1950	993606.7	2.07	23.85	114	43799.0	1.96	662.27
64	2028	733906.7	2.11	18.29	86	9346.1	1.98	143.20
100	2028	488179.6	2.19	13.01	61	2647.6	2.02	42.36
144	2051	497844.6	2.18	13.21	87	7392.2	1.98	113.78
196	2240	560592.3	2.16	14.56	86	4828.9	1.99	75.21
256	2342	529010.4	2.17	13.88	74	1784.5	2.05	29.40
324	2053	262304.5	2.36	8.11	92	3885.9	2.00	61.03
400	2142	224220.4	2.41	7.27	84	1555.3	2.06	25.95
484	2148	378792.9	2.24	10.64	77	1436.5	2.07	24.17
576	2088	151870.5	2.58	5.65	76	1432.5	2.07	24.11
676	2172	197870.1	2.46	6.68	73	677.6	2.19	12.74
784	2001	154243.5	2.57	5.70	75	830.3	2.15	15.05
900	2282	222670.1	2.41	7.23	87	1317.2	2.08	22.38
1024	2011	118466.8	2.72	4.87	81	556.7	2.24	10.90
1156	2158	158851.2	2.56	5.80	84	681.9	2.19	12.80
1296	2168	113170.7	2.74	4.75	81	531.26	2.25	10.52
1444	1992	132105.9	2.65	5.19	74	323.23	2.41	7.33
1600	2082	111026.2	2 .75	4.70	80	315.45	2.42	7.21

表4. 比特立希法利用信賴區間20%求取樣區數結果一覽表

Table 4. Densities, basal areas, and plot numbers estimated at 20% confident levels at different plots of Mt. North Tungyen broad-leaved forest by computer simulation with the Bitterlich sampling method

	Density (number / ha)				Basal area (m^2 / ha)			
Angle gauge	Average	Variance	t-value	Plot numbers	Average	Variance	t-value	Plot numbers
1: 10	147	21185.5	4.38	2.313	81	1793.1	2.05	29.53
1: 15	96	3266.2	10.83	1.387	76	613.2	2.21	11.76
1: 20	89	2700.9	1.96	0.062	80	442.9	2.30	9.17
1: 25	81	790.5	1.96	0.023	80	279.8	2.46	6.65
1: 30	84	587.7	1.96	0.013	81	83.1	3.22	3.40
1: 35	80	405.6	1.96	0.012	77	108.5	3.01	3.84
1: 40	87	206.2	1.96	0.001	80	45.7	3.83	2.66
1: 45	86	206.9	1.96	0.001	77	49.4	3.75	2.73
1: 50	86	191.9	1.96	0.001	73	52.7	3.69	2.78
1: 55	88	238.5	1.96	0.011	71	38.9	4.02	2.52
1: 60	91	247.5	1.96	0.012	69	46.5	3.81	2.67
1: 65	98	281.1	1.96	0.011	69	40.8	3.97	2.55
1: 70	96	283.9	1.96	0.011	65	35.1	4.20	2.40
1: 75	99	200.2	1.96	0.002	63	22.5	4.84	2.11
1: 80	103	163.8	1.96	0.002	61	17.2	5.43	1.93
1: 85	105	380.8	1.96	0.012	59	33.7	4.26	2.37
1: 90	101	150.7	1.96	0.001	55	12.3	6.25	1.77
1: 95	110	265.5	1.96	0.011	56	19.1	5.22	1.99
1:100	106	210.7	1.96	0.001	52	14.9	5.93	1.82

之前提下，同樣地亦可以由表4中發現，比特立希法用於調查單位面積內之胸高斷面積和，實爲一有效率之調查方法(1：30至1：40之角度尺於1.9044 ha內所需設置之樣點數不到4個)。

三、適合度測驗

爲更清楚地瞭解方區法與比特立希法之各種不同取樣處理，對原始調查林分直徑級組成的取樣代表性，以及造成比特立希法較小比例角度尺對優勢度產生低估的原因，特將方區法與比特立希法各種不同取樣面積(角度尺比例)各取100個樣區(樣點)之取樣結果與原始調查林分直徑級組成之適合度測驗卡方值摘錄於表5-8中。由於在比特立希法中藉由各入選樣木之平均胸高斷面積來反推林分之平均密度，會造成對密度明顯低估(約95%)，因此在此部分中密度之求算方式乃改採Grosenbaugh(1952)之方式，以各直徑級之平均胸高斷面積反推各直徑級之密度進而求算全林分之密度。

由於方區法之取樣爲P.P.F.取樣，因此林木株數愈多之直徑級入選機率愈大，而原始植群之直徑分布多集中在胸徑40 cm以下(約占95％)，因此可發現當樣區面積小於64 m^2時，無論在密度或優勢度皆會對胸徑較大之直徑級產生偏估，而這種偏誤將隨著樣區面積加大或樣區數增加，使得這些入選機率較低之直徑級之樣木個數達到一定之取樣標準，才能克服。

在表6中，可發現由比特立希法依各直徑級入選樣木株數所求得之各直徑級優勢度，與原始調查林分之各直徑級優勢度組成有顯著的相似性(x^2≦10)，然而亦如同先前不分直徑級求算優勢度所得之結果一樣(表2)，當角度尺比例小於1：40時會對優勢度產生低估的現象。以下謹就表6之結果來探討此一現象產生的原因。

表5. 各面積級方區法於密度及優勢度取樣結果與原始林分組成之適合度測驗卡方值(DBH≧1)

Table 5. The chi-square values derived from the fitness test between density and dominance at different plots of Mt. North Tungyen broad-leaved forest obtained by the census and those by computer simulation with the quadrate sampling method (DBH≧1)

plot	16	36	64	100	144	196	256	324	400	484	576	676	784	900	1024	1156	1296	1444	1600
chi-square for density	203.1	93.1	46.9	22.9	30.7	21.3	14.1	13.4	19.8	6.6	4.3	5.5	3.1	3.4	3.9	2.9	2.1	2.0	1.1
chi-square for dominance	85.1	244.3	31.1	20.2	40.5	18.4	13.9	8.1	10.1	3.6	5.0	6.6	1.8	2.9	4.9	2.9	2.1	1.4	1.5

表6. 各種比例尺比特立希法於密度及優勢度取樣結果與原始林分組成之適合度測驗卡方值(DBH≧1)

Table 6. The chi-square values derived from the fitness test between density and dominance at different plots of Mt. North Tungyen broad-leaved forest obtained by the census and those by computer simulation with the Bitterlich sampling methods at different angle gauges (DBH≧1)

Angle gauge	1:10	1:15	1:20	1:25	1:30	1:35	1:40	1:45	1:50	1:55	1:60	1:65	1:70	1:75	1:80	1:85	1:90	1:95	1:100
chi-square for density	258.2	255.9	98.6	127.1	71.3	55.4	8.6	16.1	4.1	73.4	56.7	57.2	54.8	106.6	82.0	124.8	76.2	45.6	40.5
chi-square for dominance	9.1	5.2	2.1	2.4	1.0	0.4	0.9	1.5	2.0	2.9	4.2	5.3	6.4	7.3	8.7	10.7	11.5	12.2	14.1

表7. 各面積級方區法於密度及優勢度取樣結果與原始林分組成之適合度測驗卡方值(DBH≧5)

Table 7. The chi-square values derived from the fitness test between density and dominance at different plots of Mt. North Tungyen broad-leaved forest obtained by the census and those by computer simulation with the quadrate sampling method (DBH≧5)

plot	16	36	64	100	144	196	256	324	400	484	576	676	784	900	1024	1156	1296	1444	1600
chi-square for density	278.5	69.2	29.7	32.1	36.7	15.9	14.9	9.6	4.9	6.1	5.9	4.5	5.4	5.4	10.3	2.7	3.8	1.8	2.3
chi-square for dominance	272.7	57.4	22.8	26.4	40.1	10.3	14.2	7.7	4.5	6.1	5.1	4.6	3.9	5.7	9.1	2.7	3.1	1.4	2.9

表8. 各種比例尺比特立希法於密度及優勢度取樣結果與原始林分組成之適合度測驗卡方值(DBH≧5)

Table 8. The chi-square values derived from the fitness test between density and dominance at different plots of Mt. North Tungyen broad-leaved forest obtained by the census and those by computer simulation with the Bitterlich sampling methods at different angle gauges (DBH≧5)

Angle gauge	1:10	1:15	1:20	1:25	1:30	1:35	1:40	1:45	1:50	1:55	1:60	1:65	1:70	1:75	1:80	1:85	1:90	1:95	1:100
chi-square for density	65.9	17.3	37.9	6.1	9.7	3.3	5.8	28.3	15.1	4.1	15.7	4.8	5.5	6.6	14.5	8.3	8.0	10.1	14.6
chi-square for dominance	5.3	3.6	2.0	1.2	0.7	0.9	0.8	1.3	2.2	3.0	4.0	5.0	6.6	8.0	9.4	9.8	11.7	12.8	14.3

由於比特立希法取樣爲取樣機率與樣木胸徑大小成比例之取樣法(P.P.S.取樣)，因爲大徑木之理論樣區面積大於小徑木之理論樣區面積，所以大徑木被抽選爲樣木的機率大於小徑木，然而隨著比特立希角度尺之比例縮小，入選之小徑木所占的比例亦隨之增加。綜合以上二項比特立希取樣法之取樣本質，再觀察表5之結果，特將角度尺比例值分爲二個階段以方便解釋，當比特立希角度尺之比例大於1：40時，由於比特立希法對樣木之選擇乃根據林木胸徑與林木離觀測點距離之比例關係，因此實際上角度尺比例值之選擇與林分內空間分布及直徑級分布有其使用上之限制，例如：使用1：10之角度尺，則直徑1 cm之林木，必須當觀測者至立木之距離小於10 cm方得入選爲樣木，然而實際上林分內之空間分布，1 cm之林木其所需之最小生存空間可能遠大於100 cm^2，因此當這種限制發生時，則會產生對小徑木優勢度之低估，而這種低估的情形將會隨著角度尺比例變小而獲得改善，例如：使用1：100之角度尺，則直徑1 cm之林木，必須當觀測者至立木之距離小於1m方得入選爲樣木，而或許實際上林分內之空間分布，1 cm之林木所需之最小生存空間小於1 m^2，因此當使用1：100之角度尺，則低估優勢度之情況將可獲得改善。

當角度尺比例小於1：40後，隨著角度尺比例愈小，小徑木入選爲樣木之機率提高，而那些相對密度較小的大直徑級林木，入選爲樣木之機率亦隨之提高，但是由於這些大徑木原本在植群組成中就僅占少數，因此當角度尺之比值小於某界限，這些大徑木之入選機率已達到最高而不再提升，而相對上小徑木之入選機率卻仍是逐漸提升，因而造成大徑木之低估。這或許就是Husch(1955)於研究結論中提出使用較大角度尺可減少對大徑

木產生低估之眞正原因。

Stage and Rennie(1994)卻認爲使用較小比例角度尺對大徑木產生低估之原因，乃是由於大徑木可被量測到之距離遠，而容易造成樣木應否入選之誤判。Husch(1955)亦認爲就理論而言，比特立希法各種不同比例角度尺之數學關係，應該是一恆定的關係，因此不同比例角度尺所獲得之結果應該不受角度尺比例所影響，而實際上會產生較小比例角度尺的低估現象，可能是由於較小比例之角度尺所形成之理論樣區面積較大，因此容易造成樣木是否入選之誤判，以及樣木間互相遮蔽之誤差。本研究中樣木之選取乃採電腦模擬取樣，各樣木是否入選均經過電腦計算選擇，沒有誤判之虞，因此於本研究中對樣木誤判應不是造成大徑木優勢度低估之眞正原因。

在密度推估方面，由於此部分之密度乃由各直徑級之優勢度除以各直徑級入選樣木平均胸高斷面積所得，因此結果類似推估優勢度之結果，在角度尺比例大於1：40時，僅對較大之直徑級較具準確性，而當角度尺比例小於1：40時，則對較小之直徑級較具有準確的推估性，對較大之直徑級產生低估，只是由於比特立希法對密度值之求算，實際上是由入選樣木胸高斷面積平均值推算而得，因此只要優勢度推估值有偏誤，密度亦產生偏誤，而且愈小的直徑級偏誤愈明顯(因爲相同的優勢度，直徑級愈小密度愈大)。就因爲如此，當角度尺比例大於1：40時，雖然對大徑木之密度較具推估性，然而因爲此時比特立希法對小徑木之優勢度產生偏估，而造成對密度的明顯偏估。

當角度尺比例小於1：40時，雖然如同前面所述，會對大徑木之優勢度產生低估，然而這並不是對密度產生偏估的主要原因，對密度產生偏估的原因絕大部分還是來自對小於5 cm直徑級之密度低估。

爲了驗證造成比特立希法於密度上之偏估是否來自胸徑小於5 cm之林木，於表7及表8中，方區法各種樣區面積取樣與比特立希法各種角度尺比例取樣僅針對胸徑大於5 cm以上之林木，由取樣所得結果與原始調查林分組成之適合度測驗中，可以發現方區法所得之結果無論是在密度或是優勢度上，其與包含5 cm胸徑以下之取樣結果在卡方值上並沒有明顯的差異(表5及表7)，此乃如同前面所述，方區法爲P.P.F.取樣，因此不去考慮5 cm以下之林木，並不會去影響到其它直徑級入選爲樣木之機率。

在比特立希法中，當取樣僅考慮5 cm以上之林木所得到之結果，在優勢度之卡方值上並沒有與包含胸徑5 cm以下之取樣結果有明顯的差異(表6及表8)，此乃因爲胸徑5 cm以下之林木優勢度爲2.98，僅占總體優勢度之3%，因此即使有偏估之現象，對卡方值並沒有明顯的影響。然而就密度而言，我們可以發現若僅考慮胸徑大於5 cm以上之林木，那麼由卡方值來看，只要當比特立希角度尺比例小於1：15時對原始調查林分之各直徑級密度組成就具取樣代表性(表8)。因此，由此可知造成比特立希法對密度產生低估之原因，實際上來自於對小徑木密度之低估。

Stage and Rennie(1994)認爲使用比特立希法必須限定一最小入選樣木胸徑，小於此等胸徑之樣木必須藉由樣區法取樣，方能獲得準確之推估值，否則由於這些小徑木之理論樣區面積太小而容易造成誤差，而對結果產生高估。然而由本研究之結果發現，若是針對優勢度來看，造成優勢度低估之主要原因還是來自於角度尺之比例選擇不當(角度尺比例小於1：40)，有無考慮小徑木對結果並沒有明顯影響。在密度之推估值有無考慮小徑木就有明顯差異，當不去限定最小入選樣木胸徑(本研究限定爲5 cm)時，會對密度造成低估的現象，結果與Stage and Rennie(1994)所述有所差異，而這種低估之現象，當限定最小入選樣木胸徑後即可獲得改善。

綜合以上所言，比特立希法使用上發生之誤差，並非單純由角度尺之比例大小所造成，實際上還牽涉了調查林分內之林木空間分布與直徑級分布，Barrett and Allen(1966)就曾說過不同比例角度尺所產生的誤差乃是因林木分布所致，並沒有理論說那種角度尺誤差最大。因此有部分學者研究中即針對研究地區之林分組成、結構提出選擇角度尺之比例應根據每樣點之平均入選樣木株數。例如Snedaker and Snedaker(1984)建議在紅樹林生態調查中，以每測點7-10株樣木能得到最佳的準確性，而Meyers and Beers(1968)及Kulow(1966)則指出使用比特立希法時對於角度尺比例之選擇，應選擇每測點平均入選樣木株數10-15株之角度尺所得之結果最爲準確。若是依本研究之結果來看，欲獲得較準確之推估值，每樣點之平均入選樣木株數必須超過7.4株。然而卻也有部分學者認爲選擇角度尺之比例大小時，事先設定入選樣木之株數，將會造成結果的偏誤(Schreuder *et al*. 1981)。唯實際上於野外調查中，使用比特立希法所造成對優勢度之偏估，多半來自使用者缺乏經驗，而且通常每14株樣木就有1株屬於判斷不易之邊際木(以目視無法判定其是否入選之林木)(Deitschman 1956)，因此比特立希法於實際上之應用，角度尺比例之選擇仍不宜過小。

結　論

一、無論是變異度法或信賴區間法在決定兩種取樣方法之最適樣區數上，於相同樣區面積之前提下，方區法在推估優勢度所需設置之理論樣區數明顯多於推估密度之所需；而比特立希法對於優勢度之推估所需設置之樣點數，明顯少於方區法，以效率來考量，實不失爲一好方法，然而究竟何種比例之角度尺方爲“適當”？這又受到調查林分之林木空間分布、直徑級分布、密度組成等綜合影響，並無一定之準則，然而若是角度尺之比例選擇不當，那麼將會對優勢度產生嚴重的低估。以本研究之研究區域而言，當角度尺比例小於1：40，則產生低估之情形，且低估之情形隨著角度尺之比例愈小，更加明顯。比特立希法對於密度求算，係以所量取到全部樣木之平均胸高斷面積加以推估，故不具調查林分平均胸高斷面積之代表性，因此產生明顯之低估，且由於取樣機率之不同，使得由此法求得之密度變異數明顯小於方區法，然因與原始林分有明顯之差異，因此無法藉由此法求得有意義之理論樣點數。

二、藉由方區法與比特立希法取樣結果與原始調查林分各直徑級組成之適合度測驗，可發現當樣區面積小於64 m²時，方區法對於密度及優勢度皆會對胸徑較大之直徑級產生偏估，而這種偏誤將隨著樣區面積加大，或樣區數增加使得這些入選機率較低之直徑級之樣木個數達到一定之取樣標準，才能克服。比特立希法於角度尺比例小於1：40所產生對優勢度之低估，實乃來自於對較大直徑級產生之低估，而產生低估之原因乃是由於隨著角度尺比例縮小，致使大徑木入選爲樣木之機率相對上變小。另由結果亦可發現若不考慮胸徑小於5 cm之直徑級，比特立希法亦可對調查林分之直徑級組成有良好之推估性，而造成對小於5 cm之直徑級密度之低估，亦可能是由於林木之空間分布及直徑級分布對比特立希法使用上產生之限制。

三、比特立希法在密度之求算上，若以各直徑級之平均胸高斷面積求算各直徑級之密度，進而求算全林分之密度，較以各樹種之平均胸高斷面積求算各樹種之密度，進而求算全林分之密度，其結果較接近眞值，此乃由於比特立希法之密度求算乃以間接之方式求得，而在天然闊葉樹林中各樹種內之林木個體間之胸徑大小差異甚大，因此用以推算各樹種密度之樣木胸高斷面積無法有效代表調查林分中各樹種之實際平均胸高斷面

積，因而發生偏誤之情形。由此觀之，若欲由比特立希法求算調查林分內之各樹種密度組成，則調查林分內各樹種種內個體之胸徑大小差異不得過大，然而這在天然林中並不可能出現；而另一種情形，則是必須於調查時將入選之各樹種再分爲若干直徑級，再依各直徑級之胸高斷面積反推各直徑級之密度，進而求算各樹種之密度，然而這勢必造成額外的野外調查工作及室內的資料分析，而與比特立希法省工、省時之立意相違背。

四、由本研究證實，由於比特立希法之取樣原理符合斷面積之取樣機率，因此在適當角度尺比例之前提下，獲得之優勢度推估性較方區法爲佳，而方區法之取樣原理則較符合密度之取樣機率，因此獲得之密度推估性較比特立希法爲佳。

五、於實際應用時，比特立希法仍有其使用上之問題，例如構造複雜林分內視覺之遮蔽、邊界木之判定、坡度校正等，這些問題將耗費許多人力與時間，並造成調查結果之偏誤。本研究係以電腦模擬取樣，在沒有人爲誤差之前提下，對此兩種取樣方法進行比較評估。於實際應用時，這些問題仍須加以考量。

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關刀溪森林生態系殼斗科植物之物候週期

The Phenological Phases of Fagaceae in the Guandaushi Forest Ecosystem

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摘 要

本研究於2000年9月至2003年8月間觀測關刀溪森林生態系內12種殼斗科植物的物候期，其中僅栓皮櫟是落葉性植物。三年之調查結果發現，抽芽期大多在2至4月。開花期則較爲歧異，其中反刺櫧、川上氏櫧、青剛櫟、三斗石櫟、短尾葉石櫟、南投石櫟、菱果石櫟與栓皮櫟8種每年開花一次，火燒柯、小西氏石櫟與石櫟3種一年內有兩次或兩次以上的開花期，而圓果青剛櫟在2001與2002年分別開花2次及1次。所有觀察物種的果熟期均在8至12月，而落果期都在9月至隔年2月間。關刀溪森林生態系中殼斗科植物所呈現的物候週期爲一年一循環或兩年一循環。

Abstract

Phenological phases of 12 species of trees belonging to the family Fagaceae in Guandaushi forest ecosystem of Taiwan were investigated monthly from September of 2000 to August of 2003. *Quercus variabilis* was found to be a deciduous tree, whereas the other 11 species were the evergreen trees. All the species had the same budding season from February to April but differed in blooming season. Eight species, *Castanopsis eyrei, Castanopsis kawakamii, Cyclobalanopsis glauca, Pasania hancei, Pasania harlandii, Pasania nantoensis, Pasania synbalanos,* and *Quercus variabilis,* bloomed once a year, while the other three species, *Castanopsis fargesii*, *Pasania konishii*, and *Pasania glabra*, bloomed twice to several times a year. Fruits of all the species became mature in August to December and fell in September to next February. The phenological phases of Fagaceae showed a cycle per year or per two years.

關鍵詞：關刀溪森林生態系、殼斗科、物候週期、台灣

Key words: Gaundaushi forest ecosystem, Fagaceae, phenological phases, Taiwan

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緒言

殼斗科植物在全球共有9屬，約有900種(Judd *et al*. 1999)，大部分產於北半球之溫帶及亞熱帶地區。台灣原生殼斗科植物有6屬43種(劉等 1994)，爲台灣中低海拔森林組成樟櫟群叢之主要樹種。在關刀溪地區殼斗科植物有5屬14種(呂及歐 1996)。

物候現象主要是受到遺傳因子及環境因子影響，不同的植物有不同的物候現象(林等 1997)。同一種植物在不同的生育地，物候現象可能不同；甚至不同的單株也會呈現不同的物候現象(何 1968；呂 1990；Seghieri *et al*. 1995)。台灣對於物候的調查大多是針對一個地區的所有植物來做觀察紀錄(章 1950；何 1968，1971；廖及何 1970；呂 1990；紀 1995；林等 1997；伍 1999)，針對惠蓀林場特定物種來做研究的有：林志銓(1999)就惠蓀林場內木荷及大頭茶的開花物候加以研究；曾麗蓉(1999)於惠蓀林場研究台灣榕的開花物候；梁立明與陳明義(2000)在關刀溪森林生態系調查台灣二葉松與台灣五葉松的物候現象。

全球環境持續變遷，長期生態研究(LTER)已經成爲重要的課題，物候現象可作爲氣候指標，亦可反映植物生育地外在環境之差異，以及每年四季之提早、遲延及異常等，因此植物物候學研究爲長期生態研究中不可或缺的一環(梁及陳 2000)。殼斗科植物在台灣森林具有重要的地位，惟尙缺乏殼斗科植物的完整物候資料。本研究針對關刀溪森林生態系內12種殼斗科植物的物候期加以研究，希望能由物候期的資料提供長期生態研究更豐富的訊息。

材料與方法

一、研究地區

研究區位於南投縣仁愛鄉中興大學實驗林之關刀溪森林生態系，爲台灣五個長期生態研究區之一。海拔高介於600-1,700m間，區內之植群包括天然闊葉林、次生闊葉林以及人工林等，天然林主要爲楠櫧林帶(*Machilus*－*Castanopsis* zone)(呂及歐 1996)。本研究調查期程從2000年9月起至2003年8月止共3年。於第四、五林班林道、松風山步道、湯公碑步道、小出山步道等路線選擇已具有結實能力的殼斗科植物設置樣木(圖1)，每隔2至4週利用望遠鏡或以高枝剪配合採集調查。對本研究較大的氣象干擾有2000年8月21-23日的碧利斯颱風、10月30至11月1日的象神颱風、2001年7月28-31日的桃芝颱風、9

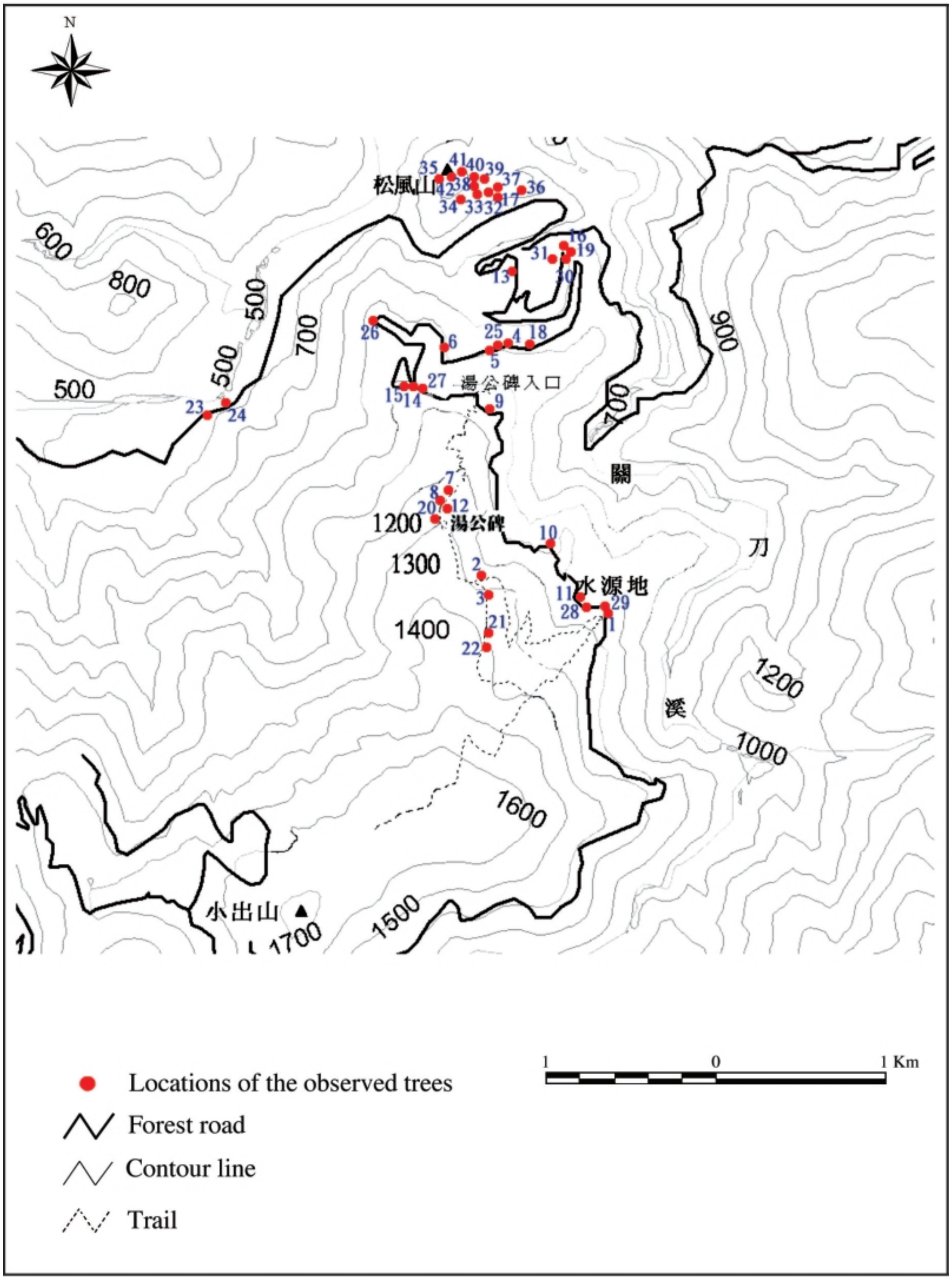


圖1. 關刀溪森林生態系殼斗科植物物候觀察樣木位置圖。

Fig. 1. Locations of the trees belonging to the family Fagaceae investigated in the Guandaushi forest ecosystem.

月6-19日的納莉颱風、9月23-28日的利奇馬颱風以及2002年7月2-4日的雷馬遜颱風等。2001年2月18日松風山區發生林火，藉此選取栓皮櫟及石櫟火燒樣木各3株，以比較火燒樣木與正常植株之物候期是否有差異。2001年11月至2002年5月底有一段較長的乾旱期發生。

二、物候觀察

於關刀溪森林生態系內進行物候觀察的物種包括：反刺櫧(*Castanopsis eyrei* (Champ.) Hutch.)、火燒柯(*Castanopsis fargesii* Fr.)、川上氏櫧(*Castanopsis kawakamii* Hay.)、青剛櫟(*Cyclobalanopsis glauca* (Thunb.) Oerst.) 、圓果青剛櫟(*Cyclobalanopsis globosa* Lin & Liu)、石櫟(*Pasania glabra* (Thunb.) Oerst.)、三斗石櫟(*Pasania hancei* (Benth.) Schot.)、短尾葉石櫟(*Pasania harlandii* (Hance) Oerst.)、小西氏石櫟(*Pasania konishii* (Hay.) Schot.)、南投石櫟(*Pasania nantoensis* (Hay.) Schot.)、菱果石櫟(*Pasania synbalanos* (Hance) Schot.)及栓皮櫟(*Quercus variabilis* Blume)共12種。共計標定42株樣木，記錄其海拔高及GPS座標如表1。每2至4週調查1次。

本研究將物候期區分爲下列8期：

1. 抽芽期(budding phase)：芽苞膨大開始抽長至芽伸出嫩葉的尖端。
2. 幼葉期(tender leaf phase)：可以明顯地看出綠色葉芽起至葉展開且葉未完全變色。
3. 展葉期(leafing phase)：葉片展開至葉完全平展並轉變爲成熟葉色爲止。
4. 落葉期(leaf falling phase)：係針對落葉樹種而言，在秋冬時葉開始掉落至葉片完全掉落。
5. 開花期(flowering phase)：由花苞開始膨大或花序抽長至花落。
6. 結果期(fruiting phase)：以雌花柱頭變黑爲幼果期之開始(圖2)到果實長大至成熟時之大小。
7. 熟果期(mature fruiting phase)：以果實開始由綠轉爲褐色定義之。
8. 落果期(fruit falling phase)：果實開始掉落至全部掉落止。

結　果

自2000年9月起至2003年8月止，各種殼斗科植物之物候觀察結果列於表2，依物候期分別說明如下：

一、抽芽至展葉期

殼斗科植物觀測樣木之抽芽期多在1月至4月間，不同物種之抽芽月份有所差異。幼葉及展葉會在抽芽後隨之生長(圖3)。

2001年所有調查樣木均只有一次抽芽期，發生在1-2月的有南投石櫟、石櫟及栓皮櫟，在2月的有反刺櫧與三斗石櫟，在2-3月

圖2. 圓果青剛櫟授粉後柱頭變黑，爲結果期之起始點。

Fig. 2. Stigmas of *Cyclobalanopsis globosa* (black after pollination, an indication of the beginning of fruiting phase).

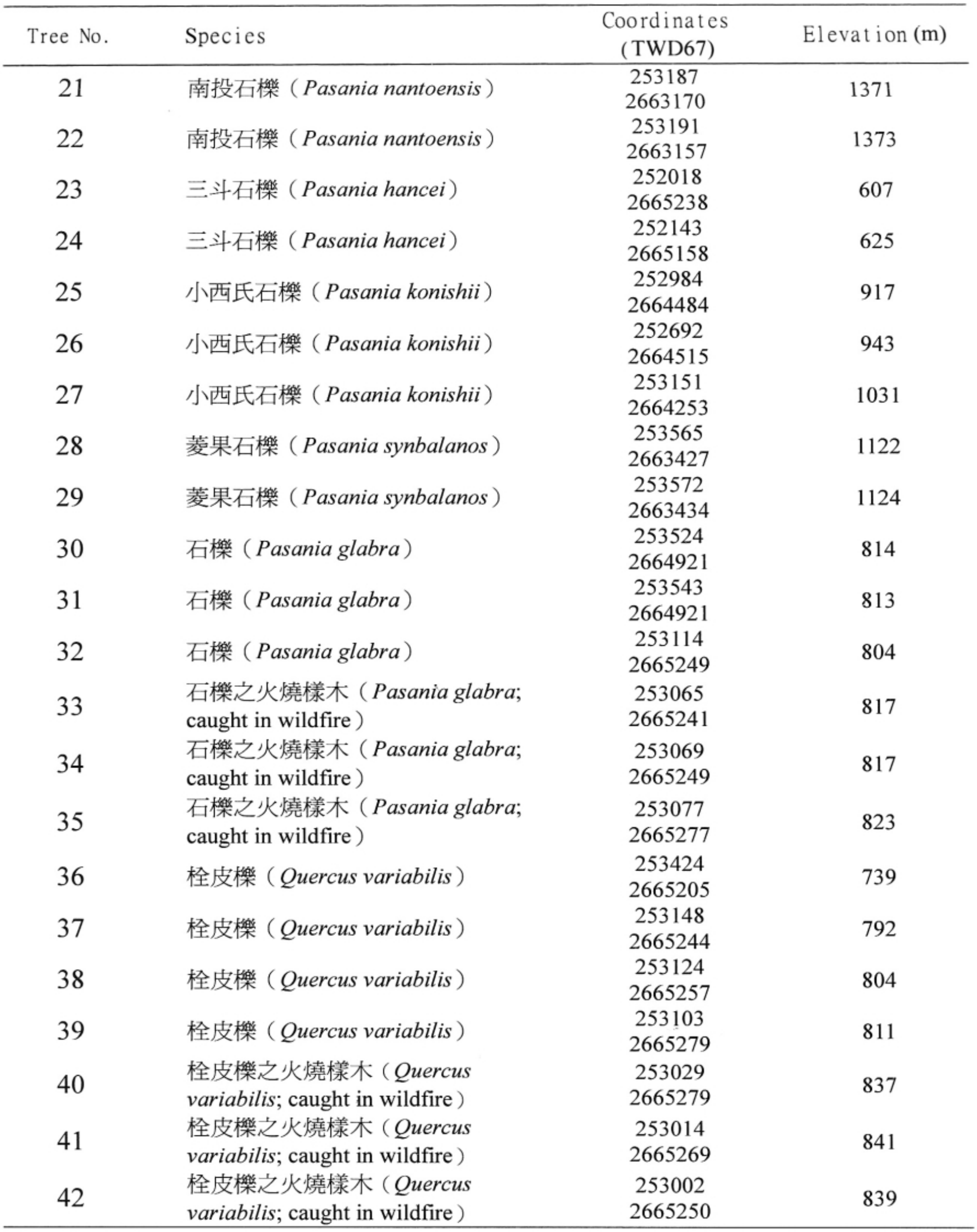
表1. 關刀溪森林生態系殼斗科植物物候調查樣木資料

Table 1. Data of the trees belonging to the family Fagaceae selected for phenological study in the Guandaushi forest ecosystem

Tree No.	Species	Coordinates (TWD67)	Elevation (m)
1	反刺櫧（*Castanopsis eyrei*）	253588 2663442	1126
2	反刺櫧（*Castanopsis eyrei*）	253006 2663460	1318
3	反刺櫧（*Castanopsis eyrei*）	253123 2663265	1354
4	川上氏櫧（*Castanopsis kawakamii*）	252977 2664445	917
5	川上氏櫧（*Castanopsis kawakamii*）	252986 2664501	917
6	川上氏櫧（*Castanopsis kawakamii*）	252876 2664609	927
7	川上氏櫧（*Castanopsis kawakamii*）	252968 2663626	1268
8	川上氏櫧（*Castanopsis kawakamii*）	252952 2663616	1272
9	火燒柯（*Castanopsis fargesii*）	253262 2664045	1057
10	火燒柯（*Castanopsis fargesii*）	253466 2663486	1112
11	火燒柯（*Castanopsis fargesii*）	253562 2663414	1121
12	火燒柯（*Castanopsis fargesii*）	252955 2663618	1273
13	青剛櫟（*Cyclobalanopsis glauca*）	253347 2664972	734
14	圓果青剛櫟（*Cyclobalanopsis globosa*）	253145 2664258	1031
15	圓果青剛櫟（*Cyclobalanopsis globosa*）	253147 2664256	1030
16	圓果青剛櫟（*Cyclobalanopsis globosa*）	253545 2664928	812
17	圓果青剛櫟（*Cyclobalanopsis globosa*）	253167 2665251	786
18	短尾葉石櫟（*Pasania harlandii*）	253088 2664427	903
19	短尾葉石櫟（*Pasania harlandii*）	253548 2664925	812
20	短尾葉石櫟（*Pasania harlandii*）	252954 2663608	1274

表1. 關刀溪森林生態系殼斗科植物物候調查樣木資料(續)

Table 1. Data of the trees belonging to the family Fagaceae selected for phenological study in the Guandaushi forest ecosystem (continued)



Tree No.	Species	Coordinates (TWD67)	Elevation (m)
21	南投石櫟（*Pasania nantoensis*）	253187 2663170	1371
22	南投石櫟（*Pasania nantoensis*）	253191 2663157	1373
23	三斗石櫟（*Pasania hancei*）	252018 2665238	607
24	三斗石櫟（*Pasania hancei*）	252143 2665158	625
25	小西氏石櫟（*Pasania konishii*）	252984 2664484	917
26	小西氏石櫟（*Pasania konishii*）	252692 2664515	943
27	小西氏石櫟（*Pasania konishii*）	253151 2664253	1031
28	菱果石櫟（*Pasania synbalanos*）	253565 2663427	1122
29	菱果石櫟（*Pasania synbalanos*）	253572 2663434	1124
30	石櫟（*Pasania glabra*）	253524 2664921	814
31	石櫟（*Pasania glabra*）	253543 2664921	813
32	石櫟（*Pasania glabra*）	253114 2665249	804
33	石櫟之火燒樣木（*Pasania glabra*; caught in wildfire）	253065 2665241	817
34	石櫟之火燒樣木（*Pasania glabra*; caught in wildfire）	253069 2665249	817
35	石櫟之火燒樣木（*Pasania glabra*; caught in wildfire）	253077 2665277	823
36	栓皮櫟（*Quercus variabilis*）	253424 2665205	739
37	栓皮櫟（*Quercus variabilis*）	253148 2665244	792
38	栓皮櫟（*Quercus variabilis*）	253124 2665257	804
39	栓皮櫟（*Quercus variabilis*）	253103 2665279	811
40	栓皮櫟之火燒樣木（*Quercus variabilis*; caught in wildfire）	253029 2665279	837
41	栓皮櫟之火燒樣木（*Quercus variabilis*; caught in wildfire）	253014 2665269	841
42	栓皮櫟之火燒樣木（*Quercus variabilis*; caught in wildfire）	253002 2665250	839

表2. 關刀溪森林生態系殼斗科植物之物候調查結果；觀察期間從2000年9月至2003年8月；各物候期之代號如後(B，抽芽期；T，幼葉期；L，展葉期；A，開花期；R，結果期；M，熟果期；F，落果期；D，落葉期)

Table 2. Phenological phases of the trees belonging to the family Fagaceae in the Guandaushi forest ecosystem (B, budding phase; T, tender leaf phase; L, leafing phase; A, flowering phase; R, fruiting phase; M, mature fruiting phase; F, fruit falling phase; D, leaf falling phase)

Species*	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ca. eyrei	2001		B	T	T,L	T,L	L	–	–	–	–	–	–
	2002	–	B	B	T,L	T,L	L,A	R	R	R	R,M	R,M,A	M,F
	2003	–	–	B,T,A	T,L,A	L,R	L,R	R	R				
Ca. kawakamii	2000									R	R,M	M,F	F
	2001	F	B	B	T,L,A	T,L,R	T,L,R	T,L,R	T,L,R	R	M	M,F	F
	2002	–	–	B,T,L	L,A	L,A,R	B,T,L,R	L,R	L,R	L,R,M	M	M,F	F
	2003	F	–	B,T,L,A	L,A	L,R	L,R	R	R				
Ca. fargesii	2000									R	R	R,M	M,F,B
	2001	–	B	B	T	L	L,A	L,R	L,R	R	M	M,F	A
	2002	R	R,A	R	R	R,A	B,T,R	L,R	B,L,R	B,T,L,R	M	M	F
	2003			B,A	T,A	T,L,R	L,R	R	R				
Cy. glauca	2001						L,R	R	R	R	R	M	F
	2002	F	–	B,A	T,R	T,R	L,R	R	R	R,M	M,F	–	–
	2003	–	–	B,T,A	T,L,A	L,R	L,R	R	R				
Cy. globosa	2000										R	R,M	R,F
	2001	R,F	R,F	R,F,A	R,B,A	R	R	R	R,B,L	R,L	A,R	R,M	B,A,R
	2002	R,B	R,B	R,T,A	R,L	R,L	R,B,T,L	R	R	R,M	M,F	–	–
	2003	–	B,T,A	B,T,L,A	L,R	L,R	R	R	R				
P. harlandii	2000									R	R,M	R,M,F	R,F
	2001	–	B	B,T	T,L,A	A,R	R	R	R	R,M	R,M	R,M,F	R,F
	2002	R	R	R,B,A	R,B,T,A	R,B,T,L,A	R,L,A	R,L,A	R	R,M	M	M,F	F
	2003	F	–	B	B,T	T,L	A	R	R				
P. nantoensis	2000										R,M	R,M	R,F
	2001	B,T	B,T	T	T,L	T,L,A	L,R	L,R	L,R	M,F	F	–	–
	2002	–	–	B,T	T,L	L	T,L,A	L,R	R,M	M	M,F	F	F
	2003	–	–	B,T	T,L	T,L,A	R	R	R				

* The abbreviation of the genus names are as the followings. Ca., *Castanopsis*; Cy., *Cyclobalanopsis*; P., *Pasania*; Q., *Quercus*.

表2. 關刀溪森林生態系殼斗科植物之物候調查結果；觀察期間從2000年9月至2003年8月；各物候期之代號如後(B，抽芽期；T，幼葉期；L，展葉期；A，開花期；R，結果期；M，熟果期；F，落果期；D，落葉期)(續)

Table 2. Phenological phases of the trees belonging to the family Fagaceae in the Guandaushi forest ecosystem (B, budding phase; T, tender leaf phase; L, leafing phase; A, flowering phase; R, fruiting phase; M, mature fruiting phase; F, fruit falling phase; D, leaf falling phase) (continued)

Species*	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
P. hancei	2000									R	R,M	R,M,F	F
	2001	—	B	T,L,A	L,A	A,R	A,R	R	R	R	R,M,F	M,F	M,F
	2002	—	B	T,L,A	L,R	L,R	B,T,A,R	A,R	R	R,M	M	M,F	F
	2003	—	—	B,T,A	T,L,A,R	L,R	L,R	R	R				
P. konishii	2000									R	R,M,F	M,F	F
	2001	A,R	B,A,R	B,T	T,L	A	R	T,L,R	R	R	R	R,M,F	—
	2002	—	A	R	B	T,L	B,T,L,A	A	R	A,R	R	R	—
	2003	—	—	B	T,L	T,L	A	R	R				
P. synbalanos	2001								R	R	R,M	R,M	R,M,F
	2002	F	F	—	—	B	T,L,A	L,A,R	R	R	R	M,F	M,F
	2003	R	R	R,B	R,T,L	R,L	A,R	R	R				
P. glabra	2000										R,M	A,R,M,F	A,R
	2001	A,R,B,T	R,B,T	R,T	T,L	T,L,R	T,L,A,R	A,R	A,R	A,R	M,F	M,F	A,M,F
	2002	—	B,T	T	T,L	L,A,R	B,T,L,R	B,T,L,R	T,L,R	T,A,R	A,R	A,M,F	R,M,F
	2003	R,F	R,B	T,L,A	L,A,R	R	R	R	R,A				
P. glabra (caught in wildfire)	2001					T,L	T,L	T,L	T,L	T,L	L	—	—
	2002	—	B,T	T,L	T,L	L	B,T,L	T,L	T,L	L	—	—	—
	2003	—	B	B,T,L,A	T,L,A,R	L,R	R	R	R,A				
Q. variabilis	2000										R	R,M,F	F,B,T
	2001	B,T,L	B,A	T,L,A	T,L	L,R	R	R	R	R	D,M,F	D,M,F	D,F
	2002	D	B,T,A	L,A,R	L,R	L,R	T,L,R	R	R	R	D,R	D,M	D,M,F
	2003	D	B,T,A	T,L,A	L,R	L,R	L,R	R	R				
Q. variabilis (caught in wildfire)	2001				T,L	T,L	T,L	T,L	L	L	—	D	D
	2002	D	B,T,A	L,A,R	L,R	L,R	B,T,L	L	—	—	D	D	D
	2003	D	B,T,A	T,L,A	L	L	L	—	—				

*The abbreviation of the genus names are as the followings. Ca., *Castanopsis*; Cy., *Cyclobalanopsis*; P., *Pasania*; Q., *Quercus*.

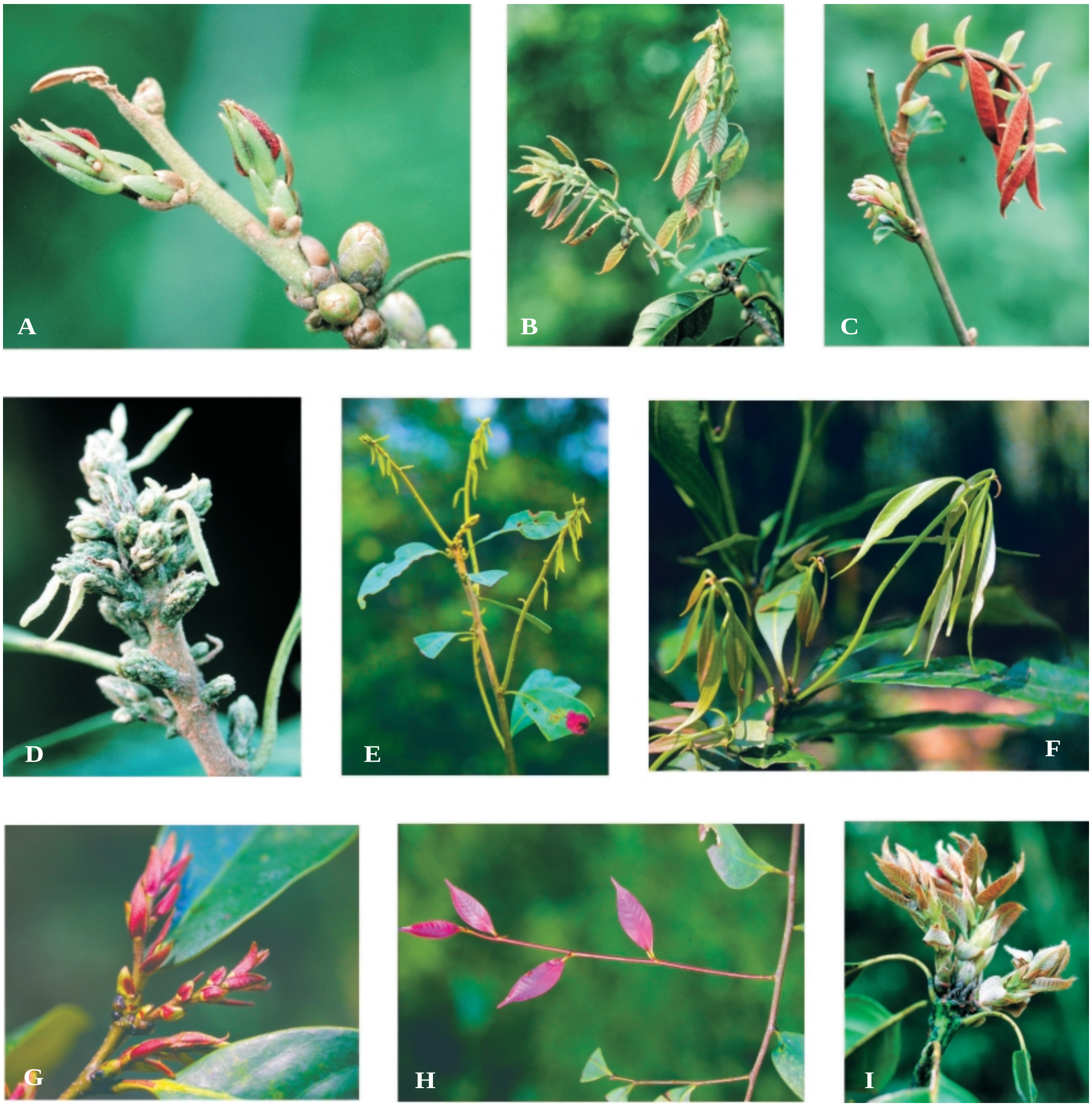


圖3. 殼斗科植物之抽芽及幼葉。(A，小西氏石櫟抽芽；B，小西氏石櫟幼葉；C，火燒柯幼葉；D，石櫟抽芽；E，石櫟幼葉；F，南投石櫟幼葉；G，川上氏櫧新芽；H，川上氏櫧幼葉；I，短尾葉石櫟幼葉。)

Fig. 3. Budding and tender leaves of Fagaceae. (A, budding of *Pasania konishii*; B, tender leaf of *Pasania konishii*; C, tender leaf of *Castanopsis fargesii*; D, budding of *Pasania glabra*; E, tender leaf of *Pasania glabra*; F, tender leaf of *Pasania nantoensis*; G, budding of *Castanopsis kawakamii*; H, tender leaf of *Castanopsis kawakamii*; I, tender leaf of *Pasania harlandii*.)

的有川上氏櫧、火燒柯、短尾葉石櫟與小西氏石櫟4種，圓果青剛櫟則在4月抽芽。

依2002年的調查，僅有一次抽芽期的有6種，其中在2月抽芽的有栓皮櫟，在2-3月的有反刺櫧，在3月的有青剛櫟與南投石櫟，短尾葉石櫟則在3-5月抽芽，菱果石櫟在5月抽芽。川上氏櫧、火燒柯、圓果青剛櫟、三斗石櫟、小西氏石櫟、石櫟與栓皮櫟的火燒樣株在2002年均出現兩次抽芽期，先在1-4月間首次抽芽，而後在6月再出現另外一次抽芽期；此外，火燒柯分別在6月及8-9月抽芽；小西氏石櫟於4月時原已抽芽長出幼葉，之後因缺水造成幼葉枯萎，6月降雨後其幼葉才又長出。在2003年，12種觀察樣木的抽芽期均發生在2-3月，其中石櫟與栓皮櫟在2月，圓果青剛櫟在2-3月，其餘9種均在3月。

12種殼斗科植物在2001年及2003年之抽芽期均在1-4月間，其中以2-3月期間抽芽最密集 (圖4)；而2002年有半數的物種出現兩次抽芽現象，推測與抽芽前長時間未降雨有關。反刺櫧的抽芽期在2001至2003年均發生在2-3月；川上氏櫧的抽芽期在2001年爲2-3月，2003年在3月抽芽，但在2002年則分別於3月及6月各發生一次。火燒柯在2001年的抽芽期爲2-3月，2003年在3月抽芽，而2002年則分別在6月及8-9月各發生一次。青剛櫟的抽芽期均在3月發生。圓果青剛櫟於2000年12月至隔年3月抽芽，2002年則分別在3月及6月各抽芽一次，2003年在3月抽芽。短尾葉石櫟在2001年的抽芽期爲2-3月，2002年在3-5月，2003年在3-4月。南投石櫟在2001年的抽芽期爲1-2月，2002及2003年均在3月。三斗石櫟在2001年的抽芽期爲2月，2002年則分別在2月及6月，2003年則在3月。小西氏石櫟在2001年的抽芽期爲1-2月，2002年則分別在4月及6月各一次，2003年在3月抽芽。菱果石櫟2002年在5月抽芽，2003年則在3月。石櫟在2001年的抽芽期爲1-2月，2002年分別在2月及6-7月，2003年在2月抽芽。栓皮櫟在2000年12月至隔年2月抽芽，2002及2003年均在2月。

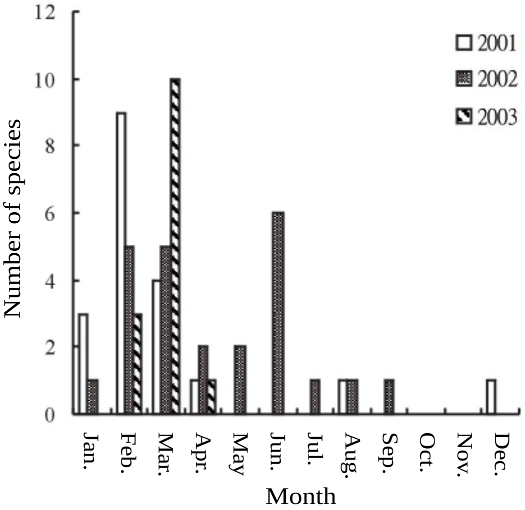


圖4. 2001至2003年各月份殼斗科抽芽種數。

Fig. 4. Numbers of species of Fagaceae at the budding phase for calendar months in 2001 to 2003.

石櫟的火燒樣木2002年分別在2月及6月各抽芽一次，2003年在2-3月抽芽。栓皮櫟的火燒樣木與未火燒樣木在2002及2003年均於2月抽芽，但火燒樣木在2002年6月多抽一次芽。

二、落葉期

所觀察的12個物種中，僅栓皮櫟有落葉現象，落葉期在2000及2001年均是從12月至隔年1月。栓皮櫟火燒樣木在2001年於11月至隔年1月落葉，而2002年的落葉期爲12月至隔年1月。

三、開花期

殼斗科有雌花及雄花序的區別，爲同株異花的植物(圖5A至圖5D)。觀察時發現多數樣株之雄花會先開而後雌花才開(圖5E、圖5F)，如此可以避免自花授粉。殼斗科植物的

圖5. 殼斗科植物之開花現象。(A，川上氏櫧雄花；B，川上氏櫧雌花；C，栓皮櫟雄花；D，栓皮櫟雌花；E，小西氏石櫟雄花謝雌花開；F，石櫟雄花謝雌花開；G，川上氏櫧花序與幼葉同時抽出；H，圓果青剛櫟花序與幼葉同時抽出；I，栓皮櫟花序與幼葉同時抽出；J，短尾葉石櫟幼葉及剛抽出之花序；K，短尾葉石櫟葉展開，花序抽長；L，三斗石櫟葉展開及開花；M，石櫟開花。)

Fig. 5. Flowers of Fagaceae. (A, staminate of *Castanopsis kawakamii*; B, pistillate of *Castanopsis kawakamii*; C, staminate of *Quercus variabilis*; D, pistillate of *Quercus variabilis*; E, monoecious inflorescence of *Pasania konishii*; F, inflorescence with both staminate and pistillate of *Pasania glabra*; G, inflorescence and budding of *Castanopsis kawakamii*; H, pistillate inflorescence and tender leaf of *Cyclobalanopsis globosa*; I, inflorescence and budding of *Quercus variabilis*; J, inflorescence and tender leaf of *Pasania harlandii*; K, inflorescence and leafing of *Pasania harlandii*; L, inflorescence and leafing of *pasania hancei*; M, inflorescence and leafing of *Pasania glabra*.)

開花時間很短，大多數的花期約爲2-4週。開花期多集中在2-6月(圖6)。其開花現象可略區分爲：(1)抽芽同時花芽也一起生長，隨著幼葉的開展，花序跟著抽長，花苞也發育膨大展開，可以同時看到花與幼葉同時生長的現象；例如川上氏櫧(圖5G)、圓果青剛櫟(圖5H)及栓皮櫟(圖5I)。(2)幼葉抽長嫩葉長出之後花序才生長，即幼葉與花序出現有一段時間區隔；例如青剛櫟、短尾葉石櫟(圖5J、圖5K)、南投石櫟、三斗石櫟(圖5L)、小西氏石櫟及菱果石櫟。(3)葉展開後才開花；如火燒柯及石櫟(圖5M)。

反刺櫧、川上氏櫧、青剛櫟、短尾葉石櫟、南投石櫟、菱果石櫟及栓皮櫟等7種每年開花一次；火燒柯、石櫟及小西氏石櫟3種一年內有兩次開花期；圓果青剛櫟於2001年分別於3-4月、10月及12月開花，但2002年僅於3月開一次花，2003年於2-3月開花；而三斗石櫟在2001年3-6月開一次花，在2002年3月及6-7月分別開花，2003年於3-4月開花，連續三年開花期均在不同的月份。

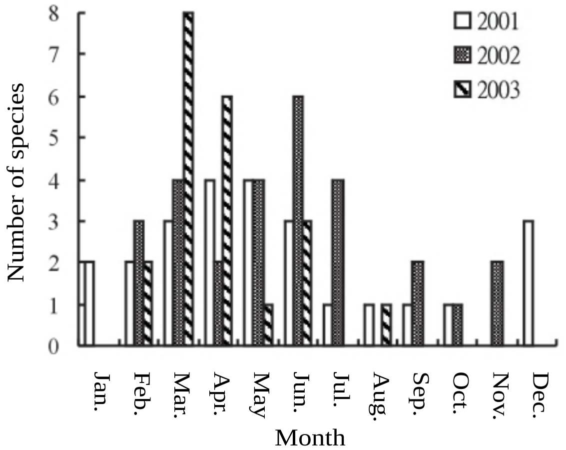


圖6. 2001至2003年各月份殼斗科植物開花之種數。

Fig. 6. Numbers of species of Fagaceae at the budding phase for calendar months in 2001 to 2003.

石櫟之火燒樣木2001及2002年連續兩年均未開花，2003年則與未遭火燒之植株同於3-4月開花；栓皮櫟的3株火燒樣木，2002年有1株於2-3月開花，但於2002年11月死亡；另外2株樣木隔了兩年才開始開花，開花期爲2003年2-3月，開花月份與未遭火燒之對照樣株同時。

四、結果期至落果期

殼斗科植物果實外殼斗之形態多樣(圖7)，爲分類之重要依據。殼斗科之結果期是物候週期中爲時最久的。所調查的12種中，開始結果的季節並不一致，與開花期有關。5至9月是其結果之高峰期(圖8)，各物種之果熟期相當接近，均在8至12月(圖9)，但是石櫟於每年8-9月果實發育已接近成熟階段時均會再開一次花(圖7L)。9-11月爲果熟盛期；而落果期在9月至隔年2月間。

短尾葉石櫟及三斗石櫟在2001年開花所結的幼果似乎並未發育，有休眠的果枝留存於樹上一年餘(圖10)，此現象有待進一步監測。

討論

2001年在關刀溪森林生態系所調查之殼斗科物種均只有一次抽芽期；2002年川上氏櫧、圓果青剛櫟、三斗石櫟、小西氏石櫟及石櫟在6月另有一次抽芽期。在2001年10月至2002年5月有一較長的乾旱期(圖11)，推測可能是長期乾旱後的降雨，促使這些物種又再度抽芽。此外，小西氏石櫟於2001年2-3月抽芽，在2002年4月時原已抽芽並長出幼葉，後因未降雨造成幼葉全數枯萎，至6月降雨後才又長出幼葉，推測此物種可能是藉由本身的形態調節來適應氣候的變化。

研究發現火燒柯、圓果青剛櫟、石櫟及小西氏石櫟在2001年有2次或2次以上的開花期；2002年火燒柯、三斗石櫟及小西氏石櫟

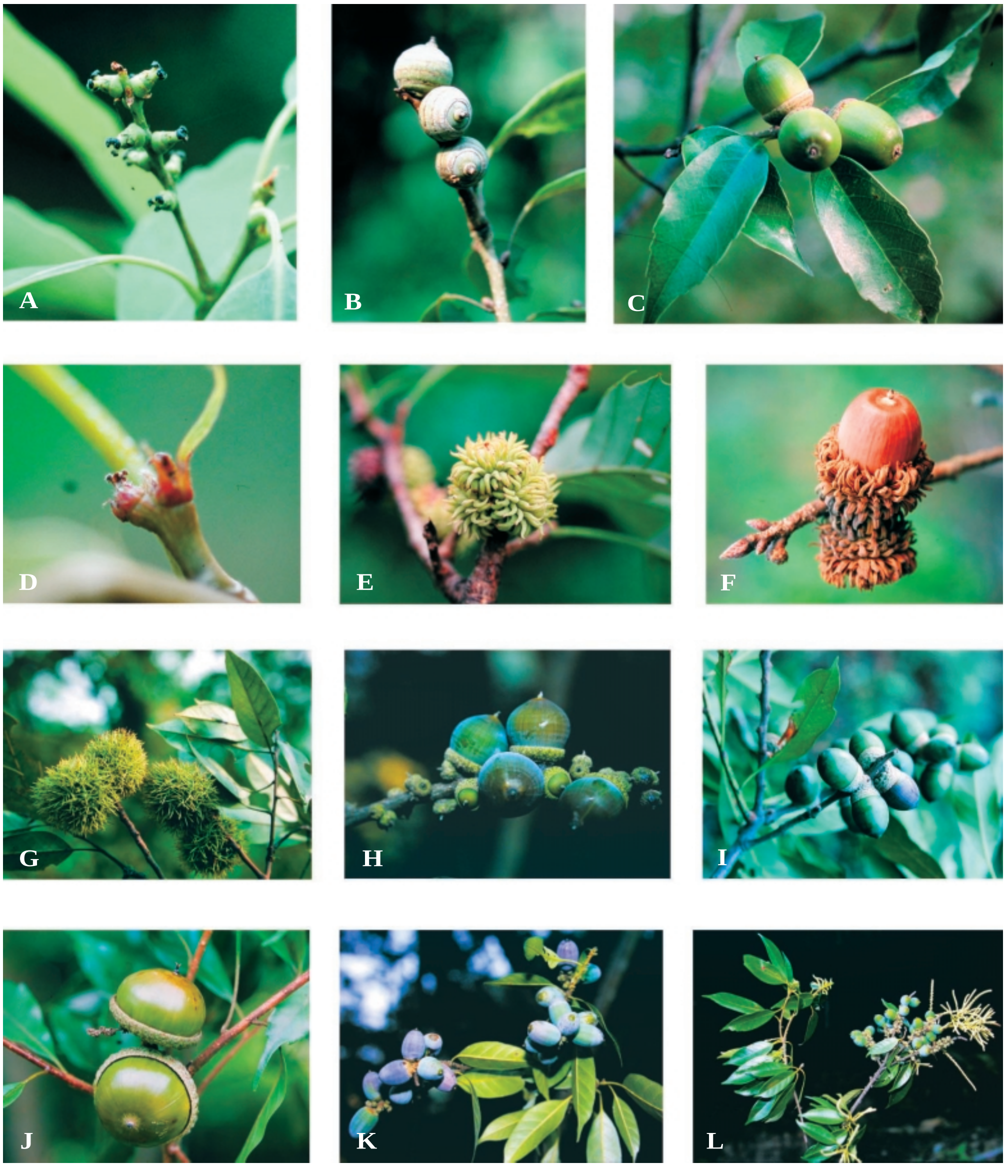


圖7. 殼斗科植物結果狀況。(A，圓果青剛櫟初果；B，圓果青剛櫟幼果；C，圓果青剛櫟熟果；D，栓皮櫟初果；E，栓皮櫟幼果；F，栓皮櫟熟果；G，川上氏櫧果實；H，短尾葉石櫟熟果；I，三斗石櫟熟果；J，小西氏石櫟熟果；K，石櫟熟果；L，石櫟近成熟之果與花序同時出現。)

Fig. 7. Fruits of Fagaceae. (A, younger immature fruiting of *Cyclobalanopsis globosa*; B, immature fruiting of *Cyclobalanopsis globosa*; C, mature fruiting of *Cyclobalanopsis globosa*; D, younger immature fruiting of *Quercus variabilis*; E, immature fruiting of *Quercus variabilis*; F, mature fruiting of *Quercus variabilis*; G, mature fruiting of *Castanopsis kawakamii*; H, mature fruiting of *Pasania harlandii*; I, mature fruiting of *Pasania hancei*; J, mature fruiting of *Pasania konishii*; K, mature fruiting of *Pasania glabra*; L, flowering phase and fruiting phase can happen simultaneously of *Pasania glabra*.)

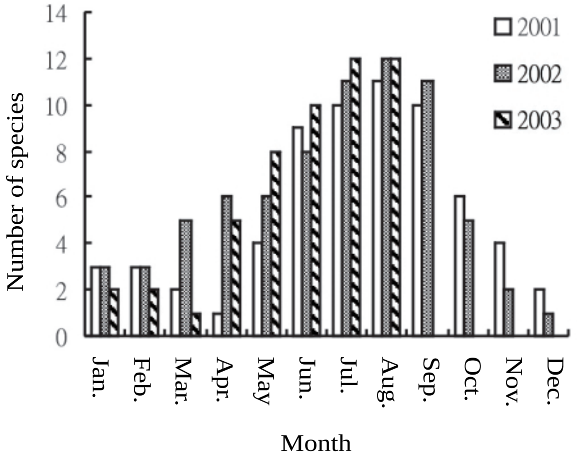


圖8. 2001至2003年各月份殼斗科結果種數。

Fig. 8. Numbers of species of Fagaceae at the fruiting phase for calendar months in 2001 to 2003.

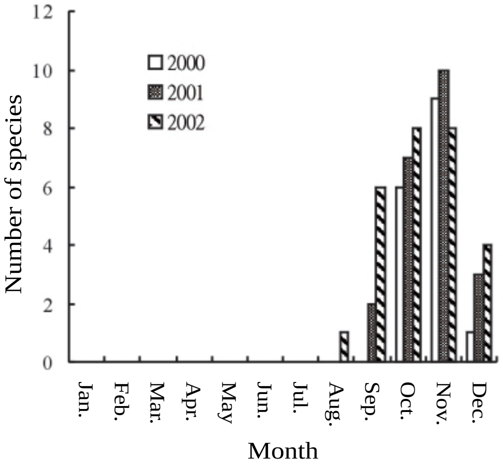


圖9. 2000至2002年各月份殼斗科果熟種數。

Fig. 9. Numbers of species of Fagaceae at the mature fruiting phase for calendar months in 2001 to 2003.

圖10. 短尾葉石櫟當年生之結果枝條(A)與休眠之果枝(B)。

Fig. 10. The new fruiting branch(A) and dormant fruiting branch(B) of *Pasania harlandii*.

有2次開花期，且在2次開花期間僅間隔1-3個月。火燒柯、圓果青剛櫟及小西氏石櫟一年開2次花，而石櫟一年則開花多次。其開二次花的機制爲何？開花後是否結果？所結之果實是否完全發育？有待進一步的觀察。這些一年開花二次以上的物種雖然均有一明顯的開花盛期出現，或許非盛期之開花現象對其更新繁殖更加重要，因台灣多颱風豪雨，而殼斗科植物之花果期與颱風期相近，若於開花期或結果期間遭颱風吹襲，可能對殼斗科植物的繁殖造成相當大的影響，但若遭颱風吹襲後再開花結實，或可使果實有比較多的機會可以發育成熟，得到較多的更新機會。這些假設有待長期監測加以證實。

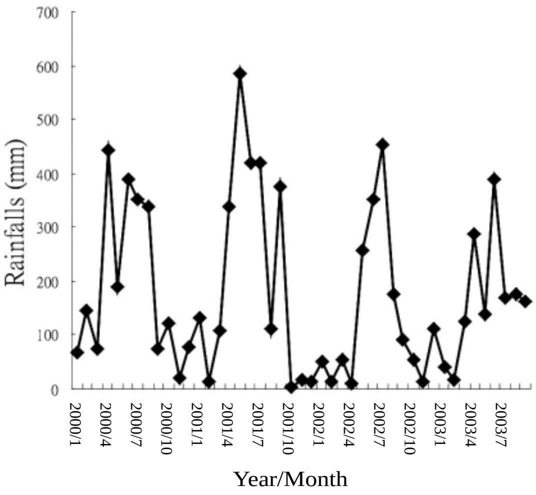


圖11. 關刀溪地區2000年1月至2003年9月之雨量。

Fig. 11. Monthly rainfalls in the Guandaushi forest ecosystem in 2000 to 2003.

一般認爲殼斗科植物之物候週期與多數植物同爲每年一個循環，但本研究發現部分殼斗科植物之物候週期可能以兩年爲一個週期，如短尾葉石櫟、石櫟及三斗石櫟，具有休眠的結果枝(圖10)會留存在樹上至隔年才開始發育膨大，果期約1年半；此外其餘未觀察到休眠結果枝的物種是否僅爲一年一循環，仍有待進一步再觀測證實。

石櫟之火燒樣木在2001及2002年連續兩年均未開花，2003年則與未遭火燒植株同時開花；栓皮櫟存活的2株火燒觀測樣木經過兩年後，於2003年同樣與未遭火燒植株同於2-3月開花。林火發生時會影響植物的物候週期，但火燒一段時間後石櫟及栓皮櫟會逐漸恢復其原來的物候週期。

結論

本研究於2000年9月至2003年8月間觀測關刀溪森林生態系內12種殼斗科植物的物候期，其中僅栓皮櫟是落葉性植物。所有觀察物種的果熟期均在8至12月，而落果期都在9月至隔年2月間。關刀溪森林生態系中殼斗科植物所呈現的物候週期爲一年一循環或兩年一循環。

三年之調查結果發現，關刀溪森林生態系內殼斗科植物之抽芽較密集的時期集中在2-4月，且由於外在環境的改變，這些物種可能是藉由本身的調節作用(生理或形態)來適應氣候的變化。例如2001年在關刀溪森林生態系所調查之殼斗科物種均只有一次抽芽期；2002年川上氏櫧、圓果青剛櫟、三斗石櫟、小西氏石櫟及石櫟在6月另有一次抽芽期，因在2001年10月至2002年5月有一較長的乾旱期，推測可能是長期乾旱後的降雨，促使其再度抽芽。

開花期則較爲歧異，當地的殼斗科植物全年均有物種在開花，且每年之開花次數變化相當大，其中反刺櫧、川上氏櫧、青剛櫟、三斗石櫟、短尾葉石櫟、南投石櫟、菱果石櫟與栓皮櫟8種每年開花一次，火燒柯、小西氏石櫟一年內有兩次的開花期，石櫟一年開花多次，而圓果青剛櫟在2001與2002年分別開花2次及1次。這些一年開花二次以上

的物種雖然均有一明顯的開花盛期出現，或許非盛期之開花現象對其更新繁殖更加重要。因台灣多颱風豪雨，而殼斗科植物之花果期與颱風期相近，若於開花期或結果期間遭颱風吹襲，可能會造成殼斗科植物落花或落果，但遭颱風吹襲後再開花結實，可使該物種有多一次的更新機會，這些假設有待長期監測加以證實。

一般認爲殼斗科植物之物候週期與多數植物同爲每年一個循環，但本研究發現部分殼斗科植物之物候週期可能以兩年爲一個週期，如短尾葉石櫟、石櫟及三斗石櫟，觀察得知其具有休眠的結果枝會留存在樹上至隔年才開始發育膨大；此外其餘未觀察到休眠結果枝的物種是否僅爲一年一循環，仍有待進一步再觀測證實。但當地殼斗科植物的果熟期多在9月至12月間。

石櫟之火燒樣木在2001及2002年連續兩年均未開花，2003年則與未遭火燒植株同時開花；栓皮櫟存活的2株火燒觀測樣木經過兩年後，於2003年同樣與未遭火燒植株同於2-3月開花。推測在林火發生時會影響植物的物候週期，但火燒對植物影響的時間過後，石櫟及栓皮櫟會逐漸恢復其原來的物候週期。

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五、 稿件全部內容包括文字、圖、表、相片及引用文獻等，研究報告以不超過10印刷頁(約18,000字)爲原則；學術論述及專論以不超過15印刷頁(約27,000字)爲原則；研究短報則以不超過 4印刷頁(約7,200字)爲原則。

肆、文稿書寫應注意事項

一、文稿須以Microsoft Word 可讀取之軟體編輯，以A4 (30cm×21cm) 白紙單面雙空行(double spaces) 列印，文稿之天、地、左、右須留白3公分，於每頁正下方註記頁碼。

二、本文敘述，應用數字編號時，其層次：

中文用：一、(一)、1、(1)、〞A...

英文用：Ⅰ、(Ⅰ)、1、(1) 、A、a、(a)....

三、中英文單位請用公制之符號，例如：kg、mg、ml、ppm、pH、cm等，數值請以阿拉伯數字表示之，年代一律用西元。

四、插圖請用白紙(或繪圖紙)以黑墨水精繪，亦可採電腦製圖，惟須以雷射印表機列印；照片限原始攝影採光面相紙沖印者，幻燈片限用原片；未按規定之插圖致圖片模糊無法製版者不予受理。

五、圖片之標題在下方，表格標題在上方，標題需中英文並列，圖的說明應中英文對照另頁繕打，不可附在繪圖及相片上面。本文中圖表順序以圖1，圖2，表1，表2 ...，Fig. 1, Fig. 2, Table l, Table 2, ...等表示。

六、圖表內容請用英文，表格不加縱線。圖、表均以A4大小列印，定稿後圖、表請送原稿。

七、引用文獻以確經引用者爲限，文中提到之文獻，請列出姓氏、年代。

八、引用文獻書寫方式：先列中、日、韓文，次列西文，其書寫方法按作者、年份、題目、發表刊物名稱(全名，不採用縮寫)、卷期及頁號順序。

例：1.中、日文期刊：柳榗、徐國士。1971。台灣稀有及有絕滅危機之動植物種類。中華林學季刊 4 (4): 89-96。

2.中、日文書籍：徐國士。1980。台灣稀有及有絕滅危機之植物。台灣省教育廳。

3.中、日文彙編書籍：徐國士。1987。台灣的稀有植物。周昌弘、彭鏡毅、趙淑妙撰(編)。台灣植物資源與保育 139-157頁。中華民國自然生態保育協會。

4.英文期刊：Clough, B. 1998. Mangrove forest productivity and biomass accumulation in Hinchinbrook Channel, Australia. Mangroves and Salt Marshes 2: 191-198.

5.英文期刊：Pimm, S. L. and J. L. Gittleman. 1992. Biodiversity : Where is it ?. Science 255: 940.

6.英文期刊：Baker, C. S., F. Cipriano and S. R. Palumbi. 1996. Molecular genetic identification for whale and dolphin products from commercial markets in Korea and Japan. Molecular Ecology 5: 671-685.

7.英文書籍：Soule, M. E. and B. A. Wilco. 1980. Conservation biology: An evolutionary-ecological approach. Sinauer Associates, Sunderand. Massachusetts.

8.英文彙編書籍：Jinchu, H. and W. Fuwen. 1990. Development and progress of breeding and rearing giant pandas in captivity within China. pp. 322-325. *In*: H. Jinchu (ed.). Research and progress in biology of the giant panda. Sichuan Publishing House of Science and Technology, Sichuan, People's Republic of China.