DOI:10.6661/TESFE.2012021 台灣昆蟲Formosan Entomol. 32: 331-344 (2012) 研究報告 Research report

Formosan Entomologist
Journal Homepage: entsocjournal.yabee.com.tw

Comparative Study of Species Composition and Seasonal Activity of Necrophilous Beetles with Emphasis on Aphodiinae and Scarabaeinae (Coleoptera: Scarabaeidae) in Subtropical and Tropical Taiwan【Research report】

熱帶與亞熱帶台灣親屍性甲蟲 - 特別是蜉金龜亞科 (Aphodiinae) 與金龜子亞科 (Scarabaeinae) (Coleoptera: Scarabaeidae) 物種組成與季節活躍的比較研究【研究報告】

Wenbe Hwang1, and Shiuh-Feng Shiao2*
黃文伯1、蕭旭峰2*

*通訊作者E-mail : sfshiao@ntu.edu.tw

Received: 2012/08/15 Accepted: 2012/11/19 Available online: 2012/12/01

Abstract

In subtropical Fushan (northern Taiwan), beetles attracted by carrion are inactive in winter, while beetles in tropical Nanjenshan (southern Taiwan) are active all year round. In subtropical Fushan distinguishing the activity periods of the four most dominant necrophilous families, Hydrophilidae, Leiodidae, Scarabaeidae and Staphylinidae, is difficult, yet in tropical Nanjenshan their activity periods are clearly separated. The diversity of necrophilous Aphodiinae and Scarabaeinae in tropical Nanjenshan is lower than that in subtropical Fushan since there is only one dominant species in Nanjenshan. In addition, the total number of necrophilous beetles was higher in the forest than in the meadow. Based on the qualitative and quantitative results of this study, we believe that the environmental factors, including temperature, wind and shade from the sun, can strongly affect the availability of the carrion used by these beetles, thereby changing their species abundance and diversity. Under intense resource competition, different strategies evolved, resulting in different patterns of species diversity, seasonal activity and niche separation between tropical and subtropical areas.

摘要

本研究比較南北台灣以屍體誘引所捕獲甲蟲的物種組成與季節性活躍，相對於南台灣地屬熱帶的南仁山受屍體吸引的甲蟲全年活躍，而甲蟲在北台灣亞熱帶福山則於冬天顯現不活躍的情況。四個最為優勢的親屍性科別 (牙蟲科、球蕈蟲科、金龜子科與隱翅蟲科) 在福山的活躍期較難區隔，但在南仁山此四個科別的活躍期則清楚分離。南仁山親屍性蜉金龜亞科與金龜子亞科的多樣性較福山為低，主要原因在於南仁山只有一個優勢種。整體來說，親屍性甲蟲在林地中的個體數目較草地為多。基於本研究結果，我們相信溫度、風與遮蔭等環境因子，強烈影響甲蟲對屍體資源的利用，進而改變物種的分布與多樣性，並基於資源的競爭而演化出不同的策略，因此得以檢測出物種多樣性、季節活躍與棲位區隔在熱帶與亞熱帶區域的不同模式。

Key words: species diversity, species abundance, niche separation, carrion fauna

關鍵詞: 物種多樣性、物種豐量、棲位區隔、屍體動物相。

台灣昆蟲 32: 331-344 (2012)
Formosan Entomol. 32: 331-344 (2012)

Comparative Study of Species Composition and Seasonal Activity of Necrophilous Beetles with Emphasis on Aphodiinae and Scarabaeinae (Coleoptera: Scarabaeidae) in Subtropical and Tropical Taiwan

Wenbe Hwang[1], and Shiuh-Feng Shiao[2*]

[1] Department of Ecoscience and Ecotechnology, National University of Tainan, Tainan City 70005, Taiwan
[2] Department of Entomology, National Taiwan University, Taipei City 10617, Taiwan

ABSTRACT

In subtropical Fushan (northern Taiwan), beetles attracted by carrion are inactive in winter, while beetles in tropical Nanjenshan (southern Taiwan) are active all year round. In subtropical Fushan distinguishing the activity periods of the four most dominant necrophilous families, Hydrophilidae, Leiodidae, Scarabaeidae and Staphylinidae, is difficult, yet in tropical Nanjenshan their activity periods are clearly separated. The diversity of necrophilous Aphodiinae and Scarabaeinae in tropical Nanjenshan is lower than that in subtropical Fushan since there is only one dominant species in Nanjenshan. In addition, the total number of necrophilous beetles was higher in the forest than in the meadow. Based on the qualitative and quantitative results of this study, we believe that the environmental factors, including temperature, wind and shade from the sun, can strongly affect the availability of the carrion used by these beetles, thereby changing their species abundance and diversity. Under intense resource competition, different strategies evolved, resulting in different patterns of species diversity, seasonal activity and niche separation between tropical and subtropical areas.

Key words: species diversity, species abundance, niche separation, carrion fauna

Introduction

When an organism dies, its remains become a resource for other organisms and can become their microhabitat. These microhabitats and the organisms themselves make up a microcommunity (Allee *et al*., 1949). Carrion decomposition

*Corresponding email: sfshiao@ntu.edu.tw

is influenced by temperature, humidity, habitat type, and the season (Reed, 1958; Lundt, 1964; Payne, 1965; Nabaglo, 1973; Swift *et al*., 1979). Scientists classify the decomposition of carrion into several phases (Fuller, 1934; Howden, 1950; Reed, 1958). The composition of carrion usually changes with the decomposition phase and with the season (Fuller, 1934; Reed, 1958; Payne, 1965; Payne and Crossley, 1966; Johnson, 1975). The most important members of the microcommunities that breed on carrion are arthropods. Coleoptera, Diptera, Hymenoptera and Araneida account for 78-90% of all organisms found on carrion (Payne, 1965; Johnson, 1975). Insects play an important role in the decomposition of carrion. If insects are prevented from reaching carrion, it will take several months for the carrion to decompose. On the other hand, when insects are present it takes only a few days (Payne, 1965). Several species of necrophilous beetles are known to use carrion, decaying fruit and fungi among other things as their food source (Halffter and Matthews, 1966; Handski, 1989). Necrophilous beetles in the subfamilies Aphodiinae and Scarabaeinae have been studied using carrion traps, and other studies have been carried out comparing various species of beetles at different altitudes (Ridsdill Smith *et al*., 1983; Lobo and Halffter, 2000).

Taiwan is located in the western Pacific Ocean. The Tropic of Cancer runs through the middle of the island resulting in a tropical climate in the southern half and a subtropical climate in the northern half. Both the seasonal weather and the vegetation influence the population density of vertebrates, leading to a variation in the potential density of carrion. Therefore, the activity periods of necrophilous species in subtropical northern Taiwan differ from the ones in tropical southern Taiwan (Hwang, 2006). To determine which factors limit the activity periods in these two ecosystems, we studied necrophilous beetles. Due to their sensitivity to changes in the physical structure of their habitat and the ease of sampling, necrophagous beetles can be used as a biological indicator (Halffter and Favila, 1993) reflecting the influence of environmental changes on biodiversity and the forest structure (Nummelin and Hanski, 1989; Halffter *et al*., 1992). The present study focused on the species composition and seasonal activity of necrophilous beetles. Its main objective was to understand the species diversity, composition, habitat preference, and seasonal changes of these necrophilous beetles in the subtropical and tropical areas of Taiwan.

Materials and Methods

A field survey was carried out from February 2001 to January 2002 in subtropical Fushan (24°45'N, 121°34'E) in northern Taiwan and in tropical Nanjenshan (22°03'N, 120°50'E) in southern Taiwan. To collect necrophilous beetles in subtropical Fushan, carcass-baited pitfall traps were set up in a forest and a meadow near Hahpen River. The study forest, located between the Fushan Botanical Garden and the Hahpen Reservation, is subtropical and lies at an altitude of 600-800 m. The study meadow is part of the grassland between the botanical garden and the Hahpen Reservation. Nanjenshan is located within Kenting National Park and is a preservation area at an altitude of 0-500 m. The tropical forest, which covers a large part of the reservation area, is situated near the Basayalu River. The traps for the beetles were set up in the meadow near Nanjen Lake.

There were eight sampling sites in each of the following habitats: subtropical forest, subtropical meadow, tropical forest, and tropical meadow. At each site, a pitfall trap was set up with a mouse carcass and a trap without a carcass as the control. The distance between traps was at least

20 m. The pitfall trap was set up as follows: a PVC pipe measuring 15 cm ID × 20 cm long was buried in the soil, with the upper rim of the pipe flush with the ground and acting as a retaining wall. A 500 mL plastic cup was placed at the bottom of the pipe to collect the beetles. A funnel, making a tight fit with the inside of the pipe was placed deep enough to reach inside the plastic cup. The ground around the pipe was covered with a piece of 60 × 60 cm steel netting. A steel wire cage with a 2 cm mesh size, and measuring 20 cm wide × 20 cm long × 10 cm high was placed on the wire netting, centered over the pipe. The steel netting covering the ground around the pipe was held down with pegs and was connected to the steel cage with nylon cable ties, so as to prevent vertebrates from digging underneath the netting to try and get at the carcass bait. The top of the steel cage was covered with a 25 × 25 cm transparent acrylic plate to keep out rain. Inside the steel cage, an 8.5 cm diameter plastic Petri dish was hung to support the carcass (Fig. 1). A fresh carcass from a 4-5-week-old mouse weighing approximately 20 g was placed in the trap twice a month for four days at a time. The beetles were collected twice a month.

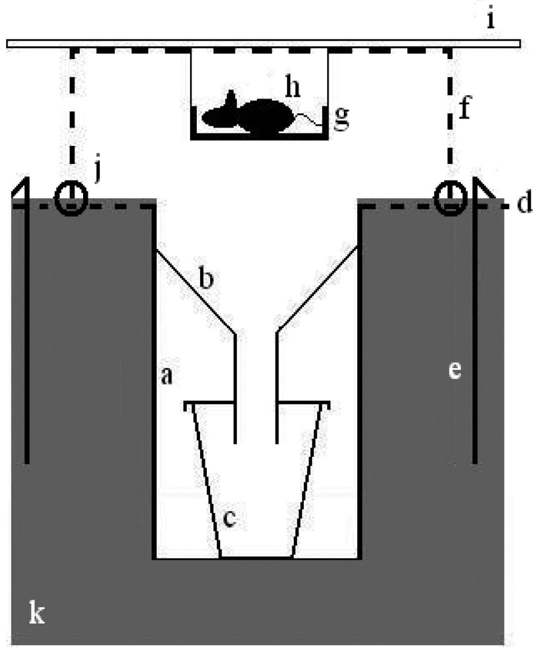


Fig. 1. Diagram of a baited pitfall trap. (a) PVC water pipe with an inside diameter of 15 cm; (b) funnel; (c) 500-mL plastic collection cup; (d) 60 × 60 cm steel netting covered with earth; (e) peg; (f) steel cage open on underside; (g) bait rack; (h) 4-5-week-old mouse carcass (ca. 20 g); (i) transparent acrylic plate; (j) nylon cable; (k) soil.

During the experiment, an automatic thermo-hygrometer (Hobo data logger, Onset Computer Corp., Pocasset, MA) was placed near the pitfall trap about 5 m from the ground, which recorded the temperature every 30 min.

Shannon-Wiener's maximum diversity index (Hmax) and evenness were used to examine the species communities of the aphodiine and scarabaeine fauna in both Fushan and Nanjenshan. We adopted the χ^2-test to compare the preference of the species and individuals of Aphodiinae and Scarabaeinae distributed in the forests and in the meadows in Fushan and Nanjenshan. Wilcoxon's signed rank test was used for comparing the two dependent treatment groups for habitat preference of one species, and the Mann-Whitney *U*-test for comparing the monthly Shannon-Wiener Indexes of necrophilous dung beetles from Fushan and Nanjenshan. The alpha level for statistical significance was set at 0.05 for all comparisons.

Results

From February 2001 to January 2002, 10,613 beetles representing 323 species in 34 families were captured in the traps. The majority of the trapped beetles were from the families Carabidae (10.1%), Histeridae (1.4%), Hydrophilidae (11.1%), Lampyridae (0.5%), Leiodidae (15.8%), Scarabaeidae (13.6%), Silphidae (1.6%), Staphylinidae (41.4%), and Trogidae (1.6%).

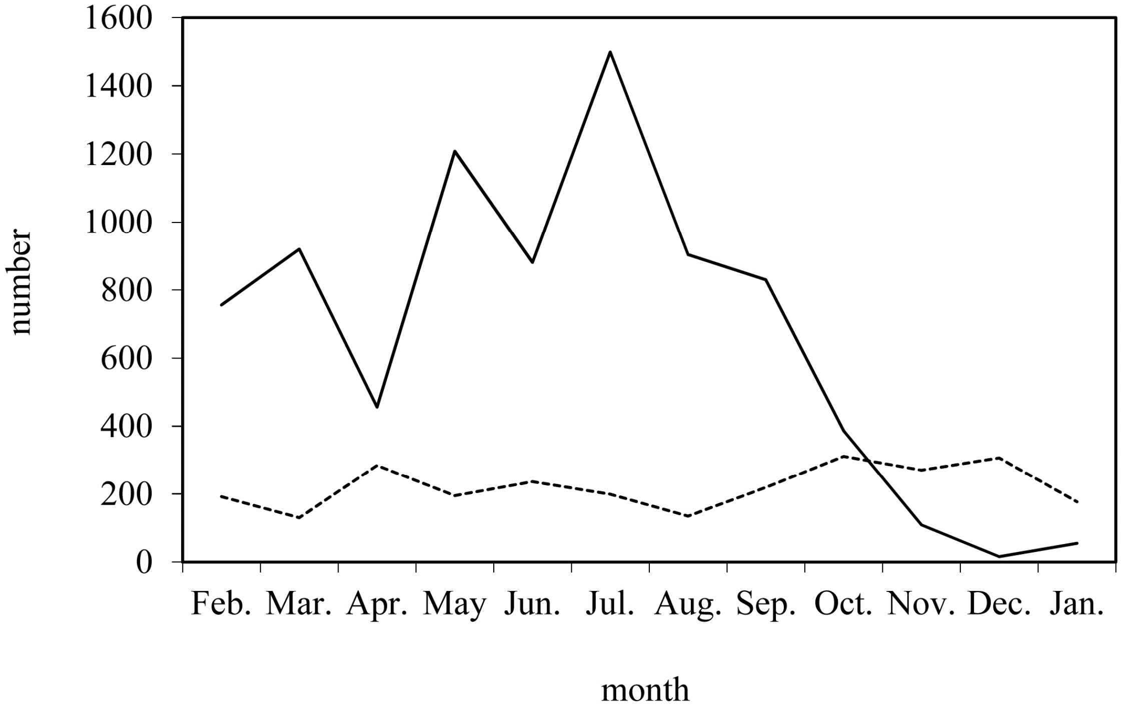


Fig. 2. The individual numbers of beetles captured in subtropical Fushan (—) and in tropical Nanjenshan (---) monthly from February 2001 to January 2002.

Of the Lampyridae, only larvae were caught. Of the trapped Scarabaeidae, there were seven melolonthides species and 21 coprophagides species. The average activity of the beetles in tropical Nanjenshan varied little during the four seasons. In contrast, the monthly activity of the beetles in subtropical Fushan declined during autumn and reached its lowest activity the winter months (Fig. 2).

The nine dominant beetle families represented 97% of all trapped beetles in Fushan. Staphylinidae was the most dominant beetle group and accounted for 46% of the trapped beetles (Fig. 3a). Leiodidae, Carabidae and Hydrophylidae combined made up 35.2% of all trapped beetles. Scarabaeidae was a subdominant group, comprising 9.7% of all trapped beetles; 98.6% of the trapped Scarabaeidae were Aphodiinae and Scarabaeinae. According to the control group, other captured scarabaeids were herbivorous species and probably only fell into the traps by chance. Silphidae, Trogidae and Histeridae were also collected, but only a few. Only three species of Silphidae were caught, and all of them in the carcass-baited traps. Both the Trogidae and Histeridae contained only one dominant species each, making up more than 92% of the trapped beetles in their respective family. Only a few lampyrid larvae were found in the carcass-baited pitfall traps.

In Nanjenshan, no Silphidae or Trogidae were captured. The other seven families represented 97.5% of all the beetles. Staphylinidae, Leiodidae, Scarabaeidae and Hydrophilidae were the dominant groups, comprising 90% of all the individuals. Of the Scarabaeidae, less than 1% of the trapped scarab beetles were herbivorous

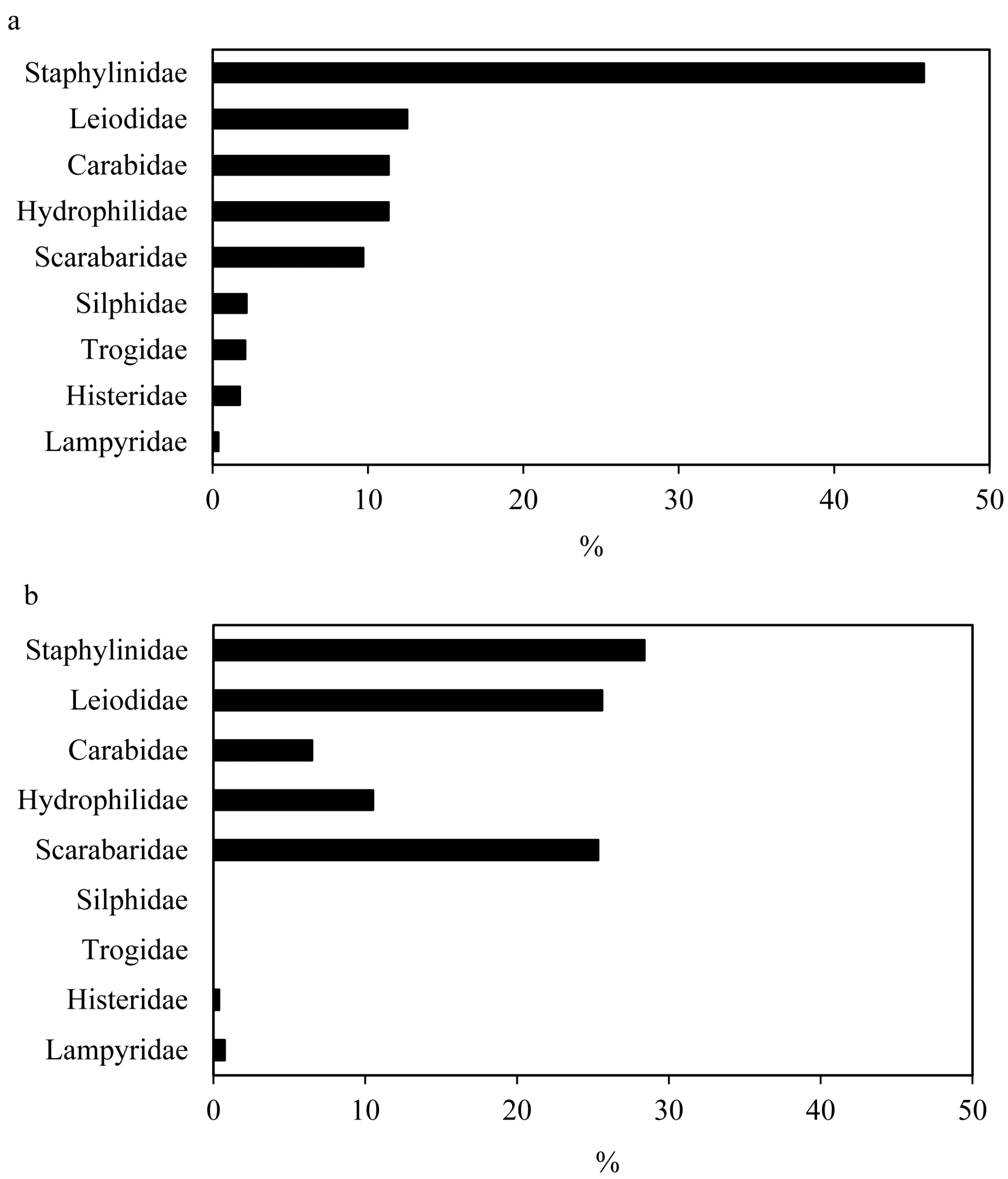
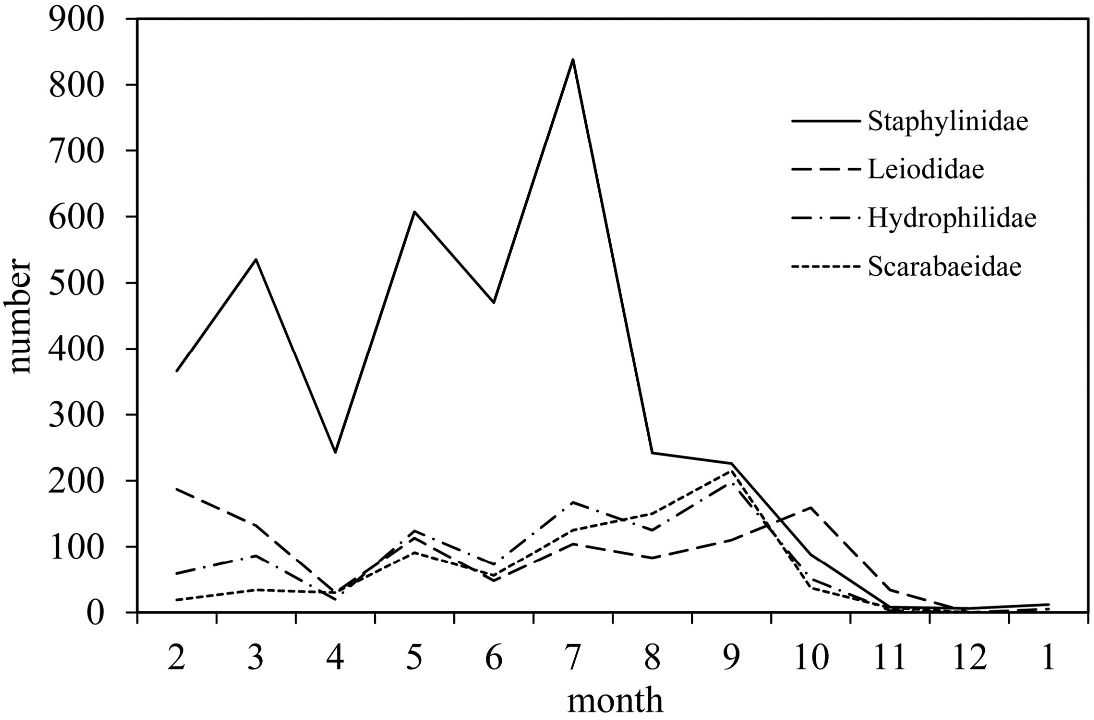


Fig. 3. Percentage of all trapped beetles belonging to nine coleopteran families in (a) Fushan and (b) Nanjenshan.

species, and the rest were aphodiines and scarabaeines. Carabidae was a subdominant group in Nanjenshan. In the tropics, the carabids were found mainly in meadows, in particular at two locations near Nanren Lake. In the tropical forest, only 10 carabids were trapped during the 12-month study, and only 10 individuals of Histeridae were trapped in Nanjenshan (Fig. 3b).

a



b

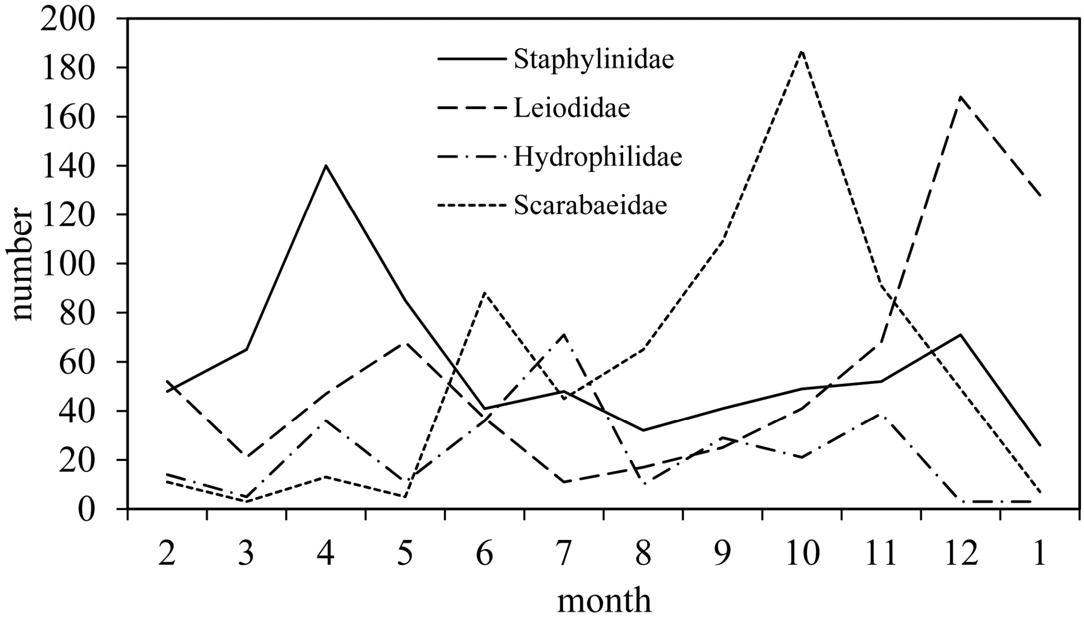


Fig. 4. Activity of the four dominant necrophilous families, Staphylinidae, Leiodidae, Hydrophilidae and Scarabaeidae (Aphodiinae and Scarabaeinae only), in (a) Fushan and (b) Nanjenshan.

Table 1. List of species and percentage of trapped Aphodiinae and Scarabaeinae in Fushan and Nanjenshan, Taiwan

Species	Fushan	Nanjenshan
Aphodius taiwanicus Petrovitz 1976	2.2	
Cassolus gotoi Masumoto 1986	11.0	
Copris fukiensis Balthasar 1941	1.6	
Haroldius hwangi Masumoto, Lee and Ochi 2005	1.4	
Onthophagus anguliceps Boucomont 1914	5.9	
Onthophagus formosanus Gillet 1924	2.0	89.9
Onthophagus hayashii Masumoto 1991	28.9	
Onthophagus hsui Masumoto, Chen and Ochi 2004	0.5	
Onthophagus kiuchianus Masumoto, Yang and Ochi 2004	15.1	
Onthophagus klapperichi Balthasar 1954	3.1	
Onthophagus miyakei Ochi and Araya 1992	0.3	
Onthophagus proletarius Harold 1875	2.6	0.1
Onthophagus roubali Balthasar 1935	1.8	
Onthophagus sauteri Gillet 1924	16.9	4.9
Onthophagus trituber Wiedemann 1823	1.8	
Onthophagus wangi Masumoto, Chen and Ochi 2004		0.1
Onthophagus yangi Masumoto, Tsai and Ochi 2006	1.7	
Panelus crenatus Nomura 1973	1.8	4.9
Paragymnopleurus ambiguous Janssens 1943	0.5	
Rhyssemus nanshanchicus Masumoto 1977	0.4	
Synapsis masumotoi Ochi 1992	0.4	

Table 2. Species diversities of the aphodiine and scarabaeine fauna in Fushan and Nanjenshan, Taiwan

Index	Fushan	Nanjenshan
Species richness	20	5
Individual number	764	673
Simpson's Index	0.85	0.19
Shannon-Wiener Index	2.25	0.41
Evenness	0.75	0.26

The activity periods of the staphylinids, leiodids, hydrophilids, scarabaeids (Aphodiinae and Scarabaeine) differed between Fushan and Nanjenshan. In Fushan, the Staphylinidae were active in spring and summer, whereas the other three families were active in autumn (Fig. 4a), with the exception of a few species of Leiodidae (the genus *Catops* Paykull), which are stenothermic and are active at low temperatures in the early spring. In comparison, in tropical Nanjenshan, these four families had different active periods (Fig. 4b). The Staphylinidae were at their most active in April, Hydrophilidae in July, Scarabaeidae in October, and Leiodidae in December.

Between February 2001 and January 2002 a total of 1,437 individuals from 21 species of Scarabaeidae were trapped in Fushan and Nanjenshan (Table 1). A total of 764 individuals from 20 species were collected in Fushan and 673 from five species in Nanjenshan. The diversity and evenness were higher in subtropical Fushan than in tropical Nanjenshan (Table 2). The monthly Shannon-Wiener

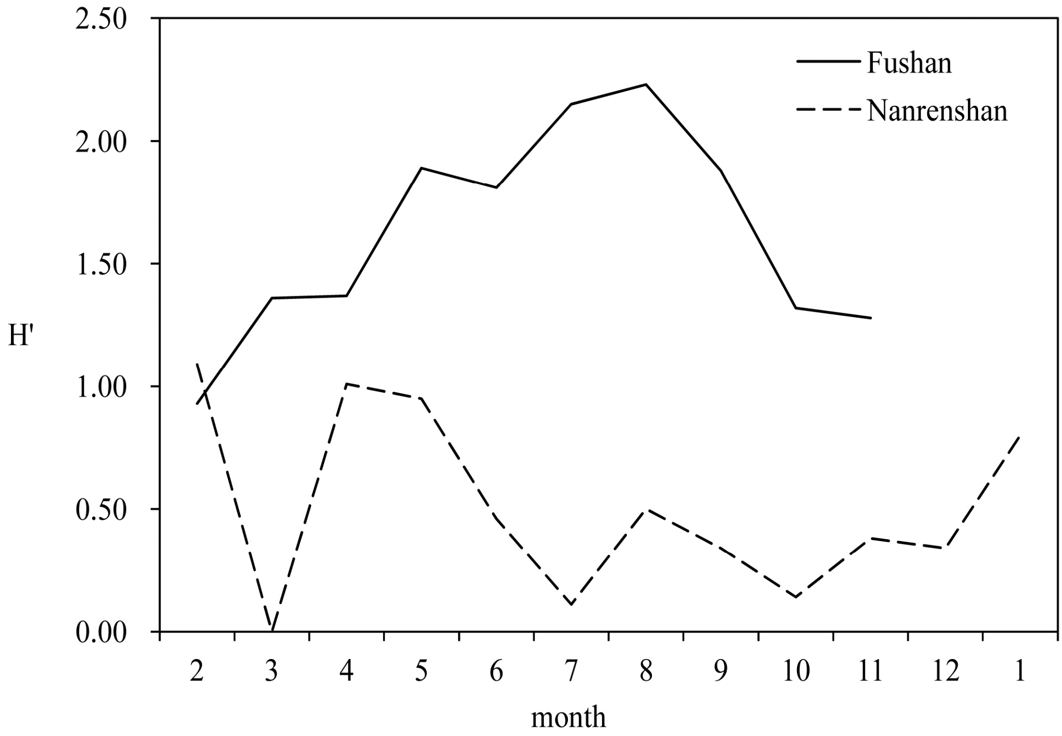


Fig. 5. The monthly Shannon-Wiener Index (H') of necrophilous dung beetles in Fushan and in Nanjenshan from February 2001 to January 2002.

Indices of necrophilous dung beetles in Fushan from February 2001 to January 2002 were compared with the indices in Nanjenshan. It was found that the diversities were significantly higher in Fushan than in Nanjenshan (Mann-Whitney U-test: $p < 0.001$) (Fig. 5). *Onthophagus hayashii*, *O. sauteri*, *O. kiuchianus* and *C. gotoi* were the four dominant species in Fushan (8.9, 16.9, 15.1, and 11.0%, respectively, of all individuals caught). In Nanjenshan, the dominant species was *O. formosanus*, amounting to 89.9% of all individuals taken. They also appeared in Fushan, but as a minority species.

In Fushan the peak activity period of scarabaeids depended upon the season. The activity period of *O. sauteri* was in the summer, while the activity of *O. kiuchianus* and *O. hayashii* approached its maximum in September, and *C. gotoi* was active at the end of the summer (Fig. 6). In the spring and at the beginning of the summer, only a few individuals of *O. formosanus* were trapped in Nanjenshan, but their activity peaked in October 2001.

To compare the species that appeared in the forest with those that appeared in the meadow, the number of species of all necrophilous Aphodiinae and Scarabaeinae in Fushan and Nanjenshan were analyzed together (χ^2-test: $p > 0.5$, $df = 1$). Although the number of species showed no habitat preferences, the number of individuals indicated a preference for the forest habitat (χ^2-test: $p < 0.001$, $df = 1$) (Table 3). *Onthophagus proletarius* and *O. trituber* preferred the meadow (Wilcoxon signed rank test: $p < 0.05$, n = 12), whereas *C. gotoi, Copris fukiensis* Balthasar, *O. hsui*, *O. formosanus*, *O. kiuchianus*, *O. klapperichi*, *O. hayashii*, and *O. sauteri* favored the

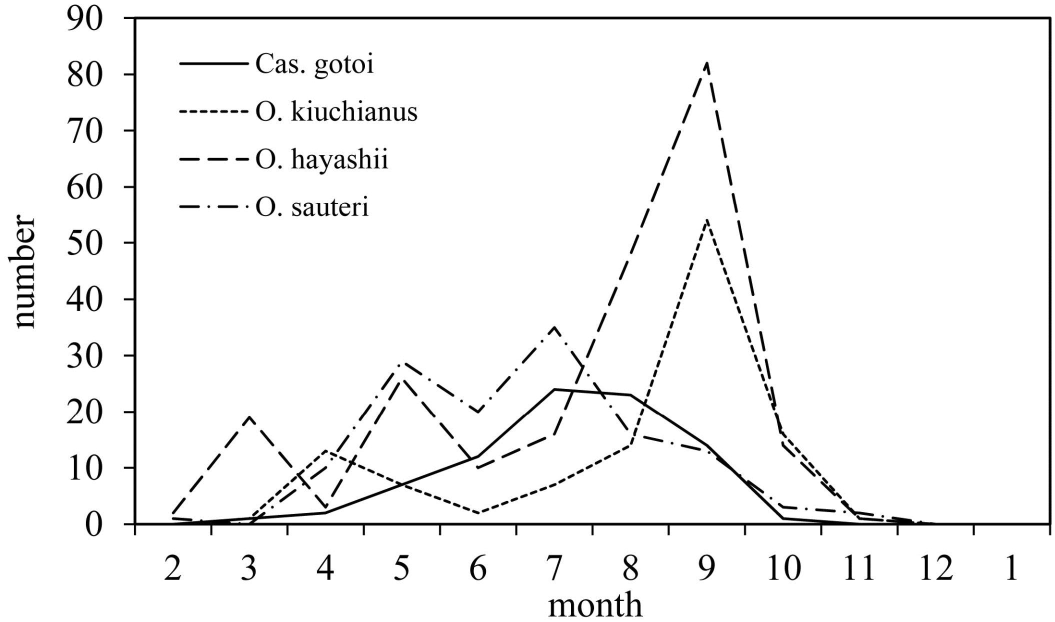


Fig. 6. The number of captured beetles of *Cassolus gotoi*, *Onthophagus kiuchianus*, *Onthophagus hayashii* and *Onthophagus sauteri* from February 2001 to January 2002 in subtropical Fushan.

Table 3. The number of species and individuals of Aphodiinae and Scarabaeinae distributed in the forest and in the meadow in Fushan and Nanjenshan, Taiwan

	Location	Fushan	Nanjenshan
No. of species	forest	17	5
	meadow	11	1
No. of individuals	forest	708	660
	meadow	56	13

forest. (Wilcoxon signed rank test: $p < 0.05$, n = 12). In Fushan, *Panelus crenatus* appeared mainly in the forest (Wilcoxon signed rank test: $p < 0.05$, n = 12), although it was caught in both the forest and in the meadow in Nanjenshan (Wilcoxon signed rank test: $p = 0.641$, n = 12).

Discussion

In our study, the carrion was protected from larger carrion eaters by a cage. Thus, we were unable to determine how much carrion is usually taken by vertebrates on open land. In temperate zones, 60-100% of the small carrion is eaten by vertebrates (Akopyan, 1953; Stoddart, 1970; Putman, 1976). Hwang (2006) found that in subtropical Fushan, 75% of the carrion placed in the field was eaten by vertebrates, while in tropical Nanjenshan, less than 20% was eaten by vertebrates. The availability of carrion depends on the rate of decomposition. The make-up of the micro-communities on the decomposing carrion depends on the environmental conditions at that time.

The factor that influences the decomposition rate the most is the temperature (Swift *et al*., 1979). The average monthly temperature in Fushan is 4.5°C lower than in Nanjenshan. In Nanjenshan during the winter months the carrion was completely decomposed within four days, while in Fushan in the winter the carrion had not even started to decompose four days after being placed outside (Hwang, 2006). In tropical Nanjenshan, the number of trapped beetles was almost constant in each month. In cooler subtropical Fushan, the persistence of the microhabitats became longer, because the slower decomposition allowed the beetles a better chance to find carrion. Thus, from spring to autumn, the number of trapped beetles in Fushan was higher than in Nanjenshan; but in the winter, the lower temperature resulted in the beetles being less active in Fushan than in Nanjenshan.

Inter- and intraspecific competitions are expected if 1) two individuals/species use the same resource, and 2) the availability of that resource is limited and decreases after use by an organism (Müller, 1983). Therefore, competition is expected between necrophilous species. Although interspecific competition can cause the exclusion of one of the competing species, it is more common for a characteristic divergence to evolve under this situation (Müller, 1983). If there is no competition for carrion micro-habitats, then all species will appear to have a similar distribution and activity pattern all year round, or there is a temporary niche differentiation of the species. In Nanjenshan the four dominant necrophilous families, Staphylinidae, Leiodidae, Hydrophilidae and Scarabaeidae had separate activity periods, while in Fushan most of their activity periods overlapped. We believe that the quality and quantity of the available resource resulted in different competitive pressures, causing different activity patterns in the tropics and the subtropics.

In the last century, it was proposed that species richness varies with latitude. The further a site is away from the equator, the lower the species richness is (Dobzhansky, 1950). However, this is not true for all animal groups (Janzen, 1981). Our results in tropical Nanjenshan and subtropical Fushan showed that the species communities of necrophilous beetles showed the opposite pattern. The carcass-baited trapped necrophilous beetle communities in Fushan were not only species richer, they also were more diverse than those in Nanjenshan, due to the difference in decomposition rate between the tropics and the subtropics. In addition, from October to April the Heng Chung area is subject to the Northeast monsoon, when strong winds blow down from the mountains to the ground at 10-17 m per second. In Nanjenshan, there were only five species of necrophilous beetles, and one of them made up 90% of the total number of beetles caught. Since Nanjenshan has a tropical climate and is warmer than subtropical Fushan, it is obvious that temperature is an important factor in the decomposition rate of a carcass (Swift *et al*., 1979; Nishida, 1984). The microhabitat on a carcass will be shorter in a warmer environment, and thus the exploitation of that carcass will be limited. This may lead to competitive exclusion between species using the same resources (MacArthur and Levins, 1964; Levins, 1968). In Nanjenshan most of the mouse carcasses were decomposed by maggots and ants (Hwang, 2011), and the necrophilous dung beetles were obviously disadvantaged in the competition for resources.

Some scarab beetles in the subfamilies Aphodiinae and Scarabaeinae (Coleoptera: Scarabaeidae) which feed partly or exclusively on feces are usually called dung beetles. All dung-beetle species in tropical grasslands are basically coprophagous (Halffter and Matthews, 1966) and use droppings of large herbivores. However, from the grasslands to the tropical forests, a complete switch in species composition was observed (Halffter and Matthews, 1966; Howden and Nealis, 1975; Janzen, 1983). Some scarab beetles species in tropical forests became necrophagous (Viljanen, 2004). Previous studies have shown that many smaller “dung beetle” species are necrophagous while most of the larger ones utilize both dung and carrion as nutrition (Hanski, 1983b; Boonrotpong *et al*., 2004). The scarab beetles that were often attracted to carcass-baited pitfall traps in Fushan were *O. hayashii*, *O. sauteri*, *O. kiuchianus* and *C. gotoi*, and the separation of their niches was not obvious. The temporal separation of their niches was only evident for *O. sauteri* and *C. gotoi*. The activity periods of *O. hayashii* and *O. kiuchianus* were almost identical, with their activity reaching its peak in September. The patchiness and temporary nature of resources (carrion) increases the chance for the coexistence of species that use the same resource (Horn and MacArthur, 1972; Slatkin, 1974; Hanski, 1981, 1983a). Estrada *et al*. (1998) found that in South America there were more dung beetle species in the forest than in pastures. The number of species decreases as the forest turns into pastures (Howden and Nealis, 1975; Klein, 1989; Montes de Oca and Halffter, 1995). The same result was also observed in the present study. The number of beetles in the forest habitat is significantly higher than that in the meadows of subtropical Fushan and tropical Nanjenshan. All wind, solar radiation, temperature and humidity conditions are not suitable for all beetle species (Hanski, 1989; Gill, 1991). Due to the rapid drying by the air in the meadows, mummified carrion becomes unattractive as a food source to necrophilous beetles.

In conclusion, necrophilous insect fauna depend mainly on the limited and somewhat unpredictable resource of animal carcasses. Therefore, surviving their environment as well as their competition is the most difficult evolutionary challenge for each carrion species. Based on the qualitative and quantitative results in this study, we believe that the environmental factors, such as temperature, wind and sunshade, strongly affect the availability of the carrion used by beetles, thereby affecting the species abundance and diversity. Different survival strategies evolved under intense resource competition, resulting in the various patterns of species diversity, seasonal activity and niche separation seen in these tropical and subtropical areas.

Acknowledgments

We would like to thank K. Masumoto, Institute of Human Living Sciences, Otsuma Women’s University, for identifying the dung beetle species, Jung-Tai Chao, Taiwan Forestry Research Institute, and Ping-Chun Lucy Hou, National Cheng Kung University, for their support and assistance in this experiment; as well as J. K. Müller, Albert-Ludwigs-Universität Freiburg i. Br., for his guidance. This work was supported by the National Science Council of Taiwan, ROC under grant nos. NSC98-2631-H-002-010 and NSC96-2422-H-002-021, by the Institute of Forensic Medicine, Ministry of Justice, Taiwan, ROC under grant nos. IFM90-M04 and IFM91-M02, and the postdoctoral fellowship funding (National Taiwan University- Aim for the Top University Project).

References

Akopyan MM. 1953. The fate of suslik corpses on the steppe. Zool Zh 32: 1014-1019.

Allee WC, Emerson AE, Park O, Park T, Schmidt KP. 1949. Principles of animal ecology. Philadelphia: W. B. Saunders Co. 837 pp.

Boonrotpong S, Sotthibandhu S, Pholpunthin C. 2004. Species composition of dung beetles in the primary and secondary forests at Ton Nga Chang Wildlife Sanctuary. Sci Asia 30: 59-65.

Dobzhansky T. 1950. Evolution in the tropics. Am Sci 38: 209-221.

Estrada A, Coates-Estrada R, Dadda AA, Cammarano P. 1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. J Trop Ecol 14: 577-593.

Fuller ME. 1934. The insect inhabitants of carrion, a study in animal ecology. Aus Counc Sci Indu Res Bull 82: 5-62.

Gill BD. 1991. Dung beetles in tropical American forest. pp 211-229. In: Hanski I, Cambefort Y (eds). Dung Beetle Ecology. Princeton University Press, Princeton.

Halffter G, Favila ME. 1993. The Scarabaeinae (Insecta: Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity in tropical rain forests and modified landscapes. Bio Int 27: 15-21.

Halffter G, Favila ME, Halffter V. 1992. A comparative study on the structure of scarab guild in tropical rain forests and derived ecosystems. Folia Entomol Mex 84: 131-156.

Halffter G, Matthews EG. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). Folia Entomol Mex 12-14: 1-312.

Hanski I. 1981. Coexistence of competitors in patchy environment with and without predation. Oikos 37: 306-312.

Hanski I. 1983a. Coexistence of competitors in patchy environment. Ecology 64: 493-500.

Hanski I. 1983b. Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forests in Sarawak, Borneo. Acta Zool Fenn 167: 1-45.

Hanski I. 1989. Dung beetles. pp 489-511. In: Lieth H, Werger MJA (eds). Tropical Rain Forest Ecosystems. Elsevier Science Publishers B.V., Amsterdam.

Horn HS, MacArthur RH. 1972. Competition among fugitive species in a harlequin environment. Ecology 53: 749-752.

Howden AT. 1950. The succession of beetles on carrion [M.S. thesis]. Raleigh (NC): North Carolina State College. 83 pp.

Howden HF, Nealis VG. 1975. Effects of clearing in a tropical rain forest on the composition of coprophagous scarab beetle fauna (Coleoptera). Biotropica 7: 77-83.

Hwang W. 2006. Konkurrenz und Aasnutzung necrophager und necrophiler Käfer in Nord- und Sudtaiwan mit einem Beitrag zur Biologie von *Nicrophorus nepalensis* Hope (Coleoptera: Silphidae) [Ph.D. dissertation]. Germany: Albert-Ludwigs-Universität Freiburg. 108 pp.

Hwang W. 2011. Environmental variables affecting community composition and carcass utilization of necrophagous ant (Hymenoptera: Formicidae) in southern and northern Taiwan. BioFormosa 46(1): 21-31.

Janzen DH. 1981. The peak of North American ichneumonid species richness lies between 38° and 42°N. Ecology 62: 532-537.

Janzen DH. 1983. Seasonal changes in abundance of large nocturnal dung beetle (Scarabaeidae) in Costa Rican deciduous forest and adjacent horse pasture. Oikos 41: 274-283.

Johnson MD. 1975. Seasonal and microseral variations in the insect population on carrion. Am Midl Nat 93: 79-90.

Klein BC. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology 70: 1715-1725.

Levins R. 1968. Evolution in changing environments. Monogr Popul Biol 2: 1-120.

Lobo JM, Halffter G. 2000. Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles

(Coleoptera: Scarabaeoidea): a comparative study. Ann Entomol Soc Am 93: 115-126.

Lundt H. 1964. Ökologische Untersuchungen uber die tierische Besiedlung von Aas im Boden. Pedobiologia 4: 158-180.

MacArthur R, Levins R. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proc Natl Acad Sci USA 51: 1207-1210.

Montes de Oca ET, Halffter G. 1995. Daily and seasonal activities of a guild of the coprophagous, burrowing beetle (Coleoptera: Scarabaeidae: Scarabaeinae) in tropical grasslands. Trop Zool 9: 159-180.

Müller JK. 1983. Konkurrenzverminderung durch ökologische Sonderung bei Laufkäfern (Coleoptera: Carabidae) [Ph.D. dissertation]. Germany: Albert-Ludwigs-Universität Freiburg. 221 pp.

Nabaglo L. 1973. Participation of intertebrates in decomposition of rodent carcass in forest ecosystem. Ekol Pol 21: 251-269.

Nishida K. 1984. Experimental studies on the estimation of postmortem intervals by means of fly larvae infesting human cadavers. Jap J Legal Med 38: 24-41.

Nummelin M, Hanski I. 1989. Dung beetles in virgin and managed forests in Kibale Forest, Western Uganda. J Trop Ecol 5: 349-352.

Payne JA. 1965. A summer carrion study of the baby pig Sus scrofa Linnaeus. Ecology 46: 592-602.

Payne JA, Crossley DJ. 1966. Animal species associated with pig carrion. Union Carbide Corporation for the U.S. Atomic Energy Commission: Oak Ridge National Laboratory, ORNL-TM-432. 70 pp.

Putman RJ. 1976. Energetics of the decomposition of animal carrion [Ph.D. dissertation]. Oxford (UK): Oxford University. 372 pp.

Reed HB. 1958. A study of dog carcass communities in Tennessee, with special reference to the insects. Am Midl Nat 59: 213-245.

Ridsdill Smith TJ, Weir A, Peck B. 1983. Dung beetles (Scarabaeidae Scarabaeinae and Aphodiinae) active in forest habitats in southwestern Australia during winter (Note). J Aust Entomol Soc 22: 307-309.

Slatkin M. 1974. Competition and regional coexistence. Ecology 55: 128-134.

Stoddart LC. 1970. A telemetric method for detecting jack rabbit mortality. J Wildl Manage 34: 501-507.

Swift MJ, Heal OW, Anderson JM. 1979. Decomposition in Terrestrial Ecosystems. Oxford: Blackwell Scientific Publication. 372 pp.

Viljanen H. 2004. Diet specialization among endemic forest dung beetles in Madagascar. Biological and Environmental Sciences [M.S. thesis]. Finland: University of Helsinki. 35 pp.

Received: August 15, 2012
Accepted: November 19, 2012

熱帶與亞熱帶台灣親屍性甲蟲－特別是蜉金龜亞科 (Aphodiinae) 與金龜子亞科 (Scarabaeinae) (Coleoptera: Scarabaeidae) 物種組成與季節活躍的比較研究

黃文伯[1]、蕭旭峰[2*]

[1] 國立台南大學生態科學與技術學系
[2] 國立台灣大學昆蟲學系

摘　要

本研究比較南北台灣以屍體誘引所捕獲甲蟲的物種組成與季節性活躍，相對於南台灣地屬熱帶的南仁山受屍體吸引的甲蟲全年活躍，而甲蟲在北台灣亞熱帶福山則於冬天顯現不活躍的情況。四個最為優勢的親屍性科別（牙蟲科、球蕈蟲科、金龜子科與隱翅蟲科）在福山的活躍期較難區隔，但在南仁山此四個科別的活躍期則清楚分離。南仁山親屍性蜉金龜亞科與金龜子亞科的多樣性較福山為低，主要原因在於南仁山只有一個優勢種。整體來說，親屍性甲蟲在林地中的個體數目較草地為多。基於本研究結果，我們相信溫度、風與遮蔭等環境因子，強烈影響甲蟲對屍體資源的利用，進而改變物種的分布與多樣性，並基於資源的競爭而演化出不同的策略，因此得以檢測出物種多樣性、季節活躍與棲位區隔在熱帶與亞熱帶區域的不同模式。

關鍵詞：物種多樣性、物種豐量、棲位區隔、屍體動物相。

*論文聯繫人
Corresponding email: sfshiao@ntu.edu.tw