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行政院農業委員會特有生物研究保育中心 55244 南投縣集集鎮民生東路 1 號

Endemic Species Research Institute, Jiji, Nantou, Taiwan

*通訊作者：cswei@tesri.gov.tw

*Corresponding author: cswei@tesri.gov.tw

摘 要

台灣獼猴在台灣受到「野生動物保育法」所保護，但獼猴危害農作物卻使這種特有靈長類的保育工作遭遇質疑與阻礙。爲協助地方主管機關發展適當的管理策略以降低人猴間的衝突，我們於 2007-2008 年間調查台南縣台灣獼猴的族群分布、密度與危害農作的概況。先進行全縣山區的台灣獼猴普查，搜尋各種台灣獼猴存在的跡象證據，並設立 17 條固定調查樣線 (總長 100.5 km)，用以估算台灣獼猴的猴群密度。遇到農民時訪問發生台灣獼猴危害的地點、受害農作物種類及受害農地的所有權歸屬。結果發現台灣獼猴分布於台南縣境內東部山區 10 個鄉鎮的 24 個村里，受獼猴危害的地區有 7 鄉鎮 13 村里。估算台灣獼猴分布的闊葉林區中平均密度爲 0.637 群/km^2 (95%信賴區間：0.524-0.751 群/km^2)，比台灣的平均值 (0.722 群/km^2) 稍低。現有證據並不支持獼猴的密度與危害程度有關。估算全縣台灣獼猴有 100 群 (95%信賴區間：82-118 群)，不到全台灣總猴群數的 1%。芒果是被最多的受訪農民(76%)陳述受害的農作物種類。將近三分之二的受訪農民 (64%) 陳述受害農地屬於承租的國有林地，而國有林地並非爲農作物生產而放租。進行台灣獼猴危害農作物的管理時，地區族群是否有滅絕的危機及受害農地的土地利用是否合法皆是需要慎重考量的面向。

Abstract

The Taiwanese macaque (*Macaca cyclopis*) is protected by Wildlife Conservation Act in Taiwan, but crop-raiding by the species hinders conservation of the endemic primate. To assist local governments in developing management strategy to reduce this human-monkey conflict, we surveyed the population distribution and density of and crop-raiding by monkeys in Tainan County in southern Taiwan in 2007 and 2008. We surveyed mountainous areas in the whole county for any evidence of occurrence of the monkey and crop damage. Seventeen line-transects with a total length of 100.5 km were established to estimate density of monkey troops. We interviewed farmers encountered in order to survey the location, crop type, and ownership of the raided farmlands. We found that the Taiwanese macaques were distributed in 24 mountainous villages of ten townships. Monkeys damaged crops in 13 villages of seven townships. Density of monkey troops in the county's broadleaf forest was 0.637 troops/km^2 (95% confidence interval: 0.524 - 0.751 troops/km^2), a little lower than average in Taiwan (0.722 troops/km^2). No evidence supported an association between density of Taiwanese macaques and the degree of crop damage. Population size was estimated to be 100 troops (95% confidence interval: 82 - 118 troops) all over the county, accounting less than 1% of the whole Taiwanese macaque population. Mango was the most frequently damaged crop as reported by 76% interviewed farmers. Ownerships of 64% raided farmland were national forest, which are not supposed to be used for crop production. It is important to consider the probable extinction of local populations and the legality of producing crops in raided farmlands while managing crop-raiding by monkeys in Tainan County.

關鍵詞：分布、密度、猴群、農作物危害、人猴衝突

Keywords：distribution, density, monkey troop, crop damage, human-monkey conflict

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前　言

台灣獼猴 (*Macaca cyclopis*) (以下亦簡稱「獼猴」) 是台灣特有且唯一的非人類靈長類動物，廣泛分布於台灣本島各山區，但未分布到各離島 (Fooden and Wu 2001)。海拔3,600 m以下是其出現區域，而海拔2,500 m 以下的闊葉林爲其主要棲息地 (李及羅 1994; 李等

2000; Fooden and Wu 2001)。台灣本島11個縣與5個直轄市的範圍內皆有台灣獼猴的分布(Fooden and Wu 2001)，而在鄉鎮層級上，至少有111個行政區有獼猴出沒 (李等 2002)。過去台灣獼猴的分布涵蓋更廣，譬如清朝人郁永河於1697年便在今日台中市清水區的大肚台地山區記錄到獼猴的活動 (陳 2001)，但現今整個大肚台地已無台灣獼猴族群的分布 (Fooden and Wu 2001)。

台灣獼猴取食農作物造成危害 (以下亦簡稱「獼猴危害」或「猴害」) 是近年媒體報導台灣獼猴的重要原因之一，蔡 (2006) 統計2002至2006年間，至少有13個報刊134則新聞報導獼猴危害，地點涵蓋本島14個縣及1個直轄市，共25個鄉鎮市。李等 (2002) 發現台灣獼猴危害農作物的現象的確遍布本島的北、東、南、西，82%的鄉鎮級行政區有猴害的問題。張等 (1995) 在南投縣的調查發現有猴害的村里占獼猴分布村里的87.5%。張 (2000) 在苗栗、台中、彰化、雲林及南投等5縣調查到26個鄉鎮市有猴害，幾乎所有山區鄉鎮皆無法倖免。有台灣獼猴分布又有農作物種植的地區就很可能有猴害的發生。獼猴危害的現象常被認爲是1989年後台灣獼猴被列爲保育類動物後才出現的，因而受害地區居民多認爲解決獼猴危害、補償農民是政府的責任 (林 2008)。但早在Swinhoe (1863) 命名台灣獼猴時，便已描述猴群會侵襲甘蔗園和危害果樹 (特別是龍眼)；1989年前台灣獼猴尚承受不小的狩獵壓力時，危害農作物的情形也屢見報導 (Poirier and Davidson 1979; 李及林 1987)。

靈長類動物危害農作物並非台灣獨有的現象，在世界許多地方亦相當普遍，像在亞洲的獼猴屬動物 (*Macaca* spp.) (張及渡邊 2009; Chakravarthy and Thyagaraj 2005; Kumar *et al.* 2008; Marchal and Hill 2009; Mishra *et al*. 2006; Priston 2009; Riley 2007; Sahoo and Mohnot 2004; Sinha *et al.* 2006; Sprague and Iwasaki 2006; Suzuki and Muroyama 2010; Wang *et al.* 2006; Watanabe and Muroyama 2005) 及在非洲的狒狒屬動物 (*Papio* spp.) (Chism 2005; Forthman *et al.* 2005; Hill 1997; Hill 2005; Hill and Webber 2010; Naughton-Treves *et al*. 1998; Tweheyo *et al.* 2005; Warren 2008; Weyher *et al.* 2006) 與綠猴屬動物 (*Chlorocebus* spp., 過去曾歸爲同一種 *Cercopithecus aehtiops*) (Boulton *et al.* 1996; Hill 1997; Saj *et al*. 2001) 皆是造成農作物受害的主要動物類群。這些靈長類智力高，是機會主義者，雜食且食性廣，適應環境的能力強，具複雜社會組織、過著成群合作的生活，因此能成功入侵農地取食作物 (Else 1991; Sillero-Zubiri and Switzer 2001)。牠們臉部皆具有頰囊 (cheek pouches) 構造，能將食物暫儲在頰囊或靠著雙手拿取農作物帶離農地進食，提升取食的效率 (Priston 2009; Warren 2008)。取食農作物讓這些靈長類獲得生存上的優勢，包括覓食時間縮短、休息與社交時間增多、較早達到性成熟、首次生育年齡下降、生育間隔縮短、出生率上升及嬰猴死亡率降低等 (Else 1991; Muroyama and Yamada 2010; Strum 1991)，如同人工餵食增加營養的情況 (Muroyama and Yamada 2010; Sugiyama and Ohsawa 1982)，因此一旦學會利用農作物，便有依賴農地提供食物的傾向，使危害情形持續而逐漸普遍。

面對靈長類危害農作物的發生，除了少數地區農民可能因宗教因素 (Riley and Priston 2010) 或可發展觀光 (Baker and Schutt 2005) 而較能容忍外，多數農民的容忍度會因作物受害而降低 (Campbell-Smith *et al.* 2010)，因爲農

民實際的受損與爲了防治危害而付出的代價不小 (Hill 2000)，且因法律對靈長類的某種程度保護而使農民在認知上放大了被害的風險 (Naughton-Treves 1998)。許多靈長類因此遭到獵捕 (Kumar *et al.* 2008; Mishra *et al.* 2006; Muroyama and Yamada 2010)，生存面臨威脅。今日許多靈長類物種有滅絕的危機，已是世界性的保育對象，靈長類危害農作物則是世界性的保育議題 (Priston 2009)。由於農作物受害會削弱地方居民對保育的支持，也使保育工作的努力受挫 (Sprague and Iwasaki 2006; Tweheyo *et al.* 2005)，因此靈長類危害農作物的問題若管理不當將會導致日後的保育危機 (Forthman *et al.* 2005)。

台南縣 (現已併入台南市，詳見「研究地點」之說明) 的開發歷史早，耕地面積是全台各縣之冠 (維基百科 2013)，但東半部仍有山脈與丘陵分布，棲息著野生台灣獼猴族群 (李等 2000; 張等 1998; 謝等 2007)。在盛產水果的玉井與南化等鄉鎮，獼猴危害的情事陸續被媒體報導 (蔡 2006)。林及張 (1994) 指出南化鄉烏山地區一群接受人工餵食的野生台灣獼猴在龍眼盛產期會遠離餵食區，入侵附近的龍眼園造成危害。南化鄉公所還曾因此補助農民捕捉造成危害的台灣獼猴。

由於獵捕屬保育類野生動物的台灣獼猴必須符合「野生動物保育法」的規範，最直接提及與危害農作物相關的條文是第 21 條：「野生動物有下列情形之一，得予以獵捕或宰殺……。但保育類野生動物除情況緊急外，應先報請主管機關處理：一、有危及公共安全或人類性命之虞者。二、危害農林作物、家禽、家畜或水產養殖者」(後略)；但另有第 18 條規定：「保育類野生動物應予保育，不得騷擾、虐待、獵捕、宰殺或爲其他利用。但有下列情形之一，不在此限：一、族群量逾越環境容許量者」(後略) (行政院農委會林務局 2013)。由於民間聽聞獼猴危害農作物時常表達是獼猴過多所致 (個人觀察)，2007 年野生動物保育地方主管機關台南縣政府亦認爲有必要從台灣獼猴族群是否已逾越環境容許量的角度思考獼猴危害的管理問題，因此委託行政院農業委員會特有生物研究保育中心進行台南縣台灣獼猴的族群分布與數量調查，並同時查訪農作物受獼猴危害的概況，試圖瞭解族群量與危害間的關係，並以此作爲猴害處理的參考依據。

材料與方法

一、研究地點

本研究調查的區域涵蓋原台南縣轄下的各鄉鎮市範圍 (東經 120 度 01 分 36 秒 - 120 度 38 分 53 秒；北緯 22 度 53 分 05 秒 - 23 度 24 分 30 秒)，由於 2010 年 12 月 25 日台南縣已與原台南市合併升格爲一新直轄市──台南市 (臺南市政府 2013)，「台南縣」此行政區現已不復存在，各原「鄉」、「鎮」、「市」更名爲「區」，但行政轄區範圍未變。因本研究進行期間 (2007 年 9 月至 2008 年 9 月)，各行政轄區仍爲台南縣與所屬鄉、鎮、市，爲反應調查期間各地的原本實際地名，本文仍以台南縣及各鄉鎮市的舊稱描述。

二、全縣普查

台灣獼猴棲息於各類森林中，但以闊葉林較爲常見，且一群台灣獼猴的活動範圍約需 1 km^2 左右 (李等 2000)，因此全縣獼猴族群普查時，將搜尋的區域侷限在山區有大面積樹林的鄉鎮，包括白河、東山、六甲、大內、玉井、

楠西、南化、新化、左鎮、龍崎等。

進行全縣普查時，利用台南縣境內主要道路，結合相銜接的產業道路與林道，以開車及走路方式，藉由自行觀察與訪問當地居民，調查各山區台灣獼猴族群分布的地點。除直接目視外，台灣獼猴的叫聲、食痕及排遺等跡象亦是判斷台灣獼猴在當地出沒的根據，居民受訪的資料亦列入參考。另行政院農業委員會特有生物研究保育中心執行之台南縣市野生動物資源調查 (鄭 2008) 在各主要山區架設 13 部紅外線自動感應相機，所拍攝到之台灣獼猴出現紀錄亦作爲本研究分布點的補充資料。

三、固定樣線調查

根據全縣普查的初步結果，選取固定樣線進行穿越線調查，藉以推估台南縣台灣獼猴主要分布地區的猴群密度。由於闊葉林是台灣獼猴的主要棲息地 (李等 2000)，因此選取闊葉林面積較大片、完整且有道路或登山小徑可接近之區域。部分有獼猴分布的鄉鎮 (如玉井)，因其境內的闊葉林與果園緊密鑲嵌，且闊葉林面積小、分布零散，不適合作爲密度估算的調查範圍，故未選取。共選定 17 條固定調查樣線，涵蓋的鄉鎮有白河、東山、楠西及南化。所有固定樣線的總長度爲 100.5 km，其中最長的爲 15.4 km，最短的爲 0.9 km，平均爲 5.9 km。海拔範圍 118 - 1,244 m (最高點爲台南縣最高峰大凍山山頂) (表 1；圖 1)。

表 1. 爲調查台南縣台灣獼猴族群密度所設立之固定調查樣線的名稱代號、地區、長度及海拔範圍

Table 1. Code, location, length, and elevation of the line transects designated to estimate the density of the Taiwanese macaques in Tainan County

Code of transect	Location		Length (km)	Elevation (m)
	Township	Region		
1	Baihe (白河鎭)	Zhentou Mountain (枕頭山)	6.9	290 - 585
2	Baihe	South Bank of Baishuei River (白水溪南岸)	3.2	169 - 281
3	Baihe	Dadong Mountain (大凍山)	12.0	502 -1,244
4	Dongshan (東山鄉)	Erjian Mountain (二尖山)	2.7	613 - 873
5	Dongshan	North Bank of Zengwen River (曾文溪北岸)	5.5	118 - 186
6	Dongshan	Jialinhu (嘉林湖)	7.6	199 - 682
7	Dongshan	Kantou Mountain (崁頭山)	5.9	590 - 977
8	Nanxi (楠西鄉)	Outside of Nanxi Tunnel (楠西隧道口)	0.9	192 - 282
9	Nanxi	Huaban Mountain (花瓣山)	4.1	149 - 841
10	Nanxi	Mazhuhu (麻竹湖)	1.9	234 - 541
11	Nanxi	Nanshan Forest Road (南山林道)	4.4	205 - 619
12	Nanhua (南化鄉)	Wushan Hiking Trail (烏山登山步道)	12.5	144 - 735
13	Nanhua	County Road # 179 in Guanshan Village (關山村 179 縣道)	15.4	235 - 423
14	Nanhua	Shuangdong (雙冬)	4.8	188 - 263
15	Nanhua	Pingkeng Productive Road (平坑產業道路)	5.7	237 - 359
16	Nanhua	Jiaxian Forest Road (甲仙林道)	3.5	251 -734
17	Nanxi & Nanhua	Sanjiaonan Mountain (三角南山)	3.6	918-1,035
	Total		100.5	118 - 1,244

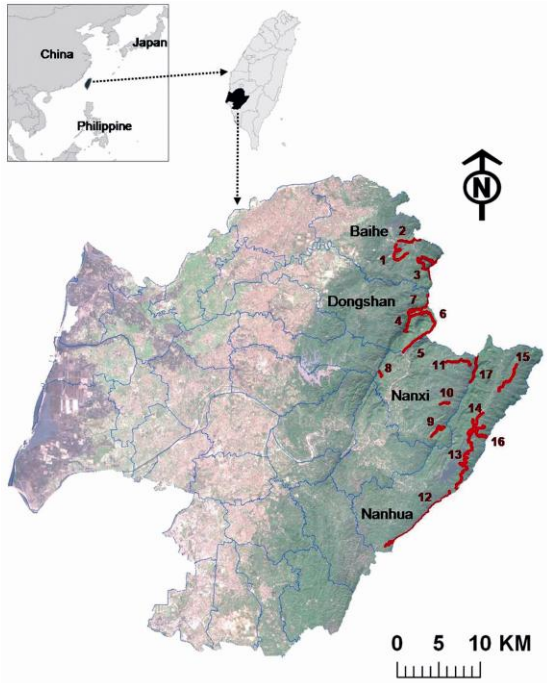

圖 1. 爲估算台南縣台灣獼猴密度所選定的 17 條固定調查樣線 (紅色線條) 位置圖，樣線代號請參照表 1。底圖是空照圖，顏色代表地表的狀況，綠色部分爲有植被地區，包括森林與農地。

Fig. 1. Map of the 17 line transects (in red lines) designated to estimate the density of the Taiwanese macaques in Tainan County. The codes of line transects are shown in Table 1. The underlying map is the true-color image of earth taken from airspace. Green areas include forests and farmlands with green plants.

進行固定樣線調查時，以緩慢步行 (每小時走 1 - 2 km)、肉眼與雙筒望遠鏡觀察，並輔以聽聞獼猴叫聲的方式，尋找台灣獼猴的個體。發現獼猴時，記錄時間、數量、年齡與性別組成、人猴間的直線距離、水平角、俯仰角、棲地類型及 GPS 座標。人猴間的直線距離是指猴群中第一隻被目擊的獼猴個體與觀察者的直線距離，以雙筒雷射測距儀 (Bushnell Corporation, USA) 測量。水平角是指觀察者與猴群之間的連接直線在水平面上與固定樣線的夾角。俯仰角是指觀察者與猴群的連接直線與水平面的夾角。由人猴間的直線距離、水平角及俯仰角可計算出猴群與固定調查樣線在水平面上的最短距離。每一條固定樣線皆進行 3 次調查，調查期間分別是：2008 年 2 月 4 日至 4 月 11 日、4 月 22 日至 7 月 4 日及 7 月 2 日至 8 月 21 日。

固定樣線的調查時間是以天亮後至上午 11 時之前與下午 2 時至天黑前爲主，以配合猴群較活躍的時間，總調查時間爲 176.6 小時。天氣方面以晴天與陰天爲主，若遇大雨則暫停調查。若雨不大，且不影響搜尋、觀測猴群的視線，則繼續調查。此乃因降雨不多時，猴群仍會繼續活動，雨大時才會移棲躲雨 (個人觀察)。

步行尋找台灣獼猴時，以滾輪測距儀記錄行進的距離，沿途並記錄各種棲地類型占樣線長度的比例。例如：步行固定樣線 100 m，沿途皆是闊葉林則記錄闊葉林 100 m；若樣線兩側各爲果園與闊葉林，或果園與闊葉林鑲嵌並存、且二者所占比例皆超過 25%，則二者所占的長度皆爲 50 m；若有 3 種棲地類型、且所占比例皆超過 25%，則 3 者所占的長度皆爲 33.3 m。同一範圍中不同棲地類型分占的百分比以目測估計。每一條固定樣線棲地類型測量的工作各進行 3 次，分析時取其平均值。

四、族群密度估算

台灣獼猴是群居性動物，常態的猴群組成包含成年雌、雄猴與未成年猴，非屬常態猴群成員的雄性孤猴與雄性光棍群占總族群量的

比例少，且結構零散不易估算，因此僅以常態猴群作爲族群密度估算的對象。由於台灣獼猴主要分布在闊葉林地 (李等 2000)，因此本研究估算的台南縣猴群密度是以全縣的闊葉林地爲目標區域，假設猴群在台南縣的闊葉林中均勻分布，且在非闊葉林中的數量極微而可以忽略。取樣時僅選用固定樣線中屬闊葉林的範圍作爲密度估算的樣區。

每次固定樣線觀察之猴群數除以某區域 (全縣、特定區域或單一樣線) 取樣範圍中測量之闊葉林所占樣線長度，即得單位取樣長度中的猴群量，以此做爲猴群的相對密度 (群/km)。相對密度即能作爲地區間族群量比較的合理根據 (Ross and Reeve 2003)。固定樣線的 3 次觀察視爲 3 次重複。以統計軟體 R 3.0.0 執行變方分析 (ANOVA)，檢測各地區間族群密度有無差異。若差異顯著則再做 Tukey 多重比較，以找出存在差異的地區。所有觀測之猴群相對密度皆取其平方根進行變方分析，以配合常態分布的前提需求。

爲估算猴群的絕對密度 (群/km^2)，須先決定調查樣線的有效觀察距離，以求得有效取樣的面積 (李等 2000; 蘇等 2011)。

有效取樣面積 ＝ 固定樣線長度 × 有效觀察距離 × 2

“× 2”是因固定調查樣線的兩側皆爲取樣範圍。

有效觀察距離受猴群可被偵測的能見度影響，因此以實際觀察到猴群時測量並計算出之猴群與固定樣線在水平面上的最短距離作爲決定有效觀察距離的參考依據 (李等 2000; 蘇等 2011)。

五、跡象記錄

進行全縣普查與固定樣線調查時，除記錄親眼目視的台灣獼猴個體外，亦會記錄沿途發現的獼猴排遺、食痕與叫聲，做爲獼猴分布點的輔助資料。若發現農民防治台灣獼猴危害農作物的相關設施 (如圍籬、布旗或反光條帶等) 亦一併記錄，作爲獼猴危害發生的佐證。獼猴的排遺可由形狀、大小與內容物判別。調查時如聽聞獼猴叫聲，研究人員會試圖找出猴群，若經 10 分鐘後仍未尋獲，則只記錄爲叫聲跡象；若尋獲猴群，則記錄爲目視資料。食痕資料包括獼猴吃天然食物或農作物的資料。另外，農作物被吃的痕跡、猴害防治設施及受害農民訪問的資料皆納入獼猴危害農作物的紀錄。

六、農民訪問

進行固定樣線與非固定樣線調查時，若遇到農民，以口頭訪談的方式，詢問農民耕種的農地是否有台灣獼猴危害農作物的情事發生。若有，則繼續詢問發生猴害的地點、受害的作物種類及耕作地的所有權屬性等資訊。由於遇到農民的場所多在農地中，農民可能因農忙或其他因素，願意回答的問題多寡不一，因此各詢問事項的回答樣本數也有所不同。研究期間共訪問了 18 位農民關於台灣獼猴危害農作物的情況。

結　果

一、全縣分布概況

綜合全縣普查與固定樣線調查的目視及各種跡象資料，台灣獼猴在台南縣境內分布的行政區包括大內、六甲、左鎮、玉井、白河、東山、南化、新化、楠西及龍崎共 10 個鄉鎮，涵蓋 24 個村里 (表 2；圖 2)。分布點主要集中在台南縣境內三大主要山脈：(一)曾文水庫西

側山脈(即表3之A山脈)，涵蓋的鄉鎮有白河、東山、六甲、楠西、大內及玉井；(二)曾文水庫東側、南化水庫西側山脈(即表3之B山脈)，涵蓋的鄉鎮有楠西、玉井及南化；(三)南化水庫東側山脈(即表3之C山脈)，涵蓋的鄉鎮爲南化鄉。大致上，台灣獼猴主要分布在山稜線兩側坡度較陡的森林中，人類開墾較多的溪谷附近已少見猴群。此3段山脈之猴群棲地除有水域阻隔，鄰近山谷的開墾農地亦使山脈間的猴群往來之可能性極低，因此後續分析將此3段山脈視爲3個台南縣台灣獼猴分布的獨立山區。

依據在地居民訪談資料，推測有5鄉鎮6村里的台灣獼猴可能來自人爲放生(表2)，推測來自放生的資訊包括：(一)獼猴個體數量少，通常1-2隻；(二)出現的年代通常距研究時期5年內；(三)行爲上較不怕人；(四)受訪居民的認知。其中在大內鄉二溪村的北嶺山地區、白河鎮六溪里、仙草里及新化鎮礁坑里的興大林場皆爲近期才出現的零星個體；左鎮鄉的草山村與龍崎鄉的龍船村爲相連的山區，當地居民表示有疑似放生的小群獼猴出沒，且有未成年個體。

表 2. 台南縣境內台灣獼猴分布與發生獼猴危害農作物的鄉鎮與村里

Table 2. Townships and villages with the Taiwanese macaques and crop-raiding in Tainan County

Township	Village	Evidence*	Artificial introduction	Crop-raiding
Danei (大內鄉)	Erxi (二溪村)	I	Y	
	Huanhu (環湖村)	I, P		Y
Lioujia (六甲鄉)	Daqiou (大丘村)	I		Y
Zuozhen (左鎮鄉)	Caoshan (草山村)	I	Y	
Yujing (玉井鄉)	Sanpu (三埔村)	I		
	Zhongzheng (中正村)	E, I		Y
	Fongli (豐里村)	I, S, P		Y
Baihe (白河鎮)	Liouxi (六溪里)	I	Y	
	Xiancao (仙草里)	I	Y	
	Guanling (關嶺里)	I, S, T		
Dongshan (東山鄉)	Qingshan (青山村)	S		
	Nanshi (南勢村)	C, E, I, S, T		Y
	Gaoyuan (高原村)	I, S		
Nanhua (南化鄉)	Xiaoluen (小崙村)	E, I, S		
	Yushan (玉山村)	E, I, P, S, T		Y
	Donghe (東和村)	E, F, I, S		Y
	Nanhua (南化村)	E, S		
	Guanshan (關山村)	E, I, P, S		Y
Xinhua (新化鎮)	Jiaokeng (礁坑里)	I	Y	
Nanxi (楠西鄉)	Mizhi (密枝村)	I, P, S		Y
	Zhaoxing (照興村)	I		Y
	Gueidan (龜丹村)	E, F, I, S		Y
	Wanqiou (灣丘村)	F, I, S		Y
Longqi (龍崎鄉)	Longchuan (龍船村)	I	Y	Y

*C: calling, E: sighting, F: food remains, I: interviews, P: facilities for pest control, S: scats, T: camera trapping

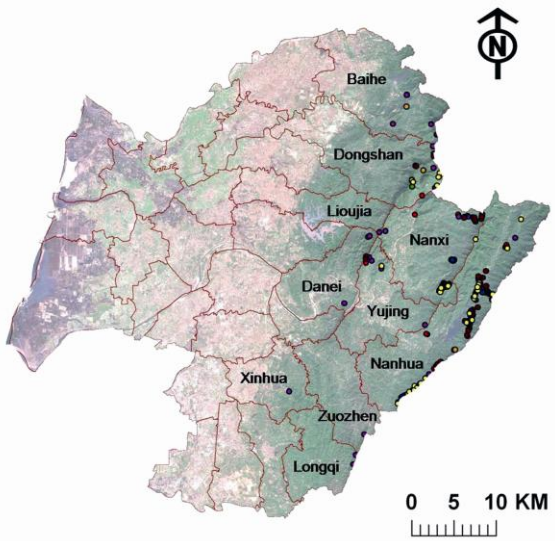

圖 2. 台南縣境內台灣獼猴出現的地點。跡象包括：目視 (黃點)、相片 (橙點)、叫聲 (綠點)、食痕 (藍點)、排遺 (褐點)、訪問 (紫點)、農民防治猴害的設施 (紅點)。底圖是空照圖，顏色代表地表的顏色，綠色部分爲有植被地區，包括森林與農地。

Fig. 2. Localities of the Taiwanese macaques verified by sighting (yellow), camera trapping (orange), calling (green), food remains (blue), scats (brown), interviews (purple), and facilities for pest control (red) in Tainan County. The underlying map is the true-color image of earth taken from airspace. Green areas include forests and farmlands with green plants.

二、獼猴族群數量與密度估算

全台南縣固定調查樣線總長 100.5 km 中，最主要的棲地類型是闊葉林，範圍有 57.5 km (57.2%)，其次依序爲竹林 21.8 km、果園 14.5 km、草生地 4.8 km、建築物 1.2 km 及裸露地 0.7 km，僅以其中闊葉林涵蓋的 57.5 km 爲估算猴群密度的取樣範圍。在 17 條固定樣線各 3 次的步行觀察中，共記錄到台灣獼猴常態猴群 22 群次、雄性孤猴 3 隻次及雄猴光棍群 1 次。常態猴群 22 群次有 8 群次出現在純闊葉林，8 群次在闊葉樹、竹林混交區，3 群次在闊葉樹、果園混交區，2 群次在闊葉樹、竹林及果園混交區，1 群次在闊葉樹、果園及草生地混交區；皆是在闊葉林中或其邊緣活動。

僅以常態猴群 22 群次進行族群密度的估算，計算各固定調查樣線的猴群密度後，將各樣線依山脈 (A、B、C) 及地區 (A1、A2、B、C1、C2) 合併估算各區域之猴群密度 (表 3)。A 山脈之 A1 區人爲活動頻繁、發現之獼猴跡象稀少，與 A2 區人爲活動較少、獼猴跡象容易發現之狀況相當不同，因此劃分此 2 區。C 山脈之 C2 區有明顯人工餵食獼猴的活動，爲探討其可能之影響，因此將 C2 區與 C1 區分別計算猴群密度。全縣闊葉林中猴群的相對密度爲 0.127 群/km，各地區的相對密度除 A1 區 (枕頭山與大凍山區) 爲 0 外，其餘地區爲 0.109 - 0.258 群/km (表 3)。A1 區的相對密度顯著低於其他各區 (5 區 ANOVA: $F = 7.727$, $d.f. = 4, 10$, $p = 0.004$; Tukey 多重比較: A1 區與其他區間皆 $p < 0.05$)，其餘各區間 Tukey 多重比較差異不顯著 ($p > 0.05$)。各山脈間的猴群相對密度 (0.064 - 0.186 群/km) 差異未達顯著水準 ($F = 2.804$, $d.f. = 2, 6$, $p = 0.138$)。A1 區 (枕頭山與大凍山山區) 的猴群密度最低，固定樣線調查時完全未發現猴群蹤跡。但根據訪問及排遺的資料，大凍山山區尚有野生族群；而枕頭山區雖有紅外線自動相機拍攝相片 1 次及零星個體被受訪者觀察到的資料，但未發現任何獼猴的排遺、食痕等跡象。

圖 3 爲進行固定樣線調查時，目擊猴群與調查樣線的最短距離分布圖，最近的距離爲

0 m (獼猴在調查樣線上)，最遠的距離爲 222 m，離調查樣線愈近，被觀察到的猴群數愈多。多數的觀察 (15/22) 皆位於垂直距離 100 m 以內，因此仿李等 (2000) 及蘇等 (2011) 選擇 100 m 作爲猴群密度估算的有效觀察距離。表 4 列出各山脈及各地區推估的猴群密度與95%信賴區間，估計台南縣闊葉林區的猴群密度爲 0.637 群/km^2。以台南縣闊葉林總面積 157 km^2 (管及陳 1995) 爲基礎，推估全台南縣的台灣獼猴有 100 群，95%的信賴區間爲 82 - 118 群。

表 3. 台南縣台灣獼猴的猴群相對密度

Table 3. Relative density of the Taiwanese macaque troops in Tainan County

Mountain range*	Region**	Code of transect	Count of monkey troop***	Length of transect in broadleaf forest (km)	Relative density (troop/km)		
A	A1	1	0 (0, 0, 0)	4.22	0	0	0.064
		2	0 (0, 0, 0)	1.48	0		
		3	0 (0, 0, 0)	5.23	0		
	A2	4	1 (0, 0, 1)	1.98	0.168	0.109	
		5	2 (1, 1, 0)	3.63	0.184		
		6	2 (1, 0, 1)	4.56	0.146		
		7	0 (0, 0, 0)	4.59	0		
		8	0 (0, 0, 0)	0.50	0		
B	B	9	3 (1, 0, 2)	2.16	0.463	0.186	0.186
		10	0 (0, 0, 0)	0.65	0		
		11	0 (0, 0, 0)	1.85	0		
		14	1 (0, 0, 1)	2.54	0.131		
		17	1 (0, 1, 0)	1.75	0.190		
C	C1	13	2 (0, 1, 1)	8.50	0.078	0.111	0.179
		15	2 (2, 0, 0)	1.88	0.355		
		16	0 (0, 0, 0)	1.66	0		
	C2	12	8 (1, 5, 2)	10.34	0.258	0.258	
Total			22 (6, 8, 8)	57.52	0.127		

* A: mountain range on the west of Zengwen Reservoir (曾文水庫); B: mountain range on the east of Zengwen Reservoir (曾文水庫); C: mountain range on the west of Nanhua Reservoir (南化水庫).

** A1: Zhentou Mountain (枕頭山) and Dadong Mountain (大凍山); A2: Erjian Mountain (二尖山) and Kantou Mountain (崁頭山); B: mountain range on the border between Nanxi (楠西) and Nanhua (南化); C1: mountains in northern Nanhua; C2: Wushan Range (烏山).

*** Total counts by three samplings, followed by each of 1st sampling, 2nd sampling, and 3rd sampling in parentheses.

表 4. 台南縣各地區台灣獼猴的猴群密度估計值

Table 4. Estimated density of the Taiwanese macaque troops in Tainan County

Mountain range	Region	Estimated density (95% confidence interval) (troop/km^2)	
		Region	Mountain range
A	A1	0	0.318 (0.193 - 0.443)
	A2	0.546 (0.332 - 0.760)	
B	B	0.931 (0.201 - 1.661)	0.931 (0.201 - 1.661)
C	C1	0.554 (0.282 - 0.825)	0.894 (0.456 - 1.332)
	C2	1.289 (0.150 - 2.429)	
Total		0.637 (0.524 - 0.751)	

* Mountain range and region codes are annotated in Table 3.

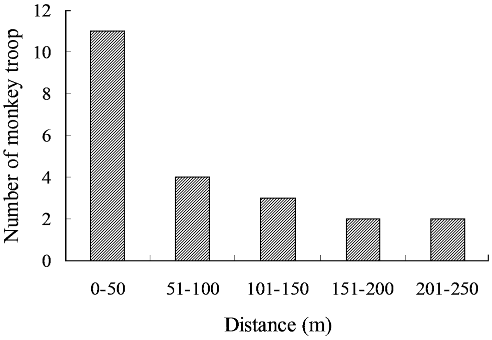

圖 3. 固定樣線調查時猴群與調查樣線的最短距離。

Fig. 3. The shortest distances from the Taiwanese macaque troops observed to the line transects.

固定樣線調查紀錄的 22 個猴群被觀測到的個體數 2 - 56 隻不等，平均每群 7.7 隻，與李等 (2002) (平均每群 6.9 隻，範圍 2 - 53 隻) 及蘇等 (2011) (平均每群 8.7 隻，範圍 1 - 56 隻) 相近，但明顯低於台灣各地猴群大小的實際觀測資料 (9 - 86 隻，多數爲 20 - 30 隻) (李等 2000, Fooden and Wu 2001)。由於以大範圍族群估算爲目標的調查無法長時間追蹤同一猴群，單次觀察常只見到猴群的部分、甚至是少數的個體，難以在短時間內掌握到每群獼猴的完整個體數，因此仿照李等 (2000) 及蘇等 (2011) 以一群 25 隻爲平均數，推估全台南縣境內的台灣獼猴族群數量爲 2,500 隻，95%的信賴區間爲 2,050 - 2,950 隻。

三、獼猴危害的概況

台南縣境內發生台灣獼猴危害農作物事件的地區至少包括大內、六甲、玉井、東山、南化、楠西及龍崎等 7 鄉鎮共 13 個村里 (表 2)，占台南縣有獼猴分布村里的 54% (13/24)，若不計僅有零星放生個體、且無猴害的 5 個村里，則台灣獼猴群分布的村里中有 68% (13/19) 發生猴害。楠西、南化及玉井皆有 2 或 2 個以上的村里有獼猴侵擾農作物，是受害較多的鄉鎮。

18 位受訪農民有 17 位陳述受害農作物的種類，共有 12 種作物遭受獼猴危害，其中以芒果 (*Mangifera indica* L.) 出現的頻度最高，有 13 位 (76%) 農民受害；其次是龍眼

(*Euphoria longana* Lam.)，受害農民有 8 位 (47%)；其餘受害作物皆僅有 1 或 2 位農民陳述 (圖 4)。台南縣山區普遍種植的麻竹 (*Dendrocalamus latiflorus* Munro)，則未在農民訪談的受害作物清單中。

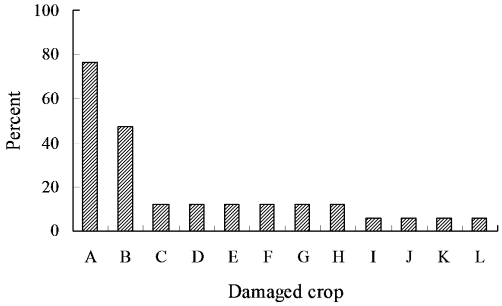

圖 4. 台南縣境內受訪農民陳述受台灣獼猴危害之農作物的種類與比例。代號：A，芒果；B，龍眼；C，柳橙；D，木瓜；E，香蕉；F，南瓜；G，番石榴；H，桂竹；I，佛手瓜；J，破布仔；K，波羅蜜；L，荔枝。(N=17)

Fig. 4. Frequency of crops damaged by the Taiwanese macaques based on interviews with farmers. Types of crop: A, *Mangifera indica* L.; B, *Euphoria longana* Lam.; C, *Citrus sinensis* Osbeck; D, *Carica papaya* L.; E, *Musa sapientum* L.; F, *Cucurbita moschata* Duchesne ex Poir.; G, *Psidium guajava* L.; H, *Phyllostachys makinoi* Hayata; I, *Sechium edule* Sw.; J, *Cordia dichotoma* G. Forst.; K, *Artocarpus heterophyllus* Lam.; L, *Litchi chinensis* Sonn. (N=17)

在受害農地的土地所有權方面，11 位受訪農民中，除 1 位 (9%) 的農地屬私有地外，其餘的皆爲農民承租之國有土地，其中 7 位 (64%) 的農地是國有林承租地，3 位 (27%) 的是國有財產局管理之國有土地。承租國有林地的受害農民遭受獼猴侵害的農作物主要是芒果 (6/7)。

討　論

一、分布概況

台灣獼猴族群在台南縣境內的分布並不普遍，僅侷限在東部山區 (圖 2)，主要分布在 3 條山脈稜線附近尚有闊葉林之處 (表 3)，這 3 條山脈分別位於曾文水庫西側、曾文水庫東側 (或南化水庫西側) 及南化水庫東側，即台南地方人士所稱「綠色長城」之東北段、東段及東南段 (大台南登山協會 2013)。這 3 條山脈的猴群密度並無顯著差異。在地區層級，枕頭山與大凍山區 (表 3 之 A1 區) 的密度顯著低於其他固定樣線調查地區，反映此區可能是台南縣台灣獼猴分布區域的邊陲地帶。台南縣的台灣獼猴族群雖出現在 10 個鄉鎮，但主要分布還是在東山、楠西及南化 3 個鄉鎮。C2 區的猴群密度在統計上雖未與 A2、B 及 C1 區不同，不過觀測到的密度稍高於他區 (表 3)，且最大的單一猴群個體數 56 隻是在該區觀測到的，是否該區內南化鄉烏山地區長期人工餵食的行爲 (林及張 1994) 已促使獼猴族群較爲快速地增長，是一值得關注的議題。

根據訪問，有 6 個村里出現的台灣獼猴可能來自人爲放生 (表 2)。過去野生動物保育的觀念未普及前，民間飼養台灣獼猴的情形並不少見，1989 年野生動物保育法施行後，法律禁止任意捕捉與飼養獼猴，且飼養的獼猴成年後不易馴服，因此容易發生棄養、放生的情況 (個人觀察)。李等 (2000) 以問卷調查即發現全台灣至少有 28 個鄉鎮市曾出現獼猴放生或逃逸的事件。2012 年 9 月 24 日聯合報報導左鎮外岡林地區有台灣獼猴入侵民宅，據居民表示一群有十多隻，行爲像放生或逃逸個體。本研究

並未在該地所屬的岡林村中調查到獼猴蹤跡，但隔鄉的草山村與龍崎鄉龍船村則皆有疑似放生的個體 (表 2)，且已形成有未成年猴的小型猴群。岡林里的獼猴族群的確有可能是由放生或逃逸個體所繁衍建立。這些有疑似放生台灣獼猴族群的村里多位於淺山、農地開發比例高的地方，猴群的成長是否導致更嚴重的人猴衝突需要多加觀察。

二、族群密度與猴害的關係

全縣固定調查樣線的總平均猴群密度 0.637 群/km^2，稍低於台灣全島闊葉林棲地 (0.7219 群/km^2) (李等 2000) 與彰化縣二水鄉山區 (0.93 群/km^2) (蘇 2012) 的猴群密度，且遠低於墾丁國家公園東半部森林性棲地 (2.90 群/km^2) 與宜蘭福山試驗林 (2.67 群/km^2) (蘇等 2011)。台南縣境內台灣獼猴族群的密度並不算高。

墾丁東半部與福山試驗林二地皆人爲干擾較少的闊葉林，猴群棲息地附近少有農地，也少有猴害的報導。二水鄉山區的猴害普遍 (張 2002)，其猴群密度除有人爲餵食的區域外，與台灣全島的密度並無明顯差異 (蘇 2012)。台南縣出現台灣獼猴危害農作物的行政區有 7 鄉鎮 13 村里，占獼猴群分布區的多數，危害情形堪稱普遍。比較台南縣與其他地區，台灣獼猴危害農作物的情形並未隨著猴群密度升高而增加，反而猴群密度較高的地方猴害較少，很可能猴群密度與猴害的多寡並無必然因果關係。至於猴群密度高反而猴害少，可能是這些猴群密度高的地方少有農業活動，棲地天然植被良好，提供獼猴充分的食物，支持較高的族群承載量；相反地，猴害多的地方，因農業活動多，天然棲地受破壞、切割的情形多而破碎化，降低了猴群的棲地品質，因而降低了猴群的密度。Kumar *et al.* (2008) 的研究也顯示同爲獼猴屬的 *M. munzala* 族群密度與危害無關。

三、影響猴害發生的因素

人類多數的農作物有較高的熱量、較低的毒性、較大的量體及較少的纖維，且農地的種植方式集中，所以比起取食天然食物，靈長類取食農作物所需的時間較少、較有效率、可以用較少的努力量獲得較多的能量 (張及渡邊 2009; Forthman *et al*. 2005; Muroyama and Yamada 2010; Osborn and Hill 2005)，因此多數農作物是靈長類偏好的食物。Hill (1997) 指出農作物的種類會影響受害與否，如玉米就是靈長類相當偏好的農作物 (Naughton-Treves *et al.* 1998)。本研究發現在台南縣普遍栽植的芒果與龍眼遭受台灣獼猴危害頗多 (圖 4)，但同在猴群分布地區廣植的麻竹卻未見猴害。在台灣其他較少遭受猴害的作物還包括檳榔、梅子、青椒及白柚等 (李等 2000; 張 2000; 蘇 2012)。可能是因獼猴不喜這些作物的味道、不善處理作物的外皮或作物尚未足夠成熟即爲農民採收，因此農作物本身的特質或種植採收的特性是影響靈長類前往取食的重要因素之一。

除了作物本身的特質外，可及性也是影響靈長類是否會利用農地的重要因素 (Muroyama and Yamada 2010)。農地與森林之間的距離對靈長類而言是作物可及性的重要指標，農地離森林愈近，發生靈長類危害的機會愈大 (Chakravarthy and Thyagaraj 2005; Chhangani *et al.* 2008; Hill 2000; Naughton-Treves 1998; Rao *et al.* 2002)。在台灣容易發生獼猴危害作物的農地也都緊鄰森林 (孫 2007; 張 2000; 蔡 2006)。台南縣的農業開發普遍，闊葉林總面積 157 km^2 (管及陳 1995) 僅占全縣面積

2,016 km^2 (維基百科 2013) 的 7.8%。這些森林多侷限在陡峭而難以開發的山區，且主要沿著山脈稜線兩側散布，其間又有不少農地鑲嵌，因此台南縣境內台灣獼猴棲息的森林區域多數狹窄，且離農地不遠，可能台南縣的猴群都不難接近相鄰的農地，獼猴進入農地取食的機會很高。

其他可能影響靈長類取食農作物的因素還包括學習的過程 (張及渡邊 2009)。靈長類需要經過學習才會接受未食用過的作物，若給牠們學習的機會，幾乎所有農作物都會成爲靈長類的食物 (Muroyama and Yamada 2010)。除了熟悉農作物，與人互動的方式也是學習的一部份，靈長類一旦學會不再對人感到恐懼，就會開始在農地出沒 (Hill 2005)。而靈長類會否懼怕人類則與人的態度與處理危害的方式有關，當農民的警覺性愈低時農作物的受害就愈多 (Osbom and Hill 2005)。所以靈長類會否危害農作物，重要的是農作物的種類及接觸農作的機會與經驗，而非族群密度。

四、猴害管理與保育

本研究推算台南縣境內台灣獼猴有 100 群 (95%信賴區間：82 - 118 群)，占全台 10,404 群 (李等 2000) 的 0.96%，所占極微。加上縣境內猴群密度並未較全台的平均水準高，「野生動物保育法」第 18 條規範「族群量逾越環境容許量者」的情況恐難適用在台南縣，主管機關面對猴害時若欲以獵捕的方式處理，可能還是依「野生動物保育法」第 21 條「野生動物……危害農林作物、家禽、家畜或水產養殖者」的相關規定處理爲宜。

獵捕是處理台灣獼猴危害農作的方法之一，卻不是萬靈丹。1998 年後，因危害農作物被獵捕移除的日本獼猴 (*M. fuscata*) 每年平均有一萬隻，但危害依舊四處發生，無適當管理計畫的捕殺對減少農作物受害並不具效益 (Muroyama and Yamada 2010)。且 Watanabe and Muroyama (2005)認爲，地區族群中的猴群數若少於 20 即爲小族群，要特別謹慎處理猴害問題，避免移除獼猴導致區域族群滅絕。台南縣境內的台灣獼猴總群數約 100 群，分散在 3 大主要山脈及一些零散山區，各地都有小族群的傾向，以捕捉移除作爲防治猴害的方法需提防區域族群滅絕的情況發生。

由於沒有單一的防治管理方法能完全排除靈長類的農業危害，最佳的策略還是綜合各種防治技術建立各地最有效的防治對策 (Wang *et al*. 2006; Watanabe and Muroyama 2005)。改變種植農作物種類是張 (2005) 列出推薦的防治技術之一，本研究發現台南縣境內普遍種植的麻竹並非台灣獼猴危害的對象，加上張 (2005) 列出推薦農民轉作的梅子、柚子及青椒等農作物，可提供遭受猴害的農民欲改變種植農作物種類時的參考。

本研究調查到受台灣獼猴危害的農地中有 64%是屬於農民承租的國有林地，而其中大多數農地受害的作物是芒果。張 (2000) 在苗栗、台中、南投、彰化及雲林等縣的調查也發現 45%的獼猴危害是發生在農民承租的國有林地上。這些原本放租目的是造林的國有林地，卻種植果樹以供農業生產，其合法性頗有疑慮。主管機關面對猴害問題處理時，宜將土地使用的合法與否列爲重要考量項目之一。

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環境昆蟲量對五色鳥(*Megalaima nuchalis*)幼鳥生長與存活之影響

Effects of arthropod abundance on nestling growth and survival of Taiwan Barbets (*Megalaima nuchalis*)

葛兆年[1] 許詩涵[1] 鄭惟仁[1] 陳銘瑝[1] 黃尹宣[1] 葉耕帆[1] 張靖[1] 羅英元[2*]

Chao-Nien Koh[1], Shih-Han Hsu[1], Wei-Jen Cheng[1], Ming-Huang Chen[1],
Yin-Hsiang Huang[1], Keng-Fan Yeh[1], Ching Chang[1] and Ying-Yuan Lo[2*]

[1] 林業試驗所森林保護組 10066 台北市中正區南海路 53 號
[2] 特有生物研究保育中心動物組 55244 南投縣集集鎮民生東路 1 號

[1] Department of Forest Protection, Taiwan Forestry Research Institute, Taipei
[2] Division of Zoology, Endemic Species Research Institute, Nantou

*通訊作者：danny@tesri.gov.tw

*Corresponding author: danny@tesri.gov.tw

摘　要

環境食物資源量影響幼鳥的生長與存活，都市地區可能因節肢動物量較自然環境低，造成都市裡的野生幼鳥存活率較低。本研究調查都市公園綠地及自然環境兩地的五色鳥幼鳥離巢率及失敗原因、環境昆蟲量、親鳥餵食昆蟲頻率、幼鳥生長速度等，發現都市公園綠地可利用的昆蟲量較少、親鳥餵食幼鳥昆蟲頻率較低、幼鳥生長較緩慢、夭折占離巢失敗比例較高，以及幼鳥體型差異較大的繁殖窩有較低餵食昆蟲頻率及較易發生夭折。本研究推測昆蟲爲五色鳥幼鳥生長的關鍵食物，都市公園綠地的昆蟲量不足可能造成五色鳥幼鳥生長遲緩及夭折率提高，建議利用棲地經營管理增加都市地區公園綠地的昆蟲資源，並杜絕對昆蟲及其棲地的破壞。

Abstract

Food abundance in the environment influences nestling growth and survival in birds. In urbanized areas, nestling survival is likely to decrease due to low arthropod abundance. We investigated the fledgling success rate of the Taiwan Barbet (*Megalaima nuchalis*) and the causes of fledgling failure in an urban green space and a natural habitat. In the two sites, arthropod abundance, arthropod provision rates by parents, nestling growth states were recorded. The results show the less arthropod abundance, the lower arthropod provision rate, slower nestling growth and more premature death of nestlings in the urban green space. Furthermore, the clutch with nestlings of distinct body size differences had lower arthropod food provision rate and more premature deaths. The results indicate that arthropods are a vital food resource for nestling growth of Taiwan Barbet. Insufficient arthropod abundance in the habitat will likely cause slow growth and premature death of nestlings. To enhance arthropod abundance in urban green space, appropriate habitat management is needed, and any damage to the arthropod community and its habitat should be prevented.

關鍵字：五色鳥、餵食頻率、離巢、都市綠地

Keywords：Taiwan Barbet, food provision rate, fledge, urban green space

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前言

都市化(urbanization)快速改變環境的地貌是眾所周知的事實(McDonnell and Pickett 1990)，並且都市住宅密集對野生動物已產生負面影響(Peterson *et al.* 2007)。都市化除了影響鳥類群聚、數量及多樣性之外(Marzluff 2001)，就個體層次而言，也影響其體型、身體狀況以及繁殖表現。雖然都市化對鳥類個體有正面或負面影響的研究結果並不一致，例如捕食壓力一般認爲會下降，但在部分都市地區卻發現仍會面臨不同於野外的掠食者，如家貓(*Felis catus*)等（Lepczyk *et al.* 2003; Thorington and Bowman 2003; Beckerman *et al.* 2007）；天然食物資源可能較缺乏，但人爲提供的食物卻也補償都市鳥類所需(Marzluff *et al.* 2001)，然而已有一些報告明確指出都市化對鳥類繁殖表現產生的影響，例如使產卵日提早(Crick *et al.* 2002)、繁殖成功率下降(Schnack 1991)、窩卵數較少或幼鳥體重較輕(Newhouse *et al.* 2008; Chamberlain *et al.* 2009)等。影響都市鳥類繁殖的可能因素包括噪音、空氣或毒物污

染、食物資源、缺乏植被、人爲干擾等(Peach *et al.* 2008)，其中，食物資源被認爲是影響都市地區鳥類繁殖表現不同於自然環境下的重要因素(Chace and Walsh 2004; Chamberlain *et al.* 2009)。例如，棲息於英國都市區域之家麻雀(*Passer domesticus*)因缺乏無脊椎動物做爲食物來源，而造成幼鳥存活率低、體重較輕(Peach *et al.* 2008)；北美的叢鴉(*Aphelocoma coerulescens*)也被認爲因節肢動物食物量的差異，造成郊區族群的幼鳥死亡率較高(Shawkey *et al.* 2004)。McIntyre (2000)回顧以往相關研究指出節肢動物量在都市地區比較少，可能原因包括棲地的切割及減少(Pyle *et al.* 1981)、污染、殺蟲劑的使用(Shawkey *et al.* 2004)等，而節肢動物是許多鳥類幼鳥的關鍵食物來源，因此都市地區鳥類繁殖失敗率的增加可能與節肢動物量的不足有關。

五色鳥屬於鬚鬍科(Capitonidae)擬鴷屬(*Megalaima*)，爲台灣特有種(Feinstain *et al.* 2008)，廣泛分布於全台中低海拔，常見於闊葉林、次生林或都市綠地之樹冠層活動(Koh and Lu 2009; Lin *et al.* 2010)，身體翠綠，保護色良好。五色鳥是一級巢洞者(Primary cavity nester)，會在枯立木或生立木上的枯枝部位打洞做巢。由於繁殖期間在巢洞中產卵、育雛，並不容易直接觀察，過往對五色鳥的繁殖生物學資料較爲缺乏。何(1990)在陽明山地區調查五色鳥繁殖行爲，結果顯示五色鳥自 3 月底開始築巢、8 月下旬結束繁殖活動，但關於繁殖成功率等繁殖表現並未有進一步探討。Lin *et al.* (2010)則在台北植物園進行五色鳥繁殖生物學研究，記錄了窩卵數、幼鳥數、孵化率以及幼鳥離巢率等資料，其結果發現幼鳥離巢率(45.4±13.7%)和同爲擬啄木屬之 *M. viridus* 及 *M. rubricapilla* 相較明顯偏低(分別爲 75.7%及 75.0%) (Yahya 1988)，而離巢失敗的幼鳥，有 27.2%的比例是在巢中夭折死亡，之後親鳥會將死亡的個體啣出巢外。但我們在陽明山地區的初步觀察中卻發現，該地區五色鳥離巢失敗之幼鳥並無如此高比例夭折死亡的現象(葛等 2012)，造成此差異之原因爲何有待研究。

台北植物園位於都市地區，其五色鳥族群可能面臨不同於自然環境的生存壓力，例如幼鳥被餵食的昆蟲較少，幼鳥被天敵捕食的比例較自然環境低等(葛等 2012)，故本研究比較台北植物園五色鳥族群與自然環境族群的幼鳥成長狀況的差異，並探討其離巢失敗之幼鳥有較高比例爲夭折死亡的現象，是否因昆蟲資源差異所造成，以期提供都市綠地經營管理之建議。

材料與方法

一、設置樣區

選定台北植物園(121.51018E, 25.031834N)及陽明山地區(中國童子軍陽明山活動中心內)(121.54808E, 25.15825N)爲調查樣區，分別代表都市綠地以及自然環境之棲地類型。台北植物園面積約 8 ha，海拔約 15 m，富涵多樣植物資源，收集植物種類超過 2,000 種；陽明山樣區占地約 6 ha，海拔約 520 至 570m，區內主要樹種爲相思樹(*Acacia confusa* Merr.)及紅楠(*Machilus thunbergii* Sieb. et Zucc.)、青剛櫟(*Cyclobalanopsis glauca* (Thunb. ex Murray) Oerst.)等該區域之原生優勢物種，另外尚有柳杉(*Cryptomeria japonica* (L. f.) D. Don.)及楓香(*Liquidambar formosana* Hance)等人工栽植樹種(葛等 2012)。

二、昆蟲資源調查

在 2012 年 3 月至 9 月五色鳥繁殖期間，於兩樣區內分別設置 3 個馬氏網(Malaise trap)，架設位置爲樹冠層。每個月收集 1 次樣本，於實驗室內進行種類鑑定(至少分類至目)，並記錄螳螂目(Mantodea)、直翅目(Orthoptera)、鞘翅目(Coleoptera)、半翅目(Hemiptera)、竹節蟲目(Phasmida)等五色鳥育雛期會餵食的種類之數量，作爲環境可利用之昆蟲資源量。

三、尋找巢洞及觀察五色鳥幼鳥在巢表現

在 2010-2012 年間於台北植物園觀察記錄樣區內五色鳥繁殖表現，陽明山樣區則於 2011 年起開始觀察。試驗期間以步行方式分別在兩樣區尋找五色鳥個體及其繁殖巢洞。尋獲巢洞後記錄其位置，並考量不破壞五色鳥巢洞，不直接測量幼鳥的體重及跗蹠長等資料，故藉由非入侵式的方法，以連接於長桿上之針孔型攝影機觀察各項成長特徵發育的狀況。五色鳥幼鳥一般第 8-10 天可看到雙翅羽鞘、第 11-14 天眼睛開始睜開、第 12-17 天後頸綠羽冒出、第 17-20 天眼睛完全打開、第 21-25 天可看到臉部及頸部藍紅兩色羽毛、第 27-30 天可看到紅色眼先。其中，後頸綠羽是可最清楚辨認的發育特徵，故選用後頸綠羽來判斷幼鳥發育的速度。另於巢洞附近安裝監視器材作爲觀察之輔助，以追蹤幼鳥離巢失敗之原因。

四、育雛期餵食觀察

幼鳥孵出後，在不干擾五色鳥的距離下以望遠鏡觀察親鳥餵食，記錄餵食頻率(次/小時)、食物種類等，食物種類分爲果實、昆蟲、無法辨識等 3 類。每次觀察時間 2 小時，約於上午 8：15-10：15 進行。每巢觀察 4-12 小時，相同鳥對在同一繁殖季內育雛 2 巢以上，則合併計算之。

五、資料分析

所有取得之資料除了敘述統計外，以 student's *t* test 比較兩樣區餵食頻率、幼鳥生長狀況之差異等，而窩內幼鳥體型異同與夭折與否的獨立性，以及其昆蟲餵食頻率的差異，分別以費氏精確檢定(Fisher exact test)和 Mann-Whitney U test 檢定之，另以簡單線性回歸分析檢視餵食頻率及幼鳥生長狀況之相關性。

結果

一、環境昆蟲量

2012 年馬氏網調查發現五色鳥可利用的昆蟲資源量在陽明山樣區會隨季節有所波動，3 月份數量最低，之後起逐月增加，至 6 月份到達高峰，而台北植物園樣區則較無顯著的起伏(圖 1)；整體而言，環境中五色鳥可利用的昆蟲種類，其數量在陽明山地區大於台北植物園。

二、育雛期餵食組成及餵食頻率

於 2011-2012 年間，分別在台北植物園及陽明山觀察五色鳥族群育雛期之餵食狀況。合計在台北植物園觀察 12 對五色鳥，共計 17 巢、總觀察時數 182 小時，以及陽明山 21 對五色鳥，共計 22 巢、總觀察時數 182 小時。總計觀察到 1274 筆餵食紀錄，其中 1164 筆(占 91.4%)能夠順利辨識餵食的食物類別。

在台北植物園地區，育雛期餵食組成中，果實的比例(佔 50.5%)略高於昆蟲，餵食昆蟲的種類以半翅目、鞘翅目爲主；在陽明山地區，育雛期餵食組成則以昆蟲的比例較高(占

67.4%)，餵食昆蟲的種類以螳螂目、直翅目爲主，且種類更爲多樣，包含螳螂目、竹節蟲目、蜚蠊目等在台北植物園未曾記錄的餵食種類。就餵食頻率(次／小時)而言，台北植物園族群育雛期平均餵食頻率爲每小時 3.6±1.3 次、平均果實餵食頻率爲每小時 1.9±0.7 次、平均昆蟲餵食頻率爲每小時 1.3±0.7 次(以上 n = 12)；陽明山族群育雛期平均餵食頻率爲每小時 3.5±1.0 次、平均果實餵食頻率爲每小時 1.1±0.8 次、平均昆蟲餵食頻率爲每小時 2.3±0.8 次(以上 n = 21) (表 1)。結果顯示兩地區五色鳥族群的平均餵食頻率沒有顯著差異(*t* test, *p* = 0.79)，但平均果實餵食頻率在植物園樣區高於陽明山樣區(*t* test, *p*＜0.01)，而平均昆蟲餵食頻率則是陽明山樣區高於植物園樣區(*t* test, *p*＜0.01)。

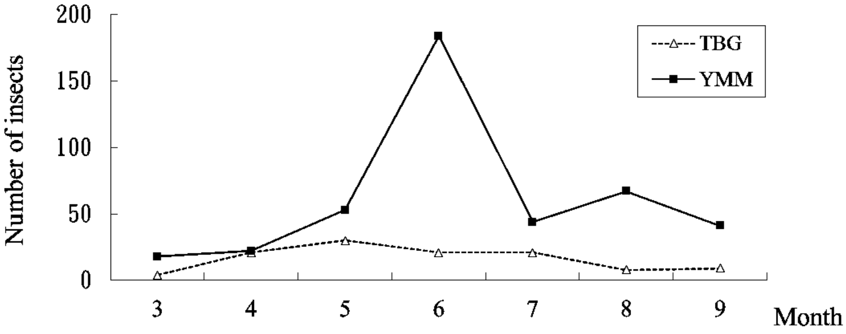

圖 1. 五色鳥繁殖期各月份在台北植物園及陽明山地區各以 3 個馬氏網調查之昆蟲資源量(TBG：台北植物園；YMM：陽明山)。

Fig. 1. Monthly abundance of insects collected from Taipei Botanical Garden (TBG) and Yang-Ming Mountain (YMM), each of which was placed with three Malaise traps during the Taiwan Barbet's breeding season.

表 1. 台北植物園及陽明山地區五色鳥育雛期餵食頻率(次/小時)之比較

Table 1. Comparisons of food provision rates (times/hr) of Taiwan Barbets between Taipei Botanical Garden and Yang-Ming Mountain

	Taipei Botanical Garden (n=12/182 hr)	Yang-Ming Mountain (n=21/182 hr)	*t**	*p*
Fruits	1.9±0.7	1.1±0.8	2.88	＜0.01
Insects	1.3±0.7	2.3±0.8	3.76	＜0.01
Unidentified	0.5±0.4	0.1±0.1	4.86	＜0.01
Total	3.6±1.3	3.5±1.0	0.26	0.79

*student's *t* test

三、餵食頻率與幼鳥發育時間之相關性

於 2011-2012 年間觀察兩樣區幼鳥後頸綠羽出現的日齡。結果顯示台北植物園幼鳥長出後頸綠羽平均日齡是 16.6±2.1 天(n=14)，在陽明山是 14.2±1.3 天(n=21)，代表台北植物園幼鳥後頸綠羽發育所需天數顯著較長(*t* test, $p < 0.01$)、生長較爲緩慢。

我們分析幼鳥被餵食頻率和長出後頸綠羽日齡的相關性，結果顯示後頸綠羽發育日齡和果實餵食頻率及總餵食頻率皆無相關，但和昆蟲餵食頻率有顯著相關(n=30, r^2=0.23, p＜0.01)，當餵食昆蟲頻率越高，則長出後頸綠羽的所需天數越少(圖 2)。

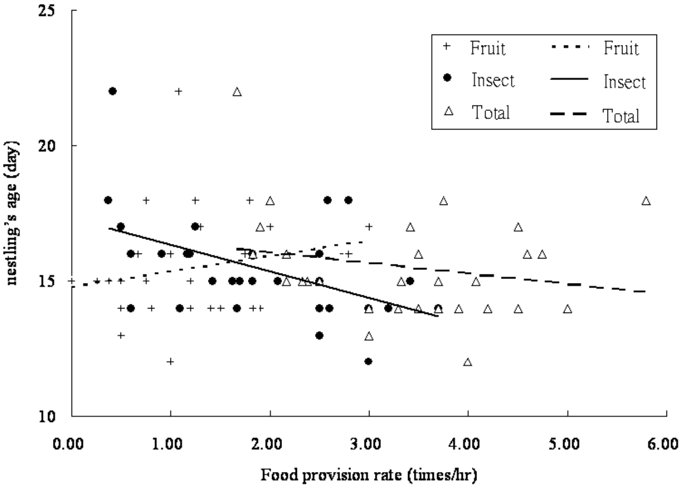

圖 2. 五色鳥幼鳥被餵食頻率與長出後頸綠羽日齡之相關性。

Fig. 2. Relationship between parent food provision rate of Taiwan Barbet and the nestling's age as the first green feather emerged on its back neck. (n = 30, fruit provision rate and nestling's age: r^2 =0.05, p=0.22 ; insect provision rate and nestling's age: r^2 = 0.23, $p < 0.01$; total food provision rate and nestling's age: r^2 =0.05, p=0.25)

四、幼鳥離巢失敗原因及比例

2011-2012 年台北植物園及陽明山兩地的幼鳥離巢失敗率分別爲 42.3% (30/71)及 53.5% (69/129)。台北植物園幼鳥離巢失敗原因大多爲夭折(60.0％, n=18)，有一半以上發生在日齡 5 至 12 天之間，其次爲氣候因素(13.3％, n=4)；陽明山地區幼鳥則絕大多數都是被捕食(91.3％, n=63)，有一半以上發生在日齡 12 至 23 天之間，夭折率僅有 2.9％ (n=2) (圖 3)，以卡方檢定結果顯示兩樣區五色鳥幼鳥離巢失敗原因有顯著不同(Chi-square test, χ^2=76.919, p<0.01)。

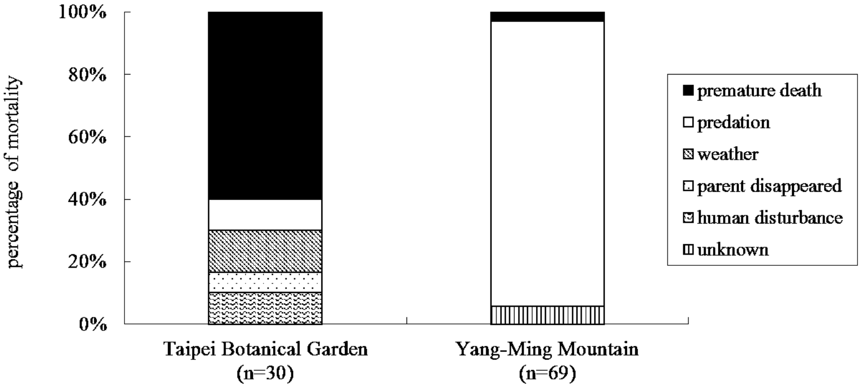

圖 3. 台北植物園及陽明山地區五色鳥幼鳥離巢失敗之原因。

Fig. 3. Causes of nestling mortality of Taiwan Barbets in Taipei Botanical Garden and Yang-Ming Mountain.

五、幼鳥體型異同與夭折及昆蟲餵食頻率

2010-2012 年於兩樣區以針孔型攝影機觀察幼鳥體型，在可確實分辨巢內幼鳥體型相對大小、並排除因氣候、天敵及人為干擾等因素而繁殖失敗窩次的條件下，共記錄 9 窩幼鳥體型有明顯大小不同，其中 2 窩幼鳥可全部成功離巢、7 窩僅部分離巢；27 窩幼鳥體型大小相當，其中有 23 窩可全部成功離巢、4 窩部分離巢。經費氏精確檢定顯示，幼鳥是否能全部離巢和窩內幼鳥是否同體型大小有關($p<$ 0.01)，亦即幼鳥體型不同的窩次較不易全部成功離巢，較易發生夭折，且夭折之幼鳥爲體型較小者。再比較幼鳥不同體型及同體型窩次的平均昆蟲餵食頻率，前者(每小時 0.5±0.5 次, n = 4)顯著低於後者(每小時 1.9±0.9 次, n = 26) (Mann-Whitney U test, Z=-2.747, $p<$0.01)。

討論

食物資源的豐富度或品質被認爲是影響鳥類繁殖表現的重要因子，假如環境食物資源充足，不僅成鳥可產下較多卵，幼鳥可能成長較快、離巢較早、體重較重、跗蹠較長，甚至影響成長後的繁殖狀態好壞(Nour *et al.* 1998; Searcy *et al.* 2004; Liker *et al.* 2008; Newhouse *et al.* 2008)。由於昆蟲含有較豐富蛋白質(Johnson 1993)，對幼鳥生長有所助益，不僅提高生長速度，亦提高其免疫力(Birkhead *et al.* 1999；Reynolds *et al.* 2003)，因此昆蟲對幼鳥是非常重要的食物來源，在缺乏昆蟲資源或餵食昆蟲較少的狀況下，幼鳥會有死亡率高、體重較輕等現象(Tremblay *et al.* 2005)。鳥類的繁殖起始時間是否處於昆蟲發生期也經常是影響繁殖成功的重要因素(Rossmanith *et al.* 2007)，任何影響食物資源多寡的環境因子，例如降雨量、氣候等，都可能影響鳥類的繁殖表現(Lin *et al.* 2007)。

就五色鳥而言，台北植物園的可利用昆蟲

量比陽明山少。都市綠地常因人爲的經營管理、美化及安全性的考量下，植被可能不如自然環境豐富，甚至因除草、施灑農藥等因素，造成昆蟲或其他無脊椎動物等食物來源較爲缺乏(Liker *et al.* 2008; Peach *et al.* 2008)。例如我們曾掃網調查台北植物園地面昆蟲，發現有除草作業的月份，直翅目昆蟲量大幅減少(葛，未發表資料)，明顯可見人爲經營管理影響環境中的昆蟲量。再者，都市綠地因生態島嶼之故，昆蟲資源受限在植被豐富的小範圍內，綠地以外的昆蟲資源相對稀少，故都市五色鳥能覓食昆蟲的範圍會比自然環境來的小。而兩地可利用昆蟲資源量的差異可能反映在親鳥餵食昆蟲頻率的不同。

本研究證實五色鳥在育雛期需要相當比例的昆蟲做爲食物來源。在陽明山以昆蟲餵食頻率較高、果實餵食頻率較少，在台北植物園則相反，但兩樣區五色鳥育雛期的總餵食頻率並無差異，表示兩樣區幼鳥雖然獲得的食物總量相當，食物組成及得到的營養成分並不一致，陽明山地區的五色鳥幼鳥所獲得蛋白質的量應較台北植物園豐富，這差異可能造成兩地區幼鳥有不同的生長速度。台北植物園族群幼鳥出現後頸綠羽所需的天數較陽明山長，表示台北植物園族群幼鳥可能生長速度較緩慢，而後頸綠羽出現的天數，和昆蟲餵食頻率有顯著相關，符合餵食昆蟲可提高幼鳥生長速度的假說(Tremblay *et al.* 2005)，說明了昆蟲是五色鳥幼鳥生長發育的關鍵性食物，應是提供了五色鳥生長發育所需的蛋白質。2012 年調查發現陽明山地區五色鳥可利用的昆蟲量在 6 月份數量達到高峰，同時記錄到該地區 17 窩五色鳥幼鳥孵化時間，其中 14 窩在 5-7 月間孵化，代表主要育雛期間大多處於昆蟲資源量較高峰的狀態，兩者在時間上的一致性亦支持昆蟲對五色鳥幼鳥生長的重要性。

在都市地區雖然有許多人爲提供的食物來源，甚至能提供鳥類度冬所需、幫助鳥類在繁殖季提早產卵，但天然食物的缺乏，仍舊使得鳥類繁殖表現下降，包括幼鳥體重較輕、死亡率較高等(Mennechez and Clergeau 2006; Chamberlain *et al.* 2009)。雖然親鳥會適時調整餵食頻率、覓食範圍或是改變食物組成來因應環境食物資源不足的狀況，但仍不足維持繁殖表現(Tremblay *et al.* 2005; Mennechez and Clergeau 2006)。這些狀況皆和本研究結果相似，台北植物園五色鳥可能以較多的果實來維持相當的餵食次數，但離巢失敗的幼鳥仍有很高的比例夭折死亡。不僅如此，本研究中陽明山地區的平均窩卵數(3.6±0.8, n=44)顯著高於台北植物園(3.1±0.6, n=23) (*t* test, $p<0.01$)，亦符合在食物資源不足的環境，鳥類會降低其窩卵數的假說(Lack 1947; Monaghan and Nager 1997)。再者，我們發現幼鳥有明顯體型大小不同的窩次，與體型相同的窩次相比，前者幼鳥較不易全部成功離巢，且通常是體型較小者在窩內夭折死亡，並且其昆蟲餵食頻率亦顯著較低，此項結果支持缺乏昆蟲資源或餵食昆蟲較少時，幼鳥死亡率較高的假說(Tremblay *et al.* 2003; Shawkey *et al.* 2004; Peach *et al.* 2008)。

除了食物資源外，尚有許多因素可能影響鳥類繁殖表現，包括巢洞品質、疾病、污染等都有可能直接影響五色鳥的繁殖表現。我們初步測量了巢樹及巢洞形質，例如巢洞深度、洞口傾角、樹冠等，以檢測台北植物園是否可能因適合樹木不足而降低巢洞品質，但測量結果發現除了台北植物園平均巢洞高度顯著比陽明山高之外(*t* test, $p<0.01$)，其他各項形質並無顯著差異(葛，未發表資料)。而是否會因都市污染的因素或化學藥劑的施灑，造成都市公園

綠地產下的幼鳥體質狀況不佳，在目前考量不破壞巢洞的情況下並無法直接對幼鳥進行免疫測試，因此尚無法驗證。綜合以上結果，我們推測富含蛋白質的昆蟲對五色鳥幼鳥生長發育而言是相當重要的食物資源，而台北植物園昆蟲資源較少及五色鳥親鳥餵食昆蟲較少可能是造成該地離巢失敗之幼鳥有較高比例夭折死亡的原因。未來將進一步以人爲餵食幼鳥試驗，驗證五色鳥幼鳥取食昆蟲比例多寡是否影響其生長狀況。

此外，本研究發現生活在自然環境的陽明山五色鳥族群，其幼鳥死亡幾乎是因爲蛇類的捕食，試驗期間多次發現臭青公(*Elaphe carinata*)捕食五色鳥幼鳥，此樣區內亦曾目擊眼鏡蛇(*Naja atra*)、黑眉錦蛇(*Orthriophis taeniura friesi*)、過山刀(*Zaocys dhumnades*)、紅斑蛇(*Dinodon rufozonatum*)等蛇類，而這些蛇類都會捕食鳥類。相較於陽明山有許多潛在的掠食者，台北植物園五色鳥幼鳥被天敵捕食的比例偏低，幾乎不受蛇類捕食的威脅。可見都市公園綠地在人爲經營管理之下可以降低天敵捕食導致野鳥繁殖失敗的比例，但也可能因除草除病蟲等作業而影響野鳥賴以存活的食物資源。昆蟲及其他無脊椎動物不僅是鳥類的覓食對象，同時也是許多生物的食物來源，建議在不違背安全性、景觀美化等都市綠地的經營考量下，仍應加強營造更豐富的植被環境、減少干擾，以更貼近自然的策略進行管理，以提升無脊椎動物的蘊含量，提供各類生物覓食所需，爲都市野生鳥類營造更適合的生存環境，也爲都市開發與野生物的生存尋求最佳平衡點。

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北台灣細胸珈蟌之翅色多型性

Wing Color Polymorphism of the Damselfly *Mnais tenuis* in Northern Taiwan

林斯正 [1] 楊平世 [2] 謝森和 [3,*]

Sue-Cheng Lin[1], Ping-Shih Yang[2] and Sen-Her Shieh[3,*]

[1] 行政院農業委員會特有生物研究保育中心　南投縣集集鎮民生東路 1 號
[2] 台灣大學昆蟲學系　台北市羅斯福路四段 1 號
[3] 靜宜大學生態人文學系　台中市沙鹿區中棲路 200 號

[1] Division of Zoology, Endemic Species Research Institute, Nantou, Taiwan
[2] Department of Entomology, National Taiwan University, Taipei, Taiwan
[3] Department of Ecological Humanities, Providence University, Taichung, Taiwan

*通訊作者：shshieh@pu.edu.tw

*Corresponding author: shshieh@pu.edu.tw

摘　要

在台灣已有報告指出細胸珈蟌(*Mnais tenuis*)翅色型爲性內多型性，雄蟌具有翅色二型性，雌蟌則有一至三種翅色型的不同看法。因此本研究的目的是以定量的方法，檢視細胸珈蟌翅色性內多型性，以及初羽化期與成熟期的珈蟌在形態上的差異。於 2012 年 3 至 4 月在台灣北部採樣 286 隻成蟲個體，測量它們的翅翼透明度、翅翼面積與體型大小等三種形態特徵，並以翅翼透明度的分布不連續判斷翅色型。結果顯示雄蟌具有「橙翅型」與「透翅型」二型性，雌蟌僅具有「透翅型」單型性，雌雄總共三種翅型。以變異數分析及 Mann-Whitney U test，分別比較此三種翅型及初羽化期與成熟期在這三種形態特徵上的差異，結果顯示透翅型雄蟌翅翼面積與體型皆顯著小於橙翅型雄蟌與透翅型雌蟌($p < 0.001$)，翅翼透明度則與雌蟌無顯著差異($p > 0.05$)。就這三種翅型而言，成熟期的珈蟌在體型上皆顯著地大於初羽化期的珈蟌($p < 0.001$)。而翅翼透明度與翅翼面積只有在成熟期橙翅型雄蟌與初羽化期橙翅型雄蟌之間有顯著差異($p < 0.001$)。

Abstract

The damselfly *Mnais tenuis* adults in Taiwan are reported to possess intra-sexual polymorphism in wing color. Male adults have two wing-color forms, but female adults have been indicated with doubt to have one to three wing-color forms. Therefore, this study was aimed to quantitatively examine wing-color polymorphisms of *Mnais tenuis* and to determine the differences in morphological features of adults between the teneral stage and mature stage. A total of 286 *Mnais tenuis* adult individuals were collected in northern Taiwan from March to April 2012. The features of these individuals, such as wing transparency, wing area, and body size, were measured, and the discrete distribution of wing-color morphs was examined according to wing transparency. A total of three morphs were identified from the discrete distribution where the males can be classified as the “orange-winged form” or “clear-winged form”, while the females classified as a single “clear-winged form”. Furthermore, the analysis of variance (ANOVA) was used to compare these features among the three morphs, and Mann-Whitney U test between teneral stage and mature stage. The results indicate that the wing area and body size of clear-winged males were significantly lower than those of both orange-winged males and clear-winged females ($p < 0.001$). But there was no significant difference in wing transparency between clear-winged males and females ($p > 0.05$). The mature adults were heavier than teneral adults for all three morphs ($p < 0.001$). However, the significant differences in wing transparency and wing area were found only between mature and teneral orange-winged males ($p < 0.001$).

關鍵詞：細胸珈蟌、翅色、多型性、豆娘、台灣

Key words：*Mnais tenuis*, wing color, polymorphism, damselfly, Taiwan

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緒　言

多型性(polymorphism)是指同種生物族群同時存在二種或多種不同形態(morph)或類型(form)個體的現象。與一般個體間連續性變異不同，多型性屬於不連續性變異，因此族群個體可容易區分並歸屬於不同的類型(Mayr and Ashlock 1991)。常見的多型性爲性別差異之雌雄二型性(sexual dimorphism)，另在雄性或雌性中也有性內多型性現象(intra-sexual polymorphism)，惟此較爲罕見。以蜻蛉目昆蟲體色爲例，雌雄一般呈現不同體色或翅色，但

雄性或雌性性內體色多型性則不多見。如台灣產約 150 種蜻蛉目昆蟲，有性內體色多型性報導者僅細胸珈蟌(*Mnais tenuis*)、長痣絲蟌(*Orolestes selysi*)、葦笛細蟌(*Paracercion calamorum dyeri*)、青紋細蟌(*Ischnura senegalensis*)、四斑細蟌(*Mortonagrion hirosei*)、褐翼勾蜓(*Chlorogomphus risi*)、短痣勾蜓(*Chlorogomphus brevistigma*)等 7 種(Lieftinck *et al.* 1984；張及汪 1997；汪 2000；葉等 2006；李及蕭 2008；曹 2011)。

雖然蜻蛉目昆蟲雄性或雌性性內體色多型性並不常見，但因其體型較大可上標操作(marking)，且生殖行爲明顯而易於觀察，故常作爲自然選汰(natural selection)與性選汰(sexual selection)對動物體色多型性影響的研究題材。特別是屬於蜻蛉目不均翅亞目(Zygoptera)的豆娘(damselfly)，因飛行力較弱且活動範圍較小更適合野外調查與室內飼養。如珈蟌科 *Mnais* 屬豆娘常用於雄性翅色多型性與交配策略(mating strategy)研究(Watanabe and Taguchi 1990；Watanabe 1991；Tsubaki *et al.* 1997；Plaistow and Tsubaki 2000；Tsubaki 2003；Hooper *et al.* 2006)，細蟌科 *Ischnura* 屬豆娘則用於雌性體色多型性研究(Robertson 1985；Cordero 1990；Andrés *et al.* 2000；李及蕭 2008)。體色多型性雖然具有物種遺傳、變異與進化等重要意涵，但當分類研究不足時，種間與種內的體色變異常混淆分類學者判斷，產生分類與鑑定問題。此外，由於成蟲體色會隨發育而改變，在未瞭解成蟲初羽化期(teneral stage)至成熟期(mature stage)的特徵變化，在體色型的界定上也容易產生紊亂。因此，對於蜻蛉目昆蟲體色多型性研究，首要探究體色特徵究竟屬於連續性或不連續性變異，再對不同發育階段進行比較，方能完成體色型歸類。

本研究之細胸珈蟌(*Mnais tenuis*)屬於溪流性大型豆娘，在台灣的分布以北部地區較多，成蟲發生期主要在 3 至 5 月(Lieftinck *et al.* 1984)。除台灣外，尚分布於華中與華東等地區(Lieftinck *et al.* 1984；Hämäläinen 2004；王 2007)。因細胸珈蟌翅色變異明顯，有關本種翅色多型性現象已多有報導。如台灣族群方面，Lieftinck *et al.* (1984)指出雄蟌具有二翅色型；張及汪(1997)與汪(2000)報導雄蟌具有透翅型(clear-winged form)與橙翅型(orange-winged form)，雌蟌具有透翅型、橙翅型與褐翅型(brown-winged form)；曹(2011)報導雄蟌與雌蟌皆有透翅型與橙翅型。Hämäläinen (2004)報導中國福建省產細胸珈蟌雄蟌具有透翅型與橙翅型，雌蟌無翅色分型；王(2007)指出河南省產細胸珈蟌，雄蟌與雌蟌皆具有翅色較淡的烟翅型與翅色較深之黃翅型。綜上所述，前人皆揭示細胸珈蟌雄蟌具有翅色二型性，至於雌蟌翅色則有單型性、二型性與三型性等不同看法。

由於往昔研究主要爲翅色型之定性描述，有關定量研究方面仍無相關報導。本研究於北台灣進行較大規模採樣，利用形質測量(morphometrics)分析翅色變異，並以變異的不連續性作爲翅色型歸類依據。其次，比較不同翅色型之體型大小，並經由文獻回顧，探討翅色型、體型與生殖策略的關係。有關初羽化期與成熟期個體的形態差異亦一併討論。

材料與方法

一、樣品採集

2012 年 3 至 4 月於台灣北部 7 採樣點進行採樣，包括新北市石門(Shimen)、萬里(Wanli)、

雙溪(Shuangxi)、平溪(Pingxi)、坪林(Pinglin)，宜蘭縣頭城(Toucheng)(圖 1)。野外採到的成蟲樣品，先依蟲體發育狀態區分爲初羽化期(teneral stage)與成熟期(mature stage)二生活期。由於初羽化期成蟌體壁與翅翼仍保持柔軟，與已硬化的成熟期成蟌明顯有別，故可在野外逕行判定(Corbet 1999)。採獲樣品直接放入四角紙袋，攜回實驗室以負 20℃冷凍保存。採集日期與採樣點地理座標見表 1。

表 1. 採樣點位置與樣品資訊

Table 1. Locations of the sampling sites and sample information

Site	Location	Collection date	Number of specimen (life stage, sex and individual)
Shimen	25.26° N, 121.58° E	2012/03/22, 2012/04/12	12 (mature♂7, teneral♂2, mature♀2, teneral♀1)
Wanli	25.17° N, 121.62° E	2012/03/23, 2012/04/12	99 (mature♂76, teneral♂6, mature♀16, teneral♀1)
Shuangxi	25.08° N, 121.85° E	2012 / 03 / 29	16 (mature♂3, teneral♂3, mature♀5, teneral♀5)
Pingxi	25.03° N, 121.73° E	2012 / 04 / 11	49 (mature♂42, teneral♂0, mature♀7, teneral♀0)
Pinglin	24.94° N, 121.68° E	2012 / 03 / 28	72 (mature♂38, teneral♂11, mature♀11, teneral♀12)
Toucheng	24.94° N, 121.87° E	2012 / 03 / 29	38 (mature♂31, teneral♂3, mature♀4, tenera♀0)

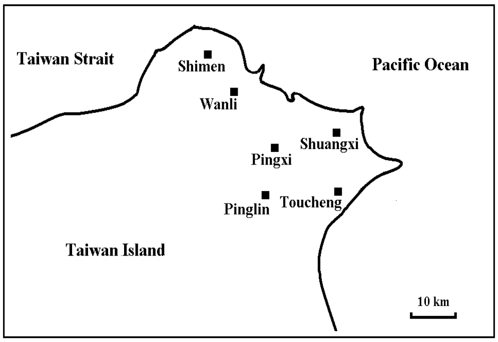

圖 1. 台灣北部細胸珈蟌採樣點位置圖。

Fig. 1. The sampling sites of *Mnais tenuis* in northern Taiwan.

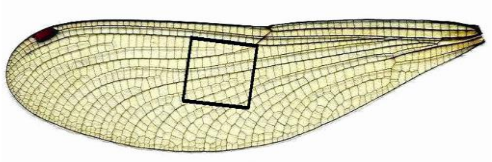

圖 2. 左前翅翅翼相對透明度測量部位(黑色方框)。

Fig. 2. Detecting area of left forewing for relative transparency (open square).

二、形質測量

(一) 左前翅翅翼相對透明度(relative transparency)

將樣品左前翅剪下，測量左前翅亞翅結(subnode)下方翅中央處一 5mm×5mm 正方形偵測面積之透明度(圖 2)。測量方法是利用顯微鏡用 Volpi Intralux® 5000-1 光源，經濾鏡過濾光線成爲 5000°K 標準色溫後，下接 Tes-1330 數位式照度計測量光強度。測量有置入翅翼的光強度(Iw)及無置入翅翼的光強度(I)，計算二者比值(Iw/I %)，得出翅翼相對透明度。

(二) 左前翅翅翼面積(wing area)

左前翅翅翼面積測量是以 Epson Stylus Photo RX630 掃描器掃描翅翼影像，並利用 Tsview 6.0 影像處理軟體計算翅翼面積。

(三) 體乾重(dry weight)

由於部份蟲體足部與翅翼脫落破損，故統一剪除樣品之前、中、後足與前、後翅。利用 Honsor FD 8080 冷凍乾燥機將樣品水份昇華乾燥，再以 Sartoris BP 121S 電子秤稱得體乾重。

三、資料分析

(一) 成熟期雄、雌蟌之翅色型歸類方式

利用翅翼相對透明度分布直方圖(histogram)呈現成熟期雄蟌(mature male adults)與成熟期雌蟌(mature female adults)的翅翼透明度變異。由分布狀態的不連續性，以及前人翅色型描述(Lieftinck *et al.* 1984；張及汪 1997；汪 2000；Hämäläinen 2004；王 2007；曹 2011)，研判翅色型類別。

(二) 成熟期雄、雌蟌各翅色型的形質比較

以單因子變異數分析(analysis of variance, ANOVA)檢定成熟期雄、雌蟌各翅色型在翅翼相對透明度、翅翼面積與體乾重間的差異，若分析結果達到 5%顯著水準，再以最小顯著差異測驗(least significant difference test, LSD)進行成對比較。使用統計軟體爲 SPSS 13.0。

(三) 初羽化期與成熟期的形質比較

由於初羽化期的樣品數較少，因此利用無母數統計法之曼-惠特尼 U 測驗(Mann-Whitney U test)檢定初羽化期與成熟期個體在翅翼相對透明度、翅翼面積與體乾重間的差異。使用統計軟體爲 SPSS 13.0。

結果與討論

一、樣品採集

研究期間於北台灣 7 採樣點共採集細胸珈蟌成蟲 286 隻，其中包括成熟期雄蟌 197 隻，初羽化期雄蟌 25 隻，成熟期雌蟌 45 隻，初羽化期雌蟌 19 隻。各採樣點調查隻數與樣品資訊見表 1。

二、成熟期雄、雌蟌之翅色型歸類

圖 3 爲成熟期雄、雌蟌翅翼相對透明度之分布直方圖。雄蟌具有二個且不連續分布峰，第一分布峰包含 144 隻個體並分布在相對透明度 34-56%間，高峰位於 40-42%間；第二分布峰包含 53 隻個體並分布在 76-92%間，高峰位於 82-84%間。雌蟌僅一分布峰且與雄蟌第二分布峰重疊，45 隻雌蟌個體分布在 76-86%間，高峰位於 82-84%間。利用多型性屬於不連續性變異之歸類依據(Mayr and Ashlock 1991)，本研究揭示雄蟌具有二型性，雌蟌僅單型性。參考前人翅色型描述(張及汪 1997；汪 2000；曹 2011)，本研究將從屬於第一分布峰，翅翼透明度低至中等(34-56%)的雄蟌翅色型歸類爲「橙翅型」；從屬於第二分布峰，翅翼透明度高(76-92%)的雄蟌歸類爲「透翅型」。雌蟌雖爲單型性，但因其翅翼透明度(76-86%)與透翅型雄蟌非常接近，故亦歸類爲「透翅型」。

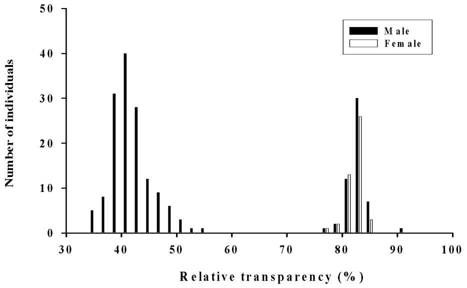

圖 3.成熟期雄、雌蟌翅翼相對透明度之直方圖。
Fig. 3. The histogram of relative transparency for mature male and female wings.

蜻蛉目昆蟲翅翼由翅痣(pterostigma)、翅脈(wing vein)以及由翅脈所包圍的翅室(wing cell)所組成。由於翅痣、翅脈與翅室皆具有顏色，在界定翅色型時需注意三者區別。翅痣顏色因與雌雄交配行爲的通訊有關，前人描述多指明翅痣顏色而不會與翅色相混淆。如細胸珈蟌雄蟌翅痣顏色由初羽化期的白色隨發育成熟轉呈橙紅色，雌蟌則皆維持爲白色(Oguma 1913；張及汪 1997；汪 2000；王 2007；曹 2011)。相反地，翅脈與翅室相互交織鑲嵌，如不指明，二者顏色容易混爲一談。特別是橙紅色至黑褐色翅脈(Oguma 1913；王 2007)，在翅室爲透明翅色時，翅脈顏色可能影響翅色判斷。過去有關細胸珈蟌雌蟌翅色多型性報導(張及汪 1997；汪 2000；王 2007；曹 2011)，可能是綜合翅脈與翅室二者顏色結果。本研究翅翼透明度偵測部位，經 Tsview 6.0 影像處理軟體對 6 隻個體補充測量結果，翅室佔總偵測面積 91.1±1.1%，翅脈僅佔 8.9±1.1%，故本研究翅色型歸類主要依據翅室特徵。

屬於不連續性變異的多型性現象，遺傳機制常爲簡單的單基因孟德爾遺傳(Mendelian inheritance) (Mayr and Ashlock 1991)。如 Tsubaki (2003)報導產於日本且翅色型亦爲雄蟌橙翅型、透翅型二型性，雌蟌透翅型單型性之 *Mnais costalis* 珈蟌，其翅色遺傳機制可用一基因座(locus)二對偶基因(allele)，橙色基因爲顯性並限於雄性表現加以解釋。由於細胸珈蟌與 *Mnais costalis* 珈蟌具有相同翅色型類別，可能亦具此遺傳性質。

三、成熟期雄、雌蟌各翅色型的形質比較

表 2 上方部分爲成熟期橙翅型雄蟌、透翅型雄蟌與透翅型雌蟌之翅翼相對透明度、翅翼面積與體乾重。就翅翼相對透明度而言，橙翅型雄蟌爲 41.9±3.6%，透翅型雄蟌爲 82.7±1.9%，透翅型雌蟌爲 82.1±1.5%。經單因子變異數分析(one-way ANOVA)結果，翅翼相對透明度上達到顯著差異(F=5362.5, p<0.001)。最小顯著差異測驗(LSD)成對比較結果，橙翅型雄蟌與透翅型雄蟌間(P<0.001)，或橙翅型雄蟌與透翅型雌蟌間(P<0.001)，皆有非常顯著差異；同屬透翅型的雄蟌與雌蟌間(p=0.336)則無顯著差異(表 3)。換言之，在翅翼透明度上，較不透明的橙翅型雄蟌確可自成一類，翅翼透明的透翅型雄、雌蟌歸類在同一型亦屬合理。

在翅翼面積上，透翅型雄蟌具較小翅翼面積(2.41±0.16cm^2)，橙翅型雄蟌(2.72±0.16cm^2)與透翅型雌蟌(2.76±0.18cm^2)皆較大(表 2 上方部分)。經單因子變異數分析結果，翅翼相對透明度上達到顯著差異(F=81.5, p<0.001)。最小顯著差異測驗成對比較結果，透翅型雄蟌無論與橙翅型雄蟌相比(p<0.001)或與透翅型雌蟌相比(p<0.001)，在翅翼面積上皆有非常顯著差異；橙翅型雄蟌與透翅型雌蟌間(p=0.165)則無顯著差異(表 3)。在體乾重上，透翅型雄蟌較低(34.0±5.8mg)，橙翅型雄蟌(49.8±7.4mg)與透翅型雌蟌(51.2±11.6mg)皆較高(表 2 上方部分)。經單因子變異數分析結果，體乾重也達到顯著差異(F=83.1, p<0.001)。最小顯著差異測驗成對比較結果，透翅型雄蟌無論與橙翅型雄蟌相比(p<0.001)或與透翅型雌蟌相比(p<0.001)，在體乾重上皆有非常顯著差異；橙翅型雄蟌與透翅型雌蟌間(p=0.313)則無顯著差異(表 3)。因此，透翅型雄蟌體型較小，橙翅型雄蟌與透翅型雌蟌體型皆較大。

細胸珈蟌透翅型雄蟌體型較小，橙翅型雄蟌體型較大現象，也見於其他種類的*Mnais*屬珈蟌。前人研究指出體型大的橙翅型雄蟌屬於領域性(territorial)生殖策略(mating strategy)，即

佔有領域並驅逐入侵領域的橙翅型雄螅與透翅型雄螅(Watanabe and Taguchi 1990；Watanabe 1991；Tsubaki *et al.* 1997)。由於捍衛領域的橙翅型雄螅在體型發育上比透翅型雄螅付出更多代價(Plaistow and Tsubaki 2000)，因此橙色翅色被認爲是提示此策略的誠實信號(honest signal)(Hooper *et al.* 2006)。反之，體型小的透翅型雄螅屬於無領域性(non-territorial)生殖策略，即不佔有領域並棲息於橙翅型雄螅領域週邊，伺機攫取雌螅進行交配，爲偷襲者(sneaker)交配方式(Watanabe and Taguchi 1990；Watanabe 1991；Tsubaki *et al.* 1997)。

由於*Mnais*屬珈螅族群一般兼具橙翅型與透翅型雄螅，顯示兩種翅色型與其代表的領域性與無領域性生殖策略各有其適應性(Watanabe and Taguchi 1990；Tsubaki *et al.* 1997)。本研究各採樣點亦皆採獲細胸珈螅橙翅型與透翅型雄螅，數量分別爲石門：1與8隻；萬里：71與12隻；雙溪：3與3隻；平溪：28與14隻；坪林：27與22隻；頭城：29與6隻(樣品數包括初羽化期與成熟期個體)。惟各採樣點的雄螅翅色型比例差異頗大，橙翅型在11%至86%間，透翅型在14%至89%間。由於各採樣點僅有1至2次調查，資料較爲粗糙，差異原因仍待後續探究。

表 2. 初羽化期與成熟期的橙翅型雄螅、透翅型雄螅與透翅型雌螅之翅翼相對透明度、翅翼面積與體乾重(n=樣品數；平均值±標準偏差)

Table 2. Wing relative transparency, wing area, and dry weight of the orange-winged male, clear-winged male, and clear-winged female in teneral and mature stages (n=sample size, mean±standard deviation)

Stage	Wing-color form and sex	n	Transparency (%)	Wing area (cm^2)	Dry weight (mg)
Mature	Orange-winged male	144	41.9 ± 3.6	2.72 ± 0.16	49.8 ± 7.4
	Clear-winged male	53	82.7 ± 1.9	2.41 ± 0.16	34.0 ± 5.8
	Clear-winged female	45	82.1 ± 1.5	2.76 ± 0.18	51.2 ± 11.6
Teneral	Orange-winged male	13	62.6 ± 4.2	2.61 ± 0.20	20.2 ± 4.8
	Clear-winged male	12	82.6 ± 1.1	2.32 ± 0.15	17.1 ± 4.8
	Clear-winged female	19	81.4 ± 2.3	2.68 ± 0.20	19.4 ± 6.1

表 3. 最小顯著差異測驗成對比較翅翼相對透明度、翅翼面積與體乾重之差異(平均差與 *p* 值)

Table 3. Pair-wise comparisons for wing relative transparency, wing area, and dry weight based on least significant difference (LSD) test (mean difference with *p*-value)

Pair-wise comparison	Transparency	Wing area	Dry weight
Mature orange-winged male versus mature clear-winged male	-40.8 (p<0.001)	31.1 (p<0.001)	15.8 (p<0.001)
Mature orange-winged male versus mature clear-winged female	-40.2 (p<0.001)	-3.9 (p=0.165)	-1.4 (p=0.313)
Mature clear-winged male versus mature clear-winged female	0.6 (p=0.336)	-35.3 (p<0.001)	-17.2 (p<0.001)

四、初羽化期與成熟期的形質比較

表 2 爲橙翅型雄蟌、透翅型雄蟌與透翅型雌蟌在成熟期(表 2 上方部分)與初羽化期(表 2 下方部分)的左前翅翼相對透明度、左前翅翼面積與體乾重。就翅翼透明度而言，橙翅型初羽化期雄蟌爲 62.6±4.2%，橙翅型成熟期雄蟌爲 41.9±3.6%，經 Mann-Whitney U test，二者具有非常顯著差異($p＜0.001$) (表 4)，即橙翅型雄蟌翅色隨成蟌發育由淺變深(圖 4. A, D)。相反地，在透翅型初羽化期雄蟌(82.6±1.1%)與成熟期雄蟌(82.7±1.9%)間($p=0.732$)，以及透翅型初羽化期雌蟌(81.4±2.3%)與成熟期雌蟌(82.1±1.5%)間($p=0.314$)，翅翼透明度皆無顯著差異(表 4)，即二生活期之翅色皆呈現較透明狀態(圖 4. B, E; C, F)。Hooper *et al.* (1999)利用同位素追蹤 *Mnais costalis* 珈蟌翅色發育，發現橙翅型雄蟌翅室具有色素前驅物(precursor)的堆積，但透翅型雄蟌則無。因此，細胸珈蟌橙翅型雄蟌翅色發育變深應與色素堆積表現有關，反之，透翅型個體在羽化期與成熟期皆無此表現而同呈透明翅色。

在翅翼面積上，橙翅型初羽化期雄蟌(2.61±0.20cm^2)與橙翅型成熟期雄蟌(2.72±0.16cm^2)間具有顯著差異($p=0.038$)(表 4)。但在透翅型初羽化期雄蟌(2.32±0.15cm^2)與透翅型成熟期雄蟌(2.41±0.16m^2)間($p=0.140$)，以及透翅型初羽化期雌蟌(2.68±0.20cm^2)與透翅型成熟期雌蟌(2.76±0.18cm^2)間($p=0.183$)皆無顯著差異(表 4)。換言之，雖然成熟期的翅翼面積皆較初羽化期爲大，但在統計上僅橙翅型雄蟌具有顯著差異。Matsubara *et al.* (2005)報導 *Calopteryx atrata* 珈蟌雄蟌，在不同年齡階段(age class)，翅翼面積並無顯著差異($p=0.1980$)。本研究中，透翅型雄蟌與透翅型雌蟌翅翼面積無明顯變化與 Matsubara *et al.* (2005)報導一致，但橙翅型雄蟌成熟期卻較初羽化期顯著較大，此差異是否與初羽化期的翅翼伸展程度有關，尚待進一步探討。

在體乾重上，橙翅型初羽化期雄蟌(20.2±4.8mg)與橙翅型成熟期雄蟌(49.8±7.4 mg)間($p＜0.001$)，透翅型初羽化期雄蟌(17.1±4.8 mg)與透翅型成熟期雄蟌(34.0±5.8 mg)間($p＜0.001$)，以及透翅型初羽化期雌蟌(19.4±6.1 mg)與透翅型成熟期雌蟌(51.2±11.6 mg)間($p＜0.001$)，皆有非常顯著差異(表 4)。簡言之，成熟期的橙翅型雄蟌、透翅型雄蟌與透翅型雌蟌明顯較重，並約爲初羽化期的 2.5、2.0 與 2.6 倍重。與幾丁質硬化後無法成長的翅翼不同，珈蟌體內的肌肉、脂肪、臟器等，在體壁硬化後，仍能進行發育而呈現體重增加現象(Plaistow and Tsubaki 2000；Matsubara *et al.* 2005)。

表 4. 曼-惠特尼 U 測驗成對比較翅翼相對透明度、翅翼面積與體乾重之差異(U 值與 p 值)

Table 4. Pair-wise comparisons for wing relative transparency, wing area, and dry weight based on Mann-Whitney U test (U score with p value)

Pair-wise comparison	Transparency	Wing area	Dry weight
Mature orange-winged male versus teneral orange-winged male	4 ($p<0.001$)	611 ($p=0.038$)	4 ($p<0.001$)
Mature clear-winged male versus teneral clear-winged male	297 ($p=0.732$)	230 ($p=0.140$)	12 ($p<0.001$)
Mature clear-winged female versus teneral clear-winged female	358 ($p=0.314$)	336 ($p=0.183$)	9.5 ($p<0.001$)

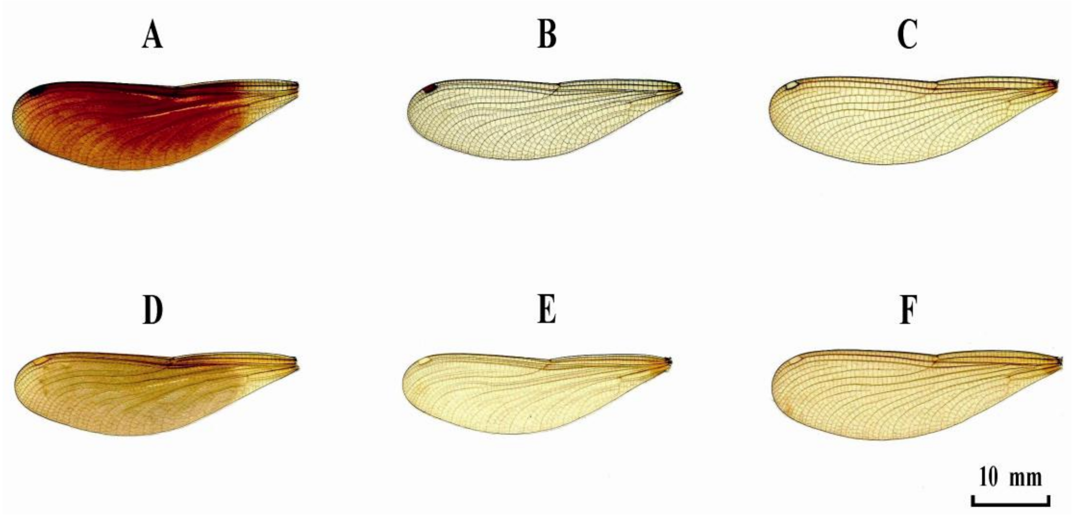

圖 4. 細胸珈蟌左前翅翼：A 成熟期橙翅型雄蟌；B 成熟期透翅型雄蟌；C 成熟期透翅型雌蟌；D 初羽化期橙翅型雄蟌；E 初羽化期透翅型雄蟌；F 初羽化期透翅型雌蟌。

Fig. 4. Left forewing of *Mnais tenuis*. A: mature orange-winged male; B: mature clear-winged male; C: mature clear-winged female; D: teneral orange-winged male; E: teneral clear-winged male; F: teneral clear-winged female.

比較特別的是透翅型雄蟌增重比例(2.0 倍)與橙翅型雄蟌(2.5 倍)或與透翅型雌蟌(2.6 倍)有較大差別。經 Mann-Whitney U test 後續分析結果，在體乾重上，透翅型初羽化期雄蟌與橙翅型初羽化期雄蟌間(*p*=0.137)，以及透翅型初羽化期雄蟌與透翅型初羽化期雌蟌間(*p*=0.367)皆無顯著差異，即初羽化期的透翅型雄蟌的體乾重與另二者接近。但在成熟期體乾重上，透翅型雄蟌與橙翅型雄蟌間(*p*<0.001)，以及透翅型雄蟌與透翅型雌蟌間(*p*<0.001)卻皆有非常顯著差異(表 3)，也就是成熟期的透翅型雄蟌體乾重與另二者明顯差異。換句話說，透翅型雄蟌體重的增加明顯少於另二者。相反地，橙翅型雄蟌與透翅型雌蟌，無論是在初羽化期的體乾重比較(Mann-Whitney U test 後續分析 *p*=0.495)或是在成熟期的體乾重比較(*p*=0.313) (表 3)皆無顯著差異，即橙翅型雄蟌體重增長狀態近似透翅型雌蟌。Anholt *et al.* (1991)指出無領域行爲的蜻蛉目雄蟲，無需花費較多能量在肌肉合成與捍衛領域上，因此體重低於雌蟲，但有領域性的雄蟲則與雌蟲體重接近。本研究中，透翅型雄蟌增重較少，橙翅型雄蟌增重近似雌蟌，配合 Anholt *et al.* (1991)歸納結果，以透翅型與橙翅型的翅色遞移代表雄蟌無領域性與有領域性之生殖策略似屬合理，然因領域行爲屬於動物行爲學研究範疇，故仍需野外行爲研究確認之。

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穿著顏色對大卷尾(*Dicrurus macrocercus*)驚飛距離的影響

Effects of Clothing Color on Flight Initiation Distance of Black Drongo (*Dicrurus macrocercus*)

林大利 [1,*]　鄭亦淳 [2]　陳威廷 [2]

Da-Li Lin[1,*], Yi-Chun Cheng[2] and Wei-Ting Chen[2]

[1]行政院農業委員會特有生物研究保育中心　55244 南投縣集集鎮民生東路 1 號
[2]國立臺灣大學森林環境暨資源學系　10617 臺北市大安區羅斯福路四段 1 號

[1] Endemic Species Research Institute, Jiji, Nantou, Taiwan
[2] School of Forestry and Resources Conservation, National Taiwan University, Taipei, Taiwan

*通訊作者：thrush1250@gmail.com

*Corresponding author: thrush1250@gmail.com

摘　要

人類活動爲影響鳥類生存及繁殖的干擾之一，其中一項影響因子爲鳥類對觀察者衣物顏色的容忍度可能不同，除了影響鳥類活動，亦會使鳥類調查結果產生偏差。本研究以驚飛距離作爲容忍度的指標，於國立臺灣大學農業試驗場以黑色、迷彩、白色、紅色及橘色穿著測試大卷尾的驚飛距離。結果發現以紅色穿著測得之驚飛距離顯著高於黑色及迷彩穿著之測值。彩度高的穿著之測値顯著高於彩度低者；亮度高的穿著之測値顯著高於亮度低者。結果支持物種信賴假說，大卷尾對與其羽色相近的黑色穿著，以及與背景相仿的迷彩服的容忍度較高；與其羽色相異甚大的紅色穿著的容忍度較低。賞鳥或調查時，應穿著彩度低、亮度低，或與背景相仿的顏色，以降低對鳥類造成的干擾。保護區經營管理方面，亦應該將鳥類對人類活動的容忍距離納入規劃核心區、緩衝區及遊憩區配置的考量。

Abstract

Human activities are a known disturbance affecting the survival and reproduction of wild birds. For instance, clothing color can affect bird activities as well as cause discrepancies in bird surveys. As such this study uses flight initiation distance (FID) as an indicator to investigate bird tolerance in different clothing colors. Five clothing colors (black, military camouflage, white, red and orange) were used to measure the FID of Black Drongo (*Dicrurus macrocercus*) in an experimental farm of National Taiwan University, Taiwan. The FID of Black Drongo when encountering red clothing was significantly larger than black clothing and military camouflage clothing. The FIDs triggered by high colorfulness were significantly greater than that of low colorfulness ones. The FIDs caused by high brightness were significantly greater than low brightness ones. The results support the species-confidence hypothesis. The Black Drongo showed higher tolerance in black and military camouflage clothing and lower tolerance in red clothing. The results suggest that it is important to wear clothes of low colorfulness, low brightness, or in colors similar to the surrounding environment during bird watching and surveys. The results also show that when managing a conservation area, it is important to take the degree of bird tolerance into consideration before designating core zone, buffer zone and recreation area.

關鍵詞：衣著顏色、驚飛距離、最適逃跑理論、物種信賴假說、臺灣

Key words：clothing color, flight initiation distance, optimal escape theory, species-confidence hypothesis, Taiwan

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緒言

人類及其伴侶動物與交通工具的活動已經被視爲影響鳥類生存的干擾之一(van der Zande and Verstrael 1985; Fox and Madsen 1997; Delaney *et al.* 1999)。人類活動對鳥類的影響，輕則暫時影響鳥類的棲地利用、覓食與繁殖，嚴重時可能導致繁殖失敗(Şekercǐoğlu 2002; Weston *et al.* 2012)。經營管理方面，適當配置核心區、緩衝區及遊憩區，盡可能降低人類活動對野生動物的影響就顯得相當重要(Şekercǐoğlu 2002; Weston *et al.* 2012)。

天敵出現時，野生動物必須在適當的時機採取應對策略，以降低被捕食的風險，其中逃脫反應是鳥類中常見的應對策略(Ydenberg and Dill 1986; Hockin *et al.* 1992)。獵物逃脫

時，獵物與天敵之間的距離稱爲驚飛距離(flight initiation distance)(Ydenbery and Dill 1986)。以驚飛距離分析逃脫行爲的成本效益分析，已經相當成功的建構獵物逃脫取捨關係(trade-off)的最佳策略模型 (Ydenbery and Dill 1986; Lima and Dill 1990; Cooper 1999; Cooper 2000; Broom and Ruxton 2005; Cooper and Frederick 2007)。最佳逃脫理論(optimal escape theory)(Ydenbery and Dill 1986)預測：當獵物被捕食的風險等於逃脫所付出的代價時，獵物就會採取逃脫策略，此時獵物與天敵的距離，稱爲最適驚飛距離(optimal flight initiation distance)。因此，掌握適當的驚飛距離，是獵物生存的重要策略。最佳逃脫理論不僅成爲探討逃脫行爲的基本概念，亦深入探討各種因子對驚飛距離的影響(Cooper *et al.* 2003)，例如天敵的種類(McLean and Godin 1989)、天敵接近的速度(Cooper 1997)、天敵的來向以及避難處的距離(Bulova 1994)。

顏色是許多鳥類溝通的重要訊息之一(Osorio and Vorobyev 2008)，鳥類身體各部位的顏色是辨識同種個體(Gill 1995)和潛在競爭者(Metz and Weatherhead 1991)的依據，也可能影響該個體在群體中的位階(Rohwer 1985)、配偶選擇(Noble 1936; Burley 1981; Burly 1986a; Burly 1986b; Ballentine and Hill 2003)與維持配對關係(Frankel and Baskett 1963; Goforth and Baskett 1965)、繁殖成功率等(Weatherhead *et al.* 1991; McGraw *et al.* 2001)。Burley(1986b)提出物種信賴假說(species-confidence hypothesis)，認爲鳥類較偏好與羽色相近的個體活動，而傾向排斥羽色差異甚大的個體。物種信賴假說也廣泛應用於研究鳥類行爲(*e.g.* Rockwell *et al.* 1985; Weltry and Baptista 1988; Gould *et al.* 2004)，尤其是躲避天敵的相關研究(McLean and Godin 1989; Bulova 1994; Cooper 1997; Cooper *et al.* 2003)。Gutzwiller and Marcum (1993)發現卡羅山雀(*Parus cardinensis*)、美洲鳳頭山雀(*Parus bicolor*)與美洲金翅雀(*Carduelis tristis*)對鮮艷橘色的穿著有強烈的排斥性。經營管理方面，許多研究以鳥類的驚飛距離作爲鳥類對遊客容忍度的指標(Knight and Temple 1995; Larson 1995; Riffell and Riffell 2002; Şekercĭoğlu 2002)。不僅是遊客的穿著與行爲會影響鳥類的生存與繁殖，鳥類調查員衣著的顏色也會使調查結果產生偏差(Gutzwiller and Marcum 1993; Riffell and Riffell 2002)。

綜上所述，本研究目標在於以驚飛距離作爲容忍度的指標，探討不同顏色、彩度與亮度的穿著，對鳥類驚飛距離的影響。本研究以大卷尾(*Dicrurus macrocercus*)爲研究對象，2008年於國立臺灣大學農業試驗場執行。以驚飛距離爲依變數(dependent variable)，並分別以觀察者穿著的顏色、彩度高低、以及亮度高低爲獨立變數(independent variables)，測試衣著顏色對大卷尾驚飛距離的影響。

材料與方法

研究地點

國立臺灣大學農業試驗場(25°02' N, 121°53' E)（圖 1）位於臺北市大安國立臺灣大學校總區東南隅，面積 5.77 ha，海拔 20 m（陳等，2008）。場內包含生態池與試驗田兩部份，主要試驗作物包含玉米、高莖作物、水稻、甘藷及草坪。場內景觀呈破碎區塊狀分布，路徑系統發達，無高大樹木或建築物等障礙遮蔽，適合追蹤及觀察鳥類行爲。

研究對象

大卷尾屬於臺灣特有亞種，分類上屬燕雀目(Passeriformes)、卷尾科(Dicruidae)、卷尾屬(*Dicrurus*)，廣泛分布於臺灣平地及海拔 1,000 m 以下的淺山地區，離島有少數紀錄，爲低海拔及平地地區的優勢鳥種。通常單獨或成小群出現於樹林、竹林之上層或邊緣，鮮少於樹林內部活動。常於犁田時飛捕土壤中被驚起的無脊椎動物，在食物豐盛的地區會群聚覓食。大卷尾以大型昆蟲爲主食，偶而捕食小型的鳥類或哺乳動物。繁殖期間的領域性強，對入侵領域內的生物攻擊性高，亦有攻擊體型較大的巨嘴鴉 (*Corvus macrorhynchos*)、鳳頭蒼鷹 (*Accipiter trivirgatus*)，甚至人類的紀錄 (林 2012)。由於大卷尾時常停棲於明顯的突出物上，適合測量驚飛距離。

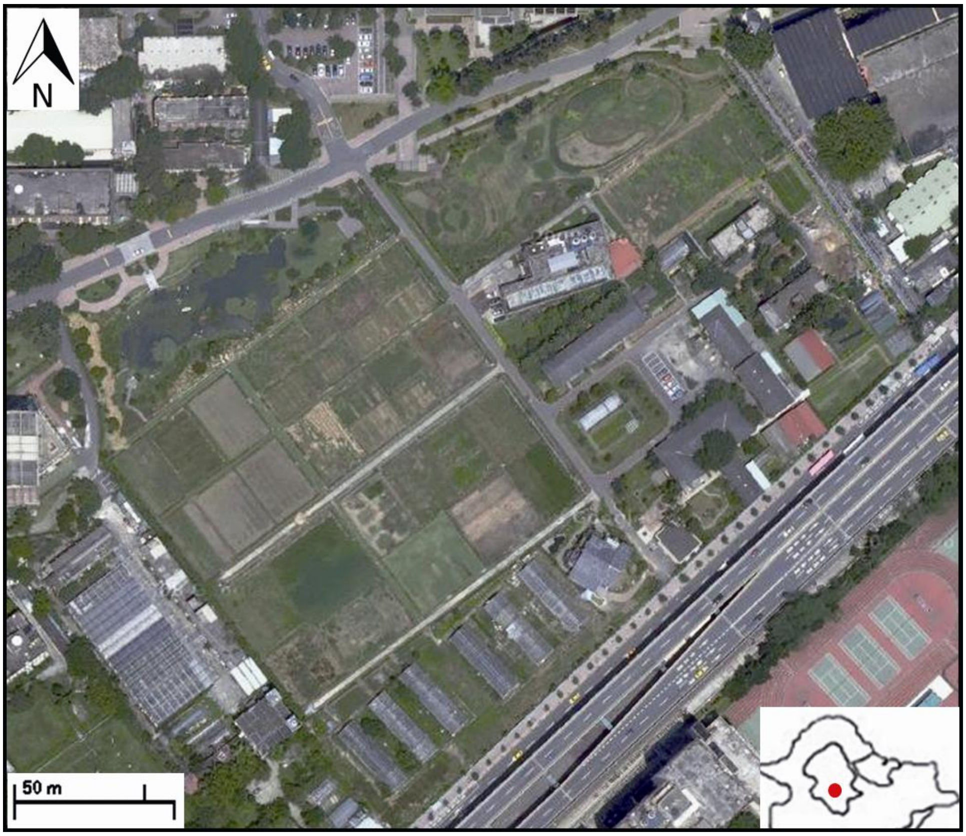

圖 1. 國立臺灣大學生物資源暨農學院農業試驗場航空照片圖。

Fig. 1. Aerial photo of the experimental farm, College of Bioresources and Agriculture, National Taiwan University.

野外資料蒐集方法

本研究於 2008 年 11 月 27 日至 12 月 12 日間，於上午 7 時至 9 時之間進行試驗。首先於農場外圍以雙筒望遠鏡(Canon: 15 × 50, IS UD 4.5°)尋找停棲高度不超過 2 m 的大卷尾。於五種顏色（紅色、橘色、黑色、白色及迷彩）的穿著中，逢機選擇一種作爲待測試的顏色。其中迷彩服爲美國 Crye Precision 設計的多環境迷彩(Multi Environmental Camouflage)，該設計使用七種色調，適用於不同環境、季節、海拔及亮度的變化。穿著長度自領口至下緣固定爲 100 cm，並超過穿著者的腰部以下，穿著者皆爲同一人，下半身均穿著相同黑色長褲、黑襪及黑色運動鞋。發現目標個體後換上測試顏色的穿著，在無遮蔽物的狀況下，自距離大卷尾約 30 m 處以時速約 1 km 的緩慢穩定步伐，直向目標個體靠近。當大卷尾飛離停棲處時，使用皮尺(Yamayo Million, 50 m)測量測試者到大卷尾原停棲處之水平距離，此距離即爲驚飛距離，並記錄測試時間、驚飛距離以及衣著顏色。

統計分析

影響大卷尾驚飛距離的獨立變數包含衣著的顏色、彩度及亮度。紅色及橘色合併爲高彩度色，黑色、白色及迷彩則合併爲低彩度色；紅色、橘色及白色合併爲高亮度色，黑色及迷彩則合併爲低亮度色；驚飛距離則爲依變數。統計分析採用 R 2.15.3 版執行單因子變異數分析、成對 t 檢定及杜凱氏檢定(Tukey’s test)；繪圖則採用繪圖軟體 Sigma Plot 10.0 版繪製。

結　果

本研究共測得 90 筆驚飛距離資料，各顏色穿著所測得之驚飛距離如下：黑色(mean = 6.45, SE = 0.71, N = 24)、白色(mean = 9.57, SE = 1.17, N = 14)、紅色(mean = 12.19, SE = 1.58, N = 17)、橘色(mean = 9.33, SE = 1.27, N = 18)、迷彩(mean = 6.76, SE = 0.61, N = 17)；高彩度色(mean = 10.72, SE = 1.02, N = 35)、低彩度色(mean = 7.34, SE = 0.49, N = 55)；高亮度色(mean = 10.39, SE = 0.80, N = 49)及低亮度色(mean = 6.57, SE = 0.48, N = 41)。

五種顏色穿著所測得的驚飛距離之間具顯著的差異(圖 2, one-way ANOVA, F = 4.833, $p < 0.010$)。紅色穿著所測得之驚飛距離顯著高於黑色(圖 2, Tukey’s test, $p < 0.010$)及迷彩穿著(圖 2, Tukey’s test, $p < 0.010$)者；與橘色穿著(圖 2, Tukey’s test, $p = 0.362$)及白色穿著(圖 2, Tukey’s test, $p = 0.517$)者之間則無顯著差異。橘色穿著之測值與黑色(圖 2, Tukey’s test, $p = 0.269$)、迷彩(圖 2, Tukey’s test, $p = 0.470$)及白色(圖 2, Tukey’s test, $p = 1.000$)者之間無顯著差異。白色穿著之測值與黑色(圖 2, Tukey’s test, $p = 0.267$)及迷彩穿著(圖 2, Tukey’s test, $p = 0.447$)之間無顯著差異。黑色穿著之測值與迷彩穿著者之間無顯著差異(圖 2, Tukey’s test, $p = 0.999$)。彩度高的穿著之測值顯著高於彩度低者 (圖 3, Paired t-test, $p < 0.010$)。亮度高的穿著之測值顯著高於亮度低者 (圖 4, Paired t-test, $p < 0.001$)。

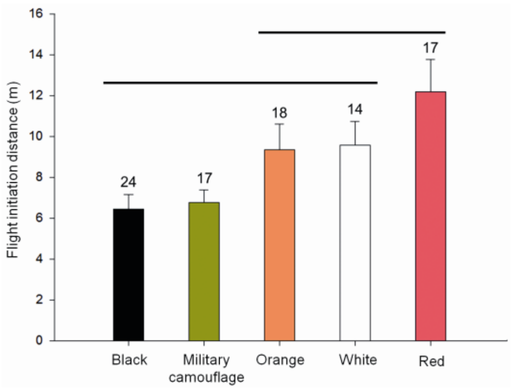

圖 2. 大卷尾對人類穿著 5 種顏色服裝的驚飛距離(flight initiation distance)之差異水平線下方之長條表示其間無顯著差異，誤差長條(error bar)爲樣本的標準機差，樣本數標示於長條圖上方。

Fig. 2. Variation of flight initiation distances of Black Drongo when encountering researchers with five different clothing colors. The bars of different colors under the same horizontal line indicate non-significant differences among them. Each error bar indicates standard error, and the numbers above the bars are sample size.

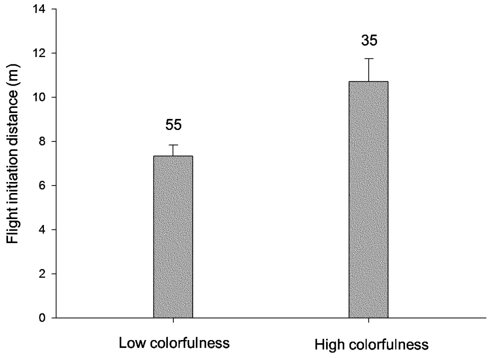

圖 3. 大卷尾對人類穿著高、低彩度服裝之驚飛距離(flight initiation distance)。圖中直條代表一個標準機差，樣本數標示於長條圖上方。

Fig. 3. Variation of flight initiation distances of Black Drongo encountering researchers with high clothing colorfulness. Each error bar represents standard error, and the numbers above each bar indicate sample size.

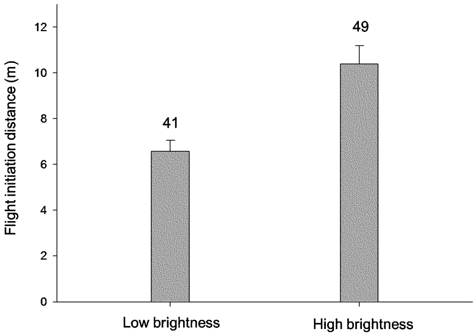

圖 4. 大卷尾對人類穿著高、低亮度服裝之驚飛距離(flight initiation distance)。圖中直條代表一個標準機差，樣本數標示於長條圖上方。

Fig. 4. Variation of flight initiation distances of Black Drongo when encountering researchers with high clothing brightness. Each error bar represents standard error, and the numbers above each bar indicate sample size.

討　論

分析結果顯示，以紅色穿著所測得之驚飛距離，顯著高於黑色及迷彩穿著的測值。彩度高的穿著所測得之驚飛距離顯著高於彩度低者。亮度高的穿著所測得之驚飛距離顯著高於亮度低者。在穿著者相同、接近速度相同的狀況下：大卷尾對衣著顏色爲紅色、高彩度、以及高亮度的警戒程度較高、容忍度較低，傾向與上述顏色穿著的觀察者保持較遠的距離；對衣著顏色爲黑色、迷彩、低彩度、以及低亮度

的警戒程度較低、容忍度較高，傾向與上述顏色穿著的觀察者保持較近的距離。

物種信賴假說(Burley 1985; Burley 1986b)認爲鳥類較青睞相同物種或與其顏色相似的個體，反之則較排斥。斑胸草雀(*Poephila guttata*)的雄成鳥具有橘紅色的喙與爪，Burley (1986a)發現比起繫上藍色或綠色腳環的雄鳥，雌鳥顯著較青睞繫上橘紅色腳環的雄鳥。Wilson *et al.* (1990)發現阿德利企鵝(*Pygoscelis adelae*)也會主動接近與自己羽色相似的鳥類模型。Johnson *et al.* (1993) 發現美洲金翅雀的雄鳥的喙會在繁殖季轉變爲鮮艷的橘色，繁殖季期間，雌鳥明顯較青睞繫上橘色腳環的雄鳥，但非繁殖季時則無此現象。

大卷尾羽色爲略帶光澤的黑色，紅色穿著不僅與其羽色大相逕庭，彩度與亮度亦較高，因此所測得之驚飛距離顯著最遠。黑色穿著可能因與其羽色相近，而測得之的驚飛距離最短；迷彩的效果使其與背景顏色相仿的程度更高，而測得較短之驚飛距離。本研究結果支持物種信賴假說，觀察者不同顏色的穿著對鳥類所測得之驚飛距離顯著不同，很可能表示鳥類對不同顏色穿著的有不同的容忍度。

若以鳥類的驚飛距離、偵測距離或警戒距離作爲鳥類對遊客容忍度的指標，在不同環境、鳥種以及各種影響因子的狀況下，所測得的驚飛距離並不盡相同(葛與鄭 2011; Glover *et al.* 2011; Weston *et al.* 2012)。穿著彩度高或亮度高的衣服，不僅較容易使鳥類警戒，尤其繁殖季期間更容易造成影響(Şekercĭoğlu 2002)。執行鳥類調查時，彩度或亮度較高的穿著也容易使調查結果產生偏差(Gutzwiller and Marcum 1993; Riffell and Riffell 2002)。因此，賞鳥或鳥類調查時，確實應穿著彩度低、亮度低，或與背景相仿的顏色，以降低對鳥類造成的干擾。經營管理方面，爲同時兼顧保育以及教育遊憩的功能，核心區、緩衝區、遊憩區的配置規劃，亦應將驚飛距離納入規劃中，使遊客與野生動物保持適當地距離。

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類禽痘症於臺灣燕雀目留鳥盛行率之初探

Preliminary investigation of the prevalence of avian pox-like lesions in resident passerines in Taiwan

林瑞興[1,*] 楊昌諺[2] 梅允文[3] 宋心怡[1]

Ruey-Shing Lin[1,*], Chang-Yan Yang[2], Yun-Wen Mei[3] and Hsin-Yi Sung[1]

[1] 行政院農業委員會特有生物研究保育中心 55244 南投縣集集鎮民生東路 1 號
[2] 國立中興大學生命科學研究所 40227 台中市國光路 250 號
[3] 臺灣省野鳥協會 40242 台中市建國南路 2 段 218 號 1 樓

[1] Endemic Species Research Institute, Jiji, Nantou, Taiwan
[2] Department of Life Sciences, National Chung Hsing University, Taichung, Taiwan
[3] Taiwan Wild Bird Association, Taichung, Taiwan

*通訊作者：rslin@tesri.gov.tw

*Corresponding author: rslin@tesri.gov.tw

摘 要

禽痘已知出現於許多鳥類中，但至今仍無其於臺灣野生鳥類盛行率和分布的相關研究。本研究運用臺灣鳥類生產力與存活率監測(MAPS Taiwan)計畫，2010-2012 年間於臺灣各地所得 50 種 1,591 隻燕雀目留鳥的繫放資料中，發現白尾鴝(9 隻)、白眉林鴝(1 隻)、山紅頭(1 隻)及繡眼畫眉(1 隻)出現類禽痘症，其盛行率分別爲 9.78%、3.23%、0.37% 及 0.28%。整體而言，臺灣留鳥出現類禽痘症的比例(0.75%)不高，但少數特定鳥種如白尾鴝的盛行率偏高。白尾鴝病例出現各地，由少數重複捕捉的病例發現，類禽痘病灶可持續 2-3 年以上，且病徵會持續加重。雖然禽痘一般不致於對大陸型島嶼留鳥造成太大負面衝擊，但類似 MAPS Taiwan 這類系統性的長期監測，將有助於早期偵測禽痘在野生鳥類中盛行率的變動。

Abstract

Avian pox has been reported in a wide range of avian species, yet nothing has been published about its prevalence and distribution in resident passerines in Taiwan. We used banding data from the Monitoring Avian Productivity and Survivorship, Taiwan (MAPS Taiwan) program from 2010 to 2012 to evaluate the prevalence of avian pox-like lesions. In total, 50 resident passerine species and 1,591 newly captured individuals were included in this study. Prevalence of avian pox-like lesions was 0.75% on average. Individual white-tailed robin *Cinclidium leucurum*, white-browed bush-robin *Tarsiger indicus*, rufous-capped babbler *Stachyridopsis ruficeps*, and gray-cheeked fulvetta *Alcippe morrisonia*, were found with lesions, and the number of cases and prevalence of avian pox-like lesions were 9 (9.78%), 1 (3.23%), 1 (0.37%), and 1 (0.28%), respectively. In contrast to most of the bird species studied which all showed a relatively low prevalence for pox virus infection, the white-tailed robin seemed to be easily infected by pox viruses. From data collected from recaptured cases, the lesions appear to last longer than two years at least. In case of an unexpected outbreak of avian pox, systematic monitoring programs of wild bird populations, such as MAPS Taiwan, would assure early detection of any such increase in the number of infected birds.

關鍵詞：禽痘病毒、白尾鴝、臺灣鳥類生產力與存活率監測、留鳥、燕雀目

Key words： avian pox virus, *Cinclidium leucurum*, MAPS Taiwan, resident birds, Passeriformes

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緒言

禽痘爲鳥類病毒性疾病之一，其疾病發展過程相當緩慢，臨床上病徵是在鳥腳趾、跗蹠或頭，或(及)在口腔和上呼吸道黏膜產生離散、增生性病變(van Riper and Forrester 2007)。禽痘爲廣泛分布的野生鳥類疾病，在許多科別中已有病例報導(van Riper and Forrester 2007)。大部分禽痘感染是溫和且鮮少造成受感染者死亡，但若病變發生在眼皮或口腔、呼吸道的黏膜，則可能有相當高的死亡率(van Riper and Forrester 2007)。此外，在長久孤立的海洋性島嶼上的鳥類族群也被發現較生活於大陸的鳥類容易受到禽痘的影響，一般認爲是因爲大陸地區宿主、病媒和病毒之間已有長遠的共演化關係(Vargas 1987; van Riper *et al.* 2002)。夏威夷、加拉巴哥(Galapagos Islands)及加那利群島(Canary

Islands)等海洋性島嶼均發現禽痘病毒(*Poxvirus avium*)於引入後快速地擴散，且其發生於原生鳥種的盛行率遠高於引入的外來鳥種，並對原生鳥類族群造成相當大的衝擊(van Riper *et al.* 2002; Atkinson *et al.* 2005; Smits *et al.* 2005; Thiel *et al.* 2005)。

雖然大部分禽痘病毒直接導致大陸型地區宿主死亡的比率並不高(van Riper and Forrester 2007)。然研究顯示，禽痘對染病個體適存度(fitness)的影響，很可能是多方面的，例如降低配對成功率、減損飛行能力、降低覓食率、降低鳥蛋孵化率及免疫能力受損等(Kleindorfer and Dudaniec 2006)。此外，近年因全球氣候變遷和外來種問題日趨嚴重，禽痘病毒也可能藉由病媒自然的分布改變或因人類蓄意、非蓄意的引入，導致病毒入侵至新的區域，進一步造成原生物種受到較大的負面影響(Lachish *et al.* 2012a, b; Lawson *et al.* 2012)。

禽痘主要的傳染途徑爲蟲類叮咬，病毒通過機械性傳播到叮咬後受損傷的皮膚而引起(Akey *et al.* 1981; van Riper *et al.* 2002)。而如同許多疾病，禽痘的發生是與密度相關的，病媒及宿主的密度愈高愈有利於禽痘傳染，因此禽痘經常好發於飼養密度高的圈養環境及鳥類復育中心(van Riper and Forrester 2007)。在溫暖潮濕的野外環境，經常有較多的病媒存在，因此禽痘盛行率偏高，尤以群集性的鳥種最爲嚴重(Forrester 1991; Young and VanderWerf 2008)。

位於北回歸線通過的臺灣島，潮濕多雨，野外蚊蟲數量相當豐富，然而至今仍無針對野外自然存活的鳥類進行過系統性調查。本研究利用自2009年開始，每年以固定努力量繫放方式監測鳥類族群的計畫－臺灣鳥類生產力與存活率監測(The monitoring avian productivity and survivorship program, Taiwan, MAPS Taiwan)(宋等 2012)所產生的資料，初步呈現臺灣燕雀目(Passerformes)留鳥類禽痘的盛行率及在各鳥種的分布情形。

材料與方法

本研究利用MAPS Taiwan計畫團隊，自2010 - 2012年於臺灣各地蒐集的繫放資料，檢視類禽痘症於燕雀目留鳥的盛行率。MAPS Taiwan自2009年開始運行，2010 - 2012 年運作的繫放站包括：新北市新店區四崁水(海拔 400m)、台中市和平區烏石坑(海拔 1,000m)、花蓮縣秀林鄉合歡山(海拔 3,000m)、南投縣仁愛鄉瑞岩(海拔 2,200m)、雲林縣林內鄉湖本(海拔 200m)、雲林縣斗六市湖山(海拔 250m)、嘉義縣中埔鄉社口(海拔 300m)及台南市龍崎區牛埔(海拔 100m)等地(圖 1)。各繫放站均依循標準作業程序進行操作(林 2012)。本研究鳥類年齡區別以1月1日爲基準，1齡鳥(hatching year)指捕捉當年12月31日之前出生，超過1齡(after hatching year)指至少爲捕捉當時前1年的1月1日至12月31日間出生的鳥，餘年齡區別以此類推。另本研究除納入MAPS Taiwan 3-9月間的繫放監測資料外，亦納入該團隊不定時舉行繫放活動所蒐集的資料。MAPS Taiwan團隊自2010年起要求所有繫放員對於出現類禽痘症的個體，特別予以註記，故本研究僅採用2010 - 2012年間的繫放資料。繫放員以肉眼檢視鳥體有無出現類禽痘病變，病變區分爲發作中和非發作中兩類。發作中的類禽痘病變係指裸露皮膚

處出現小至大型黃白色丘疹，嚴重者皮膚糜爛而結痂、脫落的情形，非發作中者則指腳趾或爪出現變形或缺失的情形(Kleindorfer and Dudaniec 2006)。雖然明顯的禽痘病變非常容易區分或發現，但由於蟎和細菌感染偶爾會在鳥的腳上產生與禽痘類似的症狀(van Riper and Forrester 2007)，而本研究並未進行病毒判定，故以類禽痘症稱之。鳥種中文名及學名依據臺灣鳥類名錄 2012 年版(阮等 2012)。

結果

2010 - 2012 年 MAPS Taiwan 累計新捕獲燕雀目留鳥個體數總計 50 種 1,591 隻(附錄 1)，其中數量比例超過 5% (80 隻)者共有 6 鳥種，分別爲繡眼畫眉 *Alcippe morrisonia* (361 隻)、山紅頭 *Stachyridopsis ruficeps* (272 隻)、頭烏線 *Schoeniparus brunnea* (139 隻)、小彎嘴 *Pomatorhinus musicus* (105 隻)、黃胸藪眉 *Liocichla steerii* (102 隻)及白尾鴝 *Cinclidium leucurum* (92 隻)。其中發現有 4 (8%)鳥種、12 (0.75%)隻個體有類禽痘病變，其中以白尾鴝 9 隻最多，其餘 3 種分別爲白眉林鴝 *Tarsiger indicus* (新捕獲個體數爲 31 隻)、山紅頭及繡眼畫眉，各僅有 1 隻的紀錄(表 1)，前述 4 鳥種分別占各鳥種捕獲個體總數的 9.78%、3.23%、0.37%及 0.28%。就捕獲個體總數前 6 名的鳥種而言，白尾鴝出現類禽痘症的比例顯著偏高($\chi^2 = 69.221$, $df = 5$, $p < 0.001$)，且病例散布各地。

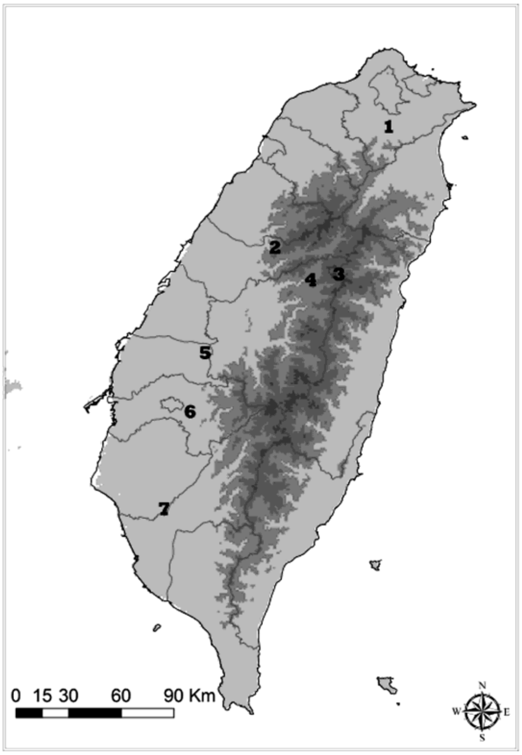

圖 1. MAPS Taiwan 繫放站分布圖。(1)新北市新店區四崁水，(2)台中市和平區烏石坑，(3)花蓮縣秀林鄉合歡山，(4)南投縣仁愛鄉瑞岩，(5)雲林縣林內鄉湖本及斗六市湖山，(6)嘉義縣中埔鄉社口及(7)台南市龍崎區牛埔。

Fig. 1. The map shows the locations of each banding site operated by MAPS Taiwan program. (1) Sikanshui, Xindian, New Taipei, (2) Wushikeng, Heping, Taichung, (3) Hehuanshan, Xiulin, Hualien, (4) Ruiyan, Renai, Nantou, (5)Huben , Linnei and Hushan, Douliu, Yunlin, (6) Shekou, Jhongpu, Chiayi, and (7) Niupu, Longci, Tainan.

4 種 12 隻出現類禽痘症的個體，分別捕獲於低海拔的新北市新店區四崁水(1 隻白尾鴝)、雲林縣林內鄉及斗六市(山紅頭 1 隻、白

尾鴝 2 隻及繡眼畫眉 1 隻)，中海拔的南投縣仁愛鄉瑞岩(6 隻白尾鴝)及高海拔的花蓮縣秀林鄉合歡山(白眉林鴝 1 隻)(表 1)。

12 隻出現類禽痘症的個體中，4 隻爲雌鳥，7 隻爲雄鳥，1 隻性別未確認。另就年齡分布而言，8 隻爲超過 1 齡、1 隻 2 齡、2 隻超過 2 齡、1 隻 1 齡(表 1)。此外，11 隻鳥禽呈現發作中狀態，僅 1 隻白尾鴝雌鳥呈現恢復後的非發作中狀態，其腳趾明顯變形及缺失(圖 2)。

12 隻出現類禽痘症的個體中，有 3 隻個體於發現有類禽痘病灶後，有多次重複捕捉的紀錄。其中 1 隻繡眼畫眉(環號 A33534)於 2010 年 8 月 12 日首次捕捉時，發現有類禽痘病灶，後於當年 9 月 9 日及 2012 年 8 月 6 日被回收。1 隻白尾鴝雌鳥(環號 B45118)於 2010 年 3 月 6 日首次捕捉時，跗蹠已有類禽痘病灶，2013 年 4 月 13 日回收時，顯著的病灶已散布於跗蹠關節、趾及嘴喙等各處(圖 3)。另有 1 隻白尾鴝雄鳥(環號 A47057)，自 2011 年 7 月 7 日首次捕捉起至 2013 年 4 月 7 日止已被捕捉 13 次，其於 2011 年 9 月 4 日被發現出現類禽痘病灶，至 2013 年 4 月 7 日其病灶仍存在且趨於嚴重(圖 4)。

表 1. 2010-2012 年出現類禽痘症個體之首次捕捉紀錄

Table 1. The first captured records of the individuals with avian pox-like lesions from 2010 to 2012

Species name	Band Number	Date (year/month/date)	Locality	Sex	Age
山紅頭(*Stachyridopsis ruficeps*)	K05374	2010/8/24	湖山(Hushan)	Male	After hatching year
白尾鴝(*Cinclidium leucurum*)	B45105	2010/3/5	湖山(Hushan)	Male	After hatching year
白尾鴝(*Cinclidium leucurum*)	Unbanded	2010/12/12	四崁水(Sikanshui)	Female	After hatching year
白尾鴝(*Cinclidium leucurum*)	B45118	2011/3/6	湖本(Huben)	Female	After hatching year
白尾鴝(*Cinclidium leucurum*)	A47057	2011/9/4	瑞岩(Ruiyan)	Male	After hatching year
白尾鴝(*Cinclidium leucurum*)	A47059	2011/7/7	瑞岩(Ruiyan)	Male	After hatching year
白尾鴝(*Cinclidium leucurum*)	A47060	2011/7/7	瑞岩(Ruiyan)	Male	After hatching year
白尾鴝(*Cinclidium leucurum*)	B25403	2012/5/26	瑞岩(Ruiyan)	Female	Second year
白尾鴝(*Cinclidium leucurum*)	B27797	2012/5/26	瑞岩(Ruiyan)	Male	After second year
白尾鴝(*Cinclidium leucurum*)	B27798	2012/5/26	瑞岩(Ruiyan)	Female	After second year
白眉林鴝(*Tarsiger indicus*)	A45320	2012/9/1	合歡山(Hehuanshan)	Male	After hatching year
繡眼畫眉(*Alcippe morrisonia*)	A33534	2010/8/12	湖山(Hushan)	Unknown	Hatching year

圖 2. 非發作中類禽痘症的案例 – 超過 1 齡白尾鴝(*Cinclidium leucurum*)雌鳥，2010 年 12 月 12 日於新北市新店區四崁水紀錄。

Fig. 2. A case of inactive avian pox-like lesions recorded from an after-hatching-year female white-tailed robin (*Cinclidium leucurum*) in Sikanshui, Xindian, New Taipei on December 12, 2012.

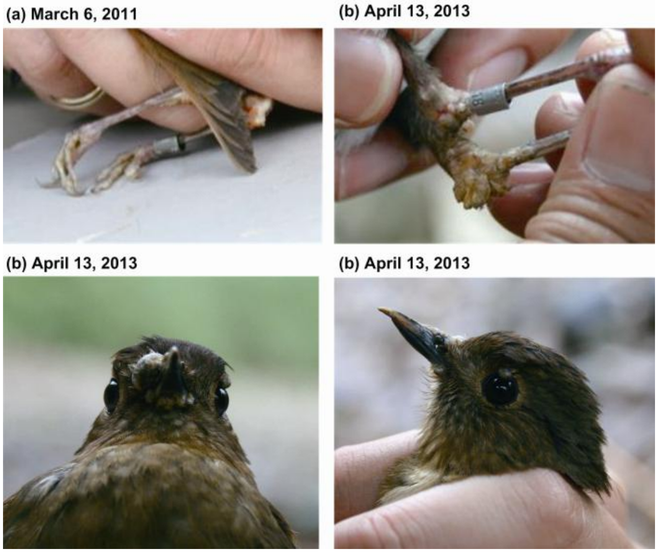

圖 3. 1 隻出現類禽痘症的白尾鴝(*Cinclidium leucurum*) (環號：B45118)雌鳥及其病變由 2011 年至 2013 年的變化。

Fig. 3. A case of a banded female white-tailed robin (*Cinclidium leucurum*) with active avian pox-like lesions captured in 2011 and recaptured in 2013. (Band number: B45118)

圖 4. 1 隻出現類禽痘症的白尾鴝(*Cinclidium leucurum*)(環號：A47057)雄鳥及其病變由 2011 年至 2013 年的變化。

Fig. 4. A case of a banded male white-tailed robin (*Cinclidium leucurum*) with active avian pox-like lesions from September 2011 to April 2013. (Band number: A47057)

討 論

禽痘病毒除南北極及少數極偏遠地帶之外，廣泛分布於世界各地，且曾有病例報告的野生鳥類至少達 20 目、70 科、278 種鳥以上(van Riper and Forrester 2007)。而臺灣曾在野生鳥類救傷案例中，於大冠鷲(*Spilornis cheela*)及鳳頭蒼鷹(*Accipiter trivirgatus*)發現有禽痘(詹等 2009; Chen *et al.* 2011)，惟至今仍無針對野生鳥類禽痘盛行率進行過系統性調查。本研究配合 MAPS Taiwan 計畫，於繫放過程中一併觀測類禽痘症於臺灣島野生留鳥中的盛行率。本研究利用所繫放的 50 種鳥中，發現有白尾鴝、白眉林鴝、山紅頭及繡眼畫眉等 4 種鳥出現類禽痘症，均爲各鳥種感染類禽痘症的首次報導。就整體盛行率而言，所繫放的 1,591 隻個體中，計有 12(0.75%)隻鳥出現類禽痘症。屬大陸型島嶼的台灣，0.75%的禽痘盛行率與已知大陸型地區盛行率主要在 0.5-1.3%相仿，相較於海洋性島嶼夏威夷原生鳥種的 6-23.5%

則明顯低了許多(van Riper *et al.* 2002; Atkinson *et al.* 2005)。然而，若就曾出現類禽痘症的鳥種來看，白尾鴝近 10% 的盛行率實屬偏高。

禽痘對染病個體適存度具多方面的負面影響(Kleindorfer and Dudaniec 2006)。雖然目前的紀錄仍屬有限，但就空間分布而言，類禽痘症於台灣由北至中南部，由低至高海拔均有病例，且於白尾鴝中盛行率特別高，另病灶持續期間長，非發作與發作中個體比例偏低的情形，均值得注意。非發作與發作中個體比例爲鳥類感染禽痘後可自然復原的指標(van Riper *et al.* 2002)。設若暴露於禽痘病毒的機會是相似的，影響禽痘於一特定鳥種族群中盛行率的主要原因爲宿主密度、宿主易受感染程度及病媒的數量(van Riper *et al.* 2002)。白尾鴝喜棲息於中海拔潮濕的森林下層，經常於林道邊陰暗的地面活動，有明顯的垂直遷移現象，族群數量並不算普遍(劉等 2012)。故就其密度和病媒數量而言，似未見有特殊之處，故很可能白尾鴝本身非常容易受到禽痘病毒的感染。

鳥在感染禽痘後，通常於身體的二區域可以以肉眼觀察到臨床病徵，一爲在無羽區，如腳趾、跗蹠、頭及眼瞼等處，出現病灶，另一區域出現在口腔、上呼吸道和咽喉黏膜部位產生離散、增生性病灶(van Riper and Forrester 2007; Ha *et al.* 2011)。本研究中並未在野生鳥類口腔、上呼吸道和咽喉黏膜部位中發現類似病變的個體，造成此結果的原因，除可能因發生率比較低之外，也可能因爲第二區域出現病灶的個體死亡率較高(van Riper and Forrester 2007)。

由本研究針對臺灣以森林性留鳥爲主的類禽痘症盛行率初步調查結果來看，多數鳥種出現類禽痘症的比例甚低，與大陸型地區的禽痘盛行率研究結果類似，顯示出臺灣島多數留鳥應與禽痘病毒已有長久互動(van Riper *et al.* 2002)。然而，無論禽痘於野生鳥類族群中盛行率爲高或低，固定的監測有助於早期發現此類流行病於野鳥中的變化(van Riper and Forrester 2007)。尤以近年因氣候變遷及外來種的交互作用，臺灣亦有可能出現如歐洲因外來蚊蟲引入新的禽痘病毒，導致白頰山雀(*Parus major*)感染禽痘的盛行率大幅提升的情形(Lachish *et al.* 2012a, b; Lawson *et al.* 2012)。由於 MAPS Taiwan 具備固定且標準化的操作程序(林 2012)，若其繫放站數量可持續增加且散布於各類棲地，可以早期偵測得野鳥禽痘盛行率資訊，一旦發現禽痘發生情形偏高時，相關研究及經營管理單位可盡早介入，強化必需的經營管理作爲。

謝誌

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附錄 1. 2010 - 2012 年 MAPS Taiwan 於各地首次捕捉之燕雀目鳥類數量統計

Appendix 1. The number and localities of new banded passerines by MAPS Taiwan from 2010 to 2012

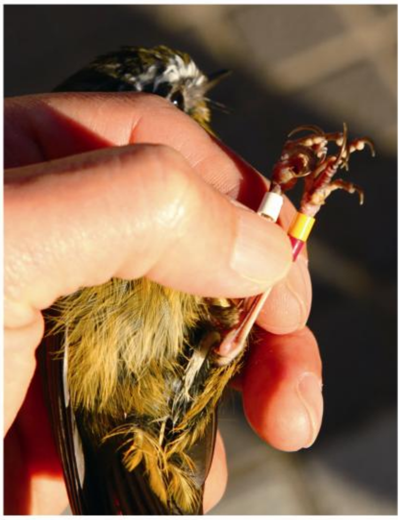
Species name	Sikanshui, Xindian, New Taipei	Daxi, Taoyuan	Wushikeng, Heping, Taichung	Jiji, Nantou	Ruiyan, Renai, Nantou	Hehuanshan, Xiulin, Hualien	Huben , Linnei and Hushan, Douliu, Yunlin,	Shekou, Jhongpu, Chiayi	Niupu, Longci, Tainan	Total
繡眼畫眉 *Alcippe mrrisonia*	45	12	74	27	18		136	49		361
山紅頭 *Stachyridopsis ruficeps*	3		46	14	30		155	14	10	272
頭烏線 *Schoeniparus brunnea*	2		24				107	6		139
小彎嘴 *Pomatorhinus musicus*	9	1	5				69	7	14	105
黃胸藪眉 *Liocichla steerii*			18		84					102
白尾鴝 *Cinclidium leucurum*	2		7		60		18	5		92
白頭翁 *Pycnonotus sinensis*				1			15		40	56
黑枕藍鶲 *Hypothymis azurea*			7	1			41	6	1	56
冠羽畫眉 *Yuhina brunneiceps*					45					45
棕面鶯 *Abroscopus albogularis*			12		21		8			41
白眉林鴝 *Tarsiger indicus*						31				31
黃胸青鶲 *Ficedula hyperythra*					23					23
綠畫眉 *Erpornis zantholeuca*	2						16	3		21
紅嘴黑鵯 *Hypsipetes leucocephalus*							10	10		20
白腰文鳥 *Lonchura striata*	1		2				16			19
褐頭花翼 *Fulvetta formosana*					1	18				19
黃羽鸚嘴 *Paradoxornis verreauxi*						18				18
白耳畫眉 *Heterophasia auricularis*			1		13					14
紋翼畫眉 *Actinodura morrisoniana*					11	3				14
台灣噪眉 *Garrulax morrisonianus*					1	12				13
火冠戴菊鳥 *Regulus goodfellowi*						12				12
台灣朱雀 *Carpodacus formosanus*						12				12
深山鶯 *Cettia acanthizoides*					2	9				11

栗背林鴝 *Tarsiger johnstoniae*						10				10
大彎嘴 *Pomatorhinus erythrocnemis*							5	1	1	7
洋燕 *Hirundo tahitica*							7			7
白環鸚嘴鵯 Spizixos semitorques				1			5			6
小翼鶇 *Brachypteryx montana*					5					5
灰頭鷦鶯 *Prinia flaviventris*									5	5
紅頭山雀 *Aegithalos concinnus*			2		3					5
綠繡眼 *Zosterops japonicus*				3			2			5
小卷尾 *Dicrurus aeneus*							4			4
台灣鷦眉 *Pnoepyga formosana*					4					4
粉紅鸚嘴 *Paradoxornis webbianus*							1		3	4
斑紋鷦鶯 *Prinia crinigera*									4	4
黃山雀 *Macholophus holsti*			1		3					4
灰鷽 *Pyrrhula erythaca*						3				3
褐頭鷦鶯 *Prinia inornata*									3	3
褐鷽 *Pyrrhula nipalensis*					3					3
青背山雀 *Parus monticolus*					2					2
茶腹鳾 *Sitta europaea*					2					2
棕噪眉 *Garrulax poecilorhynchus*			1		1					2
黃腹琉璃 *Niltava vivida*			1		1					2
煤山雀 *Periparus ater*						2				2
鷦鷯 *Troglodytes troglodytes*						2				2
台灣畫眉 *Garrulax taewanus*									1	1
斑文鳥 *Lonchura punctulata*							1			1
臺灣叢樹鶯 *Bradypterus alishanensis*							1			1
樹鵲 *Dendrocitta formosae*							1			1
Total	64	13	201	47	333	132	618	101	82	1591

White-tailed Robin, A47059, July 7, 2011

White-tailed Robin, A47060, July 7, 2011

White-browed Bush-Robin, A45320,
September 1, 2012



White-tailed Robin, B27797, May 26, 2012

附錄 2. 其餘 4 隻出現類禽痘症並具有相片紀錄的個體。

Appendix 2. The other four individuals with active avian pox-like lesions have been photographed.

Colonization Patterns of Aquatic Insects after Typhoons

颱風後水棲昆蟲之拓殖模式

Kwok-Ching Wong* and Yi-Xuan Lin

黃國靖*　林怡萱

Department of Natural Resources and Environmental Studies, National Dong Hwa University
No. 1, Sec. 2, Da Hsueh Rd., ShouFeng, Hualien, 974, Taiwan, R.O.C.

國立東華大學自然資源與環境學系

* Corresponding authors : kcwong@mail.ndhu.edu.tw

*通訊作者：kcwong@mail.ndhu.edu.tw

Abstract

To understand the colonization patterns of aquatic insects by the impacts of typhoon, an intensive investigation was carried out after typhoon hits from April 2007 to March 2008. The study found that the structure pattern of the aquatic insects community shifted back toward that of pre-typhoon period. The pre-typhoon dominant taxa *Baetis* spp. and *Ecdyonurus* spp. were replaced by *Pseudocloeon* spp. and *Rhithrogena* spp. after environmental impacts by a typhoon. *Baetis* spp. and chironomids distributed in slow running water, while *Hydroptila* sp. scattered amongst filamentous algae at the bank. Among the functional feeding groups, a higher ratio of predators was found in the early stage of colonization after typhoon disturbance. The proportion of predators decreased gradually with an increased abundance of scrapers, followed by an increase in relative abundance of collector-gatherers, which subsequently caused a decrease in scraper ratio. Population density of collector-filterers was also found to be lower than that in the pre-flood period while the ratio of piercers increased.

摘　要

本研究藉由颱風侵襲後進行較密集之調查，以了解颱風影響後水棲昆蟲之拓殖情形。調查結果顯示水棲昆蟲群聚於颱風影響後有趨向於颱風前之結構型式發展；優勢分類群於颱風引起之環境衝擊後，由 *Baetis* spp.及 *Ecdyonurus* spp.轉變爲 *Pseudocloeon* spp.及 *Rhithrogena* spp.。岸邊之調查顯示 *Baetis* spp.及搖蚊科 (Chironomidae) 偏好分布於流速較緩之河岸，*Hydroptila* sp.於河岸隨絲狀藻呈零散分布。依功能性攝食群探討，颱風影響後，水棲昆蟲拓殖初期捕食者比例較高，之後捕食者比例逐漸下降，刮食者比例上升；而刮食者相對密度升高後，集食性採食者相對密度也逐漸升高，故之後刮食者相對密度呈下降趨勢；濾食性採食者族群密度顯示較以往低；刺吸者比例較以往高。

keywords：aquatic insects, flood, disturbance, colonization, recovery

關鍵詞：水棲昆蟲、洪泛、干擾作用、拓殖、恢復

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Introduction

Taiwan is frequently hit by typhoons in the summer and autumn. Continuous and intensive rainfall causes an increase in discharge, and community structure of aquatic insects is vigorously altered (Huang 2005; Yang and Wong 2005). Contemporary climate change scenarios predict an increase in extreme weather events, which include changing precipitation patterns resulting in severe floods and droughts (IPCC 2007). Flooding is the most important natural disturbance in stream environments (Sagar 1986; Giller *et al.* 1991). Taxa abundance and population density of macroinvertebrates are reduced by increased discharge (Sagar 1986; Scrimgeour and Winterbourn 1989; Fritz and Dodds 2004). Despite the subsequent occurrence of small floods following the large flood, community structure of benthic macroinvertebrates recovers rapidly (Scrimgeour *et al.* 1988). Time required for recovery following a large flood varies, depending on factors including stream type, magnitude of disturbance and other factors under investigation, ranging from a few months to a year or more (Fisher *et al.* 1982). Rapid recolonization by macroinvertebrates after flooding is attributed by the utilization of refugia and interstitial habitats (Angradi 1997), drift from undamaged areas (Williams and Hynes 1976; Scrimgeour *et al.* 1988), and oviposition by aerial adults (Gray and Fisher 1981). Nearby areas of the flood-affected areas, such as tributaries, calmer areas and deep substrates play an important part in maintaining the resilience of aquatic ecosystems (Minshall and Petersen 1985). The relative abundance of invertebrates in nearby areas is higher since these areas might be less affected by floods. Scrimgeour *et al.* (1988) discovered that deep pools formed during flooding provided shelters for invertebrates, which act as important sources of colonists when the pool reconnects with the main channel.

The aim of the present study is to describe the aquatic insects' response to flooding caused by heavy rainfall, discriminate the characteristic and dominant species, and discuss their assemblages under different hydraulic conditions.

Materials and Methods

(1) Study Area

The study was carried out in Shakadang Stream, the first tributary of Liwu Stream basin, located in Taroko National Park in eastern Taiwan. Shakadang Stream flows 17.2km and drains 60.11km^2 directly eastward into the Pacific Ocean. The gorges of Shakadang Stream are mostly steep wall crags and the riparian vegetation is rich, comprising subtropical rainforest formation, with Ficus plants (Moraceae), large-leaved machilus (*Machilus kusanoi* (Lauraceae)) and red bark slugwood (*Beilschmiedia erythrophloia*) as dominant species.

Two sites were selected for sampling and designed to stable hydrological gradients across the Shakadang Stream, as aquatic insects there are susceptible to extreme hydraulic impacts. The sites were located about 1km (Site 1) and 1.6km (Site 2) upstream of the Shakadang Bridge respectively (Fig. 1).

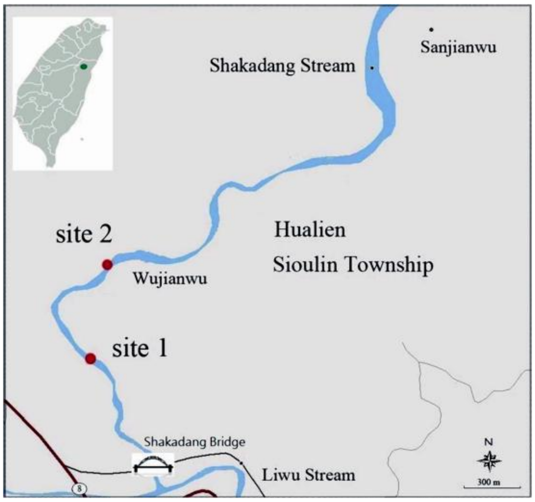

Fig. 1. The locations of the sampling sites (Site1-2) along the Shakadang Stream.

(2) Collection of environmental variables

Environmental variables were sampled in each site, totaling three samples for each variable. Current velocity and depth were measured with a Global Flow Probe FP101 for each sample. Conductivity, dissolved oxygen, pH, temperature, and turbidity were measured with portable sensors in each sampling occasion. We used a modified Went-worth scale to record the dominant grain size class in the quadrat (Surber sampler 50cm x 50cm), ranging from gravel to boulder (gravel 0-2cm, pebble 2-5cm, small cobble 5-10cm, medium cobble 10-20cm, large cobble 20-30cm, boulder >30cm).

(3) Collection of aquatic insects

Samples were collected at both banks and the middle of the stream at monthly intervals from April 2007 to March 2008 using a Surber net sampler (50cm x 50cm, mesh size 0.7mm).

Besides the above sampling design, we also took three replicate samplings at each site (along the left stream bank and 1m from the shore) between 12th August, 2007 and 24th November, 2007 to compare the distribution and abundance of aquatic insects before and after typhoon hits. After typhoon Pabuk hit on 9th August, 2007 and typhoon Sepat from 18th to 19th August, 2007, samplings were carried out at three-day intervals using the same method as that for the monthly samplings. Specimens were also sampled from 9th to 15th and 15th to 29th September, 2007 at six-day and 14-day intervals respectively. Samples were collected at seven day intervals after typhoon Krosa stuck on 6th October, 2007 and lasted for 49 days.

Each sample was preserved in 80% ethanol, labeled, and returned to the laboratory for examination. At the laboratory, organisms were sorted, identified to the lowest possible taxonomic level, counted, and kept in 75% ethanol.

(4) Statistical Analysis / Data Analysis

The number of organisms in each taxon in each sampling (both bank and middle stream, or three replicates sampling at left stream bank) was pooled for data analysis. Data transformation was performed prior to analysis: abundance of aquatic insects was log(x+1)-transformed, environmental variables were log(x)-transformed, while arcsine square root transformation (arcsin ($p^{1/2}$)) was applied to percentage data (Zar 1996). Pearson's correlation coefficient was used to determine whether the various environmental parameters were correlated with the abundance of aquatic insect taxa. Temporal and spatial changes of aquatic insect community structure were analyzed by non-metric multi-dimensional scaling (MDS) using the PRIMER v.5 software package (Clark and Warwick 1994; Clarke and Gorley 2001).

Results

1. Environmental features

The annual rainfall during the study period was 3,050mm with a peak occurring in August (963.5mm). Water temperature ranged from 17.5℃ (February) to 26.5℃ (July). Minimal water depth was 3.3cm (September) and maximum 105cm (August). Water velocity varied between 0.59m/s (September) and 4.18m/s (August). Minimum discharge was 0.53m^3/s (July) and maximum 41.39m^3/s (August) (Table 1). Substratum was dominated by medium cobble (31%) and small cobble (26.89%) (Table 2).

Table 1. Range, mean, and standard deviation of main environmental variables of sampling sites

	Minimum-maximum (mean±SD) Site 1 Site 2		
Variables	Before typhoon	After typhoon (1-49-days)	After typhoon (49-days-later)
	Apr.- Jul.	Aug.- Nov.	Dec.- Mar.
Water temperature (℃)	20.20-25.30 (23.00±2.00)	19.13-23.20 (20.89±1.19)	17.90-19.30 (18.80±0.59)
	21.4-26.50 (24.43±1.98)	18.47-23.80 (20.39±1.32)	17.50-19.00 (18.08±0.58)
Depth (cm)	25.17-12.69 (7.33±41.67)	3.33-78.00 (20.94±19.66)	9.33-19.67 (13.33±3.88)
	6.33-20.67 (11.75±5.96)	9.00-105.00 (41.50±33.60)	6.33-10.67 (8.92±1.66)
Current velocity (m/s)	1.29-2.43 (1.77±0.44)	0.79-4.18 (1.93±0.96)	1.18-2.260 (1.70±0.38)
	0.69-1.52 (1.26±0.34)	0.59-4.06 (1.91±1.00)	1.00-1.48 (1.20±0.20)
Discharge (m^3/s)	1.10-14.07 (6.17±4.82)	0.75-22.69 (5.49±6.49)	1.33-3.96 (2.82±1.01)
	0.53-4.05 (1.99±1.34)	1.36-41.39 (15.47±11.80)	1.42-3.53 (2.46±0.76)

Table 2. Substrate composition of sampling sites in Shakadang Stream

%	Gravel 0-2cm	Pebble 2-5cm	Small cobble 5-10cm	Medium cobble 10-20cm	Large cobble 20-30cm	Boulder >30cm
Site 1	7.43	16.48	23.26	31.67	10.87	10.29
Site 2	6.21	14.77	30.68	30.30	15.23	2.80
Site 1 and 2	6.84	15.64	26.89	31.00	13.00	6.63

2. Aquatic insect community structure

Community structure of aquatic insects underwent huge changes after a typhoon attack. Samples from site 1 and 2 collected after typhoons Pabuk, Sepat and Krosa deviated from the samples prior to the typhoon attacks. With time, samples tended to resume a similar species composition with those before typhoon (Fig. 2, 3).

Structure of aquatic insect community among the two sampling sites was compared between the pre-typhoon and post-typhoon periods (Fig. 2, 3). Six samplings were conducted at site 1 after typhoon Sepat struck in mid August 2007. The community structure was found to be different between 12 days (31st August, 2007) to 49 days (29th September, 2007) after typhoon Sepat. Subsequent change in community structure has been recorded after another typhoon Krosa came in early October 2007, though the change was of a smaller scale. The variation of dynamic changes in aquatic insect community recorded between December 2007 and March 2008 was found to be gentler. The result indicated that the community structure became more stable and less stochastic over time as the impact of typhoon attack subsided gradually (Fig. 2).

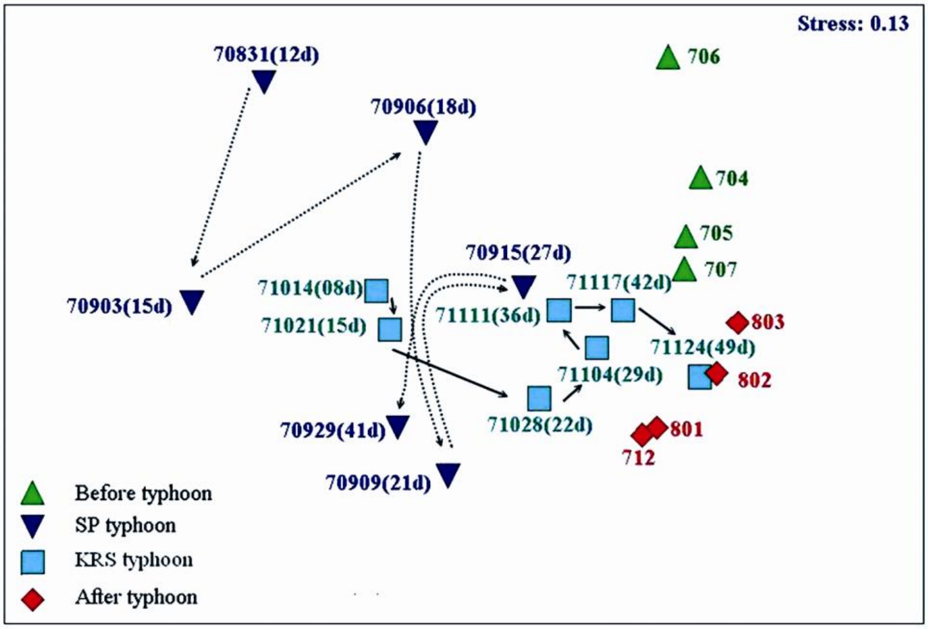

Fig. 2. MDS plots of community structure of aquatic insects at site 1 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first digit indicates the year, the second and third digits indicate the month, the fourth and fifth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 70831 (12d) indicates 31st August, 2007 and 12 days after typhoon. The number 803 indicates March 2008. SP typhoon: Sepat typhoon. KRS typhoon: Krosa typhoon.

A change in aquatic insect community structure at site 2 was recorded before and after typhoon attack (Fig. 3). The community structure was relatively stable and demonstrated little variation in the pre-typhoon period. A slight change in community structure has been noted after attack by typhoon Pabuk in early August 2007. The attack of typhoon Sepat 15 days later resulted in a different change in community structure. The change in aquatic insect community structure reached maximum at 41 days after the attack. The change in community structure recorded eight days after attack by typhoon Krosa (early October 2007) was of small scale. Like site 1, community structure observed during subsequent weekly samplings (14th October, 2007- 24th November, 2007) shifted toward the pre-typhoon structure pattern (Fig. 3).

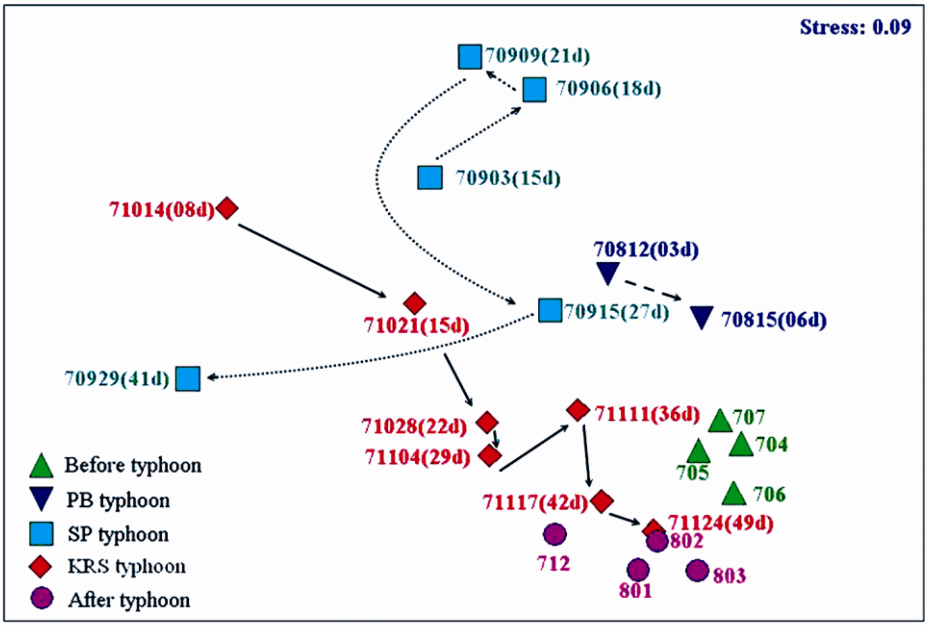

Fig. 3. MDS plots of community structure of aquatic insects at site 2 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first digit indicates the year, the second and third digits indicate the month, the fourth and fifth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 70831 (12d) indicates 31st August, 2007 and 12 days after typhoon. The number 803 indicates March 2008. PB typhoon: Pabuk typhoon. SP typhoon: Sepat typhoon. KRS typhoon: Krosa typhoon.

The relationship between physio-chemical environmental variables and the abundance of the dominant aquatic insects are demonstrated in Table 3. Conductivity, pH, current velocity, water depth, water temperature, and turbidity were highly correlated to *Baetis* spp.; *Pseudocloeon* spp., *Epeorus erratus*, and *Rhithrogena* spp appeared to have a significant positive correlation with dissolved oxygen (DO) and pH, but negative correlation with water temperature and turbidity. *Hydroptila* sp. showed significant negative correlation with current velocity and water depth. Except for the larvae of caddisfly, *Hydroptila* sp. appeared to have a significant positive correlation with pebbles. The five remaining mayflies were negatively correlated with the small substrate particles, such as gravels and pebbles (Table 3).

Table 3. The correlation coefficients and p values of *Baetis* spp., *Pseudocloeon* spp., *Ecdyonurus* spp., *Epeorus erratus*, *Rhithrogena* spp., *Hydroptila* sp., and environmental variables in the Shakadang Stream

Environment variables	*Baetis* spp.	*Pseudocloeon* spp.	*Ecdyonurus* spp.	*Epeorus erratus*	*Rhithrogena* spp.	*Hydroptila* sp.
Conductivity	0.19***	0.06	0.25***	0.01	0.06	0.10
DO	-0.11*	0.29***	-0.33***	0.23***	0.30***	-0.01
pH	0.21***	0.24***	-0.06	0.20***	0.23***	0.04
Current velocity	-0.25***	-0.05	-0.19**	0.01	-0.04	-0.11*
Water depth	-0.25***	-0.26***	0.07	-0.17**	-0.21***	-0.11*
Water temperature	-0.18**	-0.39***	0.15**	-0.35***	-0.46***	-0.07
Gravel	-0.12*	-0.20***	-0.16**	-0.16**	-0.15**	-0.03
Pebble	-0.01	-0.09	-0.14**	-0.12*	-0.01	0.11*
Small cobble	0.08	0.01	-0.01	-0.03	0.03	0.08
Medium cobble	0.05	0.10	0.11*	0.08	0.09	-0.02
Large cobble	-0.03	0.03	0.04	0.03	0.00	-0.10
Boulder	-0.05	0.02	0.04	0.09	-0.05	-0.06
Turbidity	-0.31***	-0.31***	-0.19**	-0.20**	-0.27***	-0.08

*：$p < 0.05$； **：$p < 0.01$；***：$p < 0.001$

3. Dominant taxa

Analysis of the pooled samples collected by the banks and the middle stream found *Baetis* spp. and *Ecdyonurus* spp. to be the dominant taxa prior to typhoon (Fig. 4, 5). *Pseudocloeon* spp. was the most abundant numerically and increased most rapidly after typhoon damage, thus it became the dominant species (Fig. 4, 5). *Ecdyonurus* spp. was one of the dominant species before typhoon and its population drastically decreased after typhoon while the abundance of *Rhithrogena* spp., also a Heptageniidae member, increased (Fig. 4, 5). The relative abundance of *Epeorus erratus* was also higher than that in the pre-typhoon period (Fig. 4, 5).

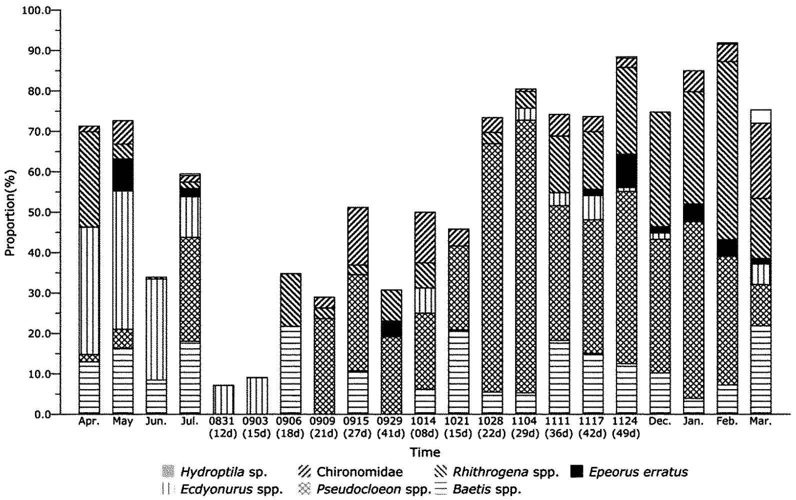

Fig. 4. Proportion of the dominant taxa abundance at site 1 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 0831 (12d) indicates 31st August and 12 days after typhoon.

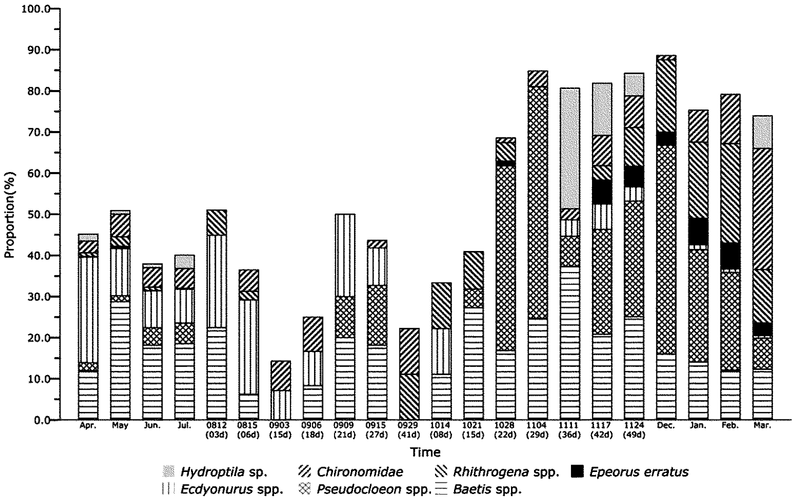

Fig. 5. Proportion of the dominant taxa abundance at site 2 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 0812 (03d) indicates 12th August and three days after typhoon.

After the typhoon Krosa struck, three replicate samples collected along the left stream bank at site 2 were pooled and analyzed. The most abundantly found species was *Baetis* spp. and not *Pseudocloeon* spp. (Figure 6).

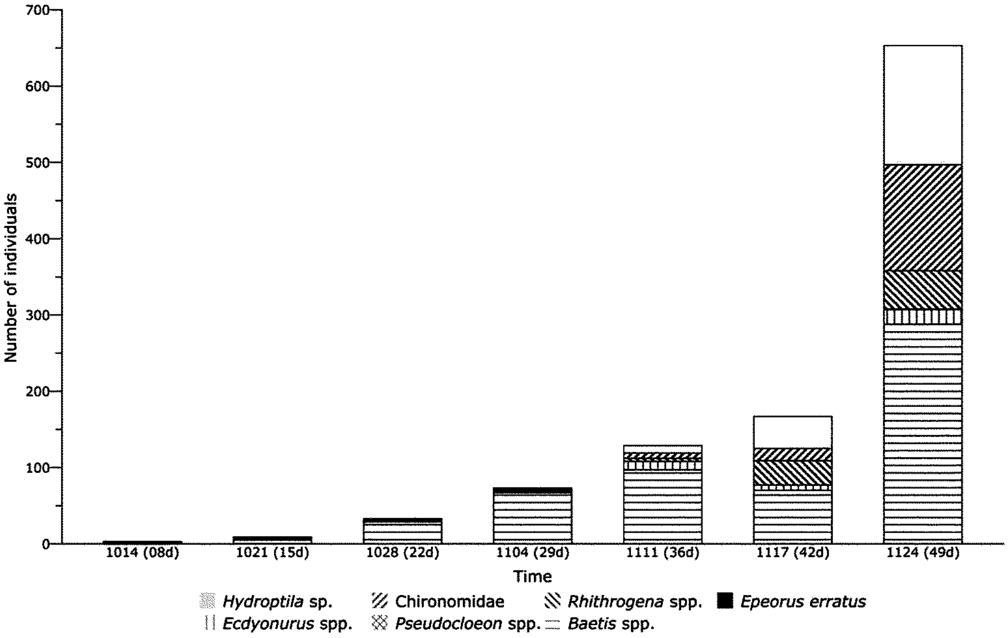

Fig. 6. Abundance of the dominant taxa along the left stream bank of site 2 in the Shakadang Stream from 14th October, 2007 to 24th November, 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 1014 (08d) indicates 14th October and eight days after typhoon.

4. Colonization of aquatic insects at the bank

In site 2, the number of *Hydroptila* sp. prior to typhoon damage was small, with a highest record of 15 specimens. A total of 35 *Hydroptila* sp. specimens were collected at both banks and the middle stream, while 156 specimens were collected in three replicate samplings at the left stream bank in 49 days after typhoon Krosa (Fig. 6). In the same period, a total of 49 chironomids were collected at both banks and the middle stream, while three replicate samplings at the left stream bank collected 139 specimens (Fig. 6).

In site 1, heavy rainfall brought by the typhoons Pabuk, Sepat, and Krosa raised the stream water level and flooded the land which was originally undrained. The water rose until the water-level reached 9m far from the original shore. A total of 16 insect specimens belonging to 11 taxa, including Baetidae, Heptageniidae, Perlidae, Hydropsychidae and Chironomidae, were collected by the bank. The water level subsided 15 days after typhoon, and the left stream bank was three meters away from the original bank where 24 insect specimens belonging to 10 taxa were collected, with the addition of Tipulidae besides the above-mentioned taxa. The left stream bank was 1.5 meters away from the original bank 22 days after typhoon and 104 insect specimens belonging to 13 taxa were collected, with Simuliidae and Euphaeidae newly added to the samples. Water level dropped, from a position 0.4m from the original edge to a stable position 29-49 days after typhoon. Taxa richness of aquatic insects increased from 17 to 25, and the number of specimens collected increased from 196 to 303. New taxa collected were Caenidae, Leptophlebiidae, Elmidae, Psephenidae, Blepharoceridae, *Protohermes grandis*, Hydroptilidae, Leptoceridae, Philopotamidae, Rhyacophilidae, and *Gumaga* sp. Numeric abundance of *Pseudocloeon* spp., *Epeorus erratus*, and *Rhithrogena* spp. increased the most.

Discussion

There are many more factors determining population dynamic and different population size over various growth periods. Ecological theory predicts that the K-selected species will dominate stable or predictable conditions, whereas r-selected species will increasingly dominate as the level of disturbance increases (Warwick 1986; Warwick *et al.* 1987). The r-selected species are frequently fast-growing, small body size, and have opportunistic strategy (high fecundity) (Reznick *et al.* 2002). Species of this type go through irregular and unstable boom-and-bust cycles in population size, and usually have a high level of mortality among the young. This means that beside biological characteristics, environmental influence is also a factor that determines population size. If the life history has been well-studied in all aquatic insect species, the mechanism and relationship within the population dynamic can perhaps be fully understood. If not, information about the basic biology of aquatic insects would be useful. Therefore, this study is an attempt to understand and explain the population fluctuation of aquatic insect under extreme environmental change that is all dependent on the basic biology of aquatic insects.

1. Dominant Taxa

(1) *Baetis* spp. and *Pseudocloeon* spp.

As reported in previous studies, the colonizing ability of *Baetis* spp. is strong (Ciborowski and Clifford 1984; Mackay 1992; Zuellig *et al.* 2002), thus it is the dominant taxon in the community structure of aquatic insects after flooding (Molles 1985; Vieira *et al.* 2004; Rader *et al.* 2008). The present study found that the number of *Baetis* spp. individuals showed significant negative correlation with current velocity (r = -0.25, $p < 0.001$) (Table 3). The number of *Pseudocloeon* spp. did not show significant correlation with current velocity (Table 3). Movement of *Baetis* spp. is mainly accomplished by swimming while *Pseudocloeon* spp. moves by crawling (Merritt and Cummins 1996) and thus can withstand a higher maximum current velocity than *Baetis* spp. High current flow also hindered sedimentation of organic matters, which brought down food supply and renders environment unfavorable for collector-gatherers like *Baetis* spp. Current velocity increased after typhoon, which was more prominent in the middle of the stream, and *Baetis* spp. preferred areas near the banks where the current was slower.

Twenty-two to 49 days after typhoon, the current velocity was between 0.92- 1.96 m/s and 0.17- 0.93 m/s along the right bank and left bank respectively. Since *Baetis* spp. was the dominant species before the typhoon and the maximum current velocity that it can tolerate is lower than that of *Pseudocloeon* spp. *Baetis* spp. dominated in the samples collected in the left bank, with a highest record of 117 specimens collected 49 days after typhoon while only 12 specimens of *Pseudocloeon* spp. were collected. *Pseudocloeon* spp. dominated the right bank 49 days after typhoon, with a total of 174 *Pseudocloeon* spp. specimens collected, while only 48 *Baetis* spp. were harvested. Since the flow of the right bank was faster and attached algae were available in the substrate for scrapers, more *Pseudocloeon* spp. specimens were collected from the right bank. When the samples were pooled for counting, *Pseudocloeon* spp. dominated site 2 while *Baetis* spp. was dominant in sites from the left stream bank.

Investigations from the left stream bank of site 1 showed that the increase in abundance of *Pseudocloeon* spp. was higher than that of *Baetis* spp., and this finding was different from the results of site 2. The left stream bank in site 2 was a gradually sloping bank, and the current velocity was slower after the water receded where it was suitable for *Baetis* spp. inhabitation. Because the left stream bank in site 1 was a steeply sloping bank, even though the waters began to recede, the stream water still flowed faster. As higher velocity in general was not considered a favorable environment for *Baetis* spp., *Pseudocloeon* spp. out-numbered *Baetis* spp. at site1.

In general, the ability of aquatic insect to cling to the substratum decides its survival chance after typhoon (Townsend *et al.* 1997). The insect would be drifted to the downstream or die if failed to cling to the substratum or refugia. Since *Pseudocloeon* spp. is a better clinger than *Baetis* spp., it dominated in areas having fast current after typhoon.

(2) *Ecdyonurus* spp., *Epeorus erratus*, and *Rhithrogena* spp.

Ecdyonurus spp. was the dominant species before typhoon. Since *Ecdyonurus* spp. showed significant negative correlation with current velocity (r= -0.19, $p < 0.01$) (Table 3), the increase in current velocity after typhoon decreased its abundance. Investigation by the bank also revealed that *Rhithrogena* spp. individuals out-numbered *Ecdyonurus* spp., and *Ecdyonurus* spp. did not establish along the bank with slow current. Vieira *et al.* (2004) pointed out that aquatic insects with weak adult dispersal ability and those with specialized feeding requirements, like heptageniid scrapers, could only establish stable population until attached algae re-established and floods magnitudes, substratum instability, suspended sediment loads were reduced.

The level of stream rose after typhoon, draining the land on the bank and scoured the attached algae on the substratum. The shades were dense along the bank, and the algae needed time to grow and provide food for scrapers after typhoon, so the population of *Ecdyonurus* spp., a heptageniid scraper collected in this study, decreased after typhoon. In contrast, generalists like *Epeorus erratus* and *Rhithrogena* spp. (both are collector-gatherers) displayed good population recovery ability (Townsend *et al.* 1997; Vieira *et al.* 2004).

2. Colonization of Aquatic Insects by the Bank

The genus *Hydroptila* mostly has univoltine cycle (one-year cycle) (Anderson 1967; Cloud and Stewart 1974).The number of *Hydroptila* sp. specimens collected at site 2 was abundant 49 days after typhoon Krosa hit (Figure 6). *Hydroptila* members are small in body size with a length of 5mm, use fine sand for case building (Kawai 1985; Wiggins 1996), and show a significant negative correlation with current velocity and water depth ($r = -0.11$, $p < 0.05$；$r = -0.11$, $p < 0.05$) (Table 3). Examination of *Hydroptila* sp. specimens show that the larval case reached around 5.5mm in length, so the larvae were assumed to be an older-instar and not the newly hatched individuals.

Hydroptila spp. was found distributed along the bank since current velocity and water depth in this area decreased rapidly after typhoon and the substratum contained fine sand. And the filamentous algae were found more abundant in slow flow and shallow water (Bohlen *et al.* 2003; Spencer 2003). *Hydroptila* sp. is a piercer and its distribution was found to be scattered with the presence of filamentous algae which it feeds on.

Fisher *et al.* (1982) conducted a study at Sycamore Stream in Arizona and the results showed that filamentous algae grew gradually 5 weeks after flood and the consumption ratio of filamentous algae by macroinvertebrate increased, which is similar with the results found in the present study.

Chironomids larvae were the most abundant organisms collected at site 2 along the left stream bank 49 days after typhoon attack. The life cycle of midges of the chironomids may be as short as a few weeks to one month (Kawai 1985), so it is likely that chironomids collected after flooding were not the same generation in the pre-flood period. Short life cycle, colonization through adult oviposition, and high reproductive rate are important factors in population recovery (Gray and Fisher 1981; Fisher *et al.* 1982; Kondo *et al.* 2001). The larvae of Chironomidae have the largest range of suitable conditions of any family of aquatic insects, a fact that enables them to be the first colonists of many new habitats (Daly *et al.* 1978). Since the chironomids are collector-gatherers and are free-living, they were more abundant in areas with a high sediment ratio of fine sand and low current velocity.

3. Functional Feeding Groups

The insects most abundantly found after typhoon attacks were taxa with strong crawling and moving ability (Baetidae, Heptageniidae, Perlidae and Hydropsychidae), or those preferring a benthic composition of fine sand (Gomphidae). Predators usually display a good ability for chasing their prey, clingers have a flattened body that avoids the main thrust of the current, and burrowers adapt well to the soft and small substrates (Wooton *et al.* 1996; Townsend *et al.* 1997; Matthaei *et al.* 1999; Maria *et al.* 2010). As perlids are clingers and gomphids are burrowers, they contribute a large proportion of individuals collected in the earliest recovery stage. Although predators out-numbered members from other functional feeding groups, only ten predator specimens were collected, not especially a large number.

According to a study conducted at Sycamore Creek in Arizona (Fisher *et al.* 1982), algae were scoured by flash flood but recovered quickly, reaching a biomass of 100g/m^2 within two weeks. Current velocity decreased gradually after typhoon, attached algae on the substrate accrued, and *Pseudocloeon* spp. gradually colonized. The number of perlids and gomphids collected changed little, around 20, resulting in a gradual decline of predator ratio and an increase in scraper ratio. The collector-gatherers, *Epeorus erratus* and *Rhithrogena* spp., subsequently carried out colonization. Although the larvae of the mayfly family Baetidae, known to be common in fast-flowing habitat, the adaptive ability to higher current velocity may differ in different species (Matzinger and Bass 1995). During higher current velocity, *Pseudocloeon* spp was more abundant than *Baetis* spp., and the latter started to colonize when the current velocity declined. *Baetis* spp. is a collector-gatherer and its relative density increased with the scrapers, and the scraper increase was then slowed down by the increasing ratio of the collector-gatherers. The major collector-filterers collected was Hydropsychidae and its number increased slowly because filter-feeding was affected by the increase of suspending granules in the water after typhoon, and its population density were found to be lower than the pre-flood period. The population size of piercers was small and no samples were collected in the early post-flood period. Filamentous algae-consuming *Hydroptila* sp. collected at site 2 was more abundant 36-49 days after typhoon Krosa. The ratio of piercers was found to be higher comparing with the pre-flood period (Figure 7, 8).

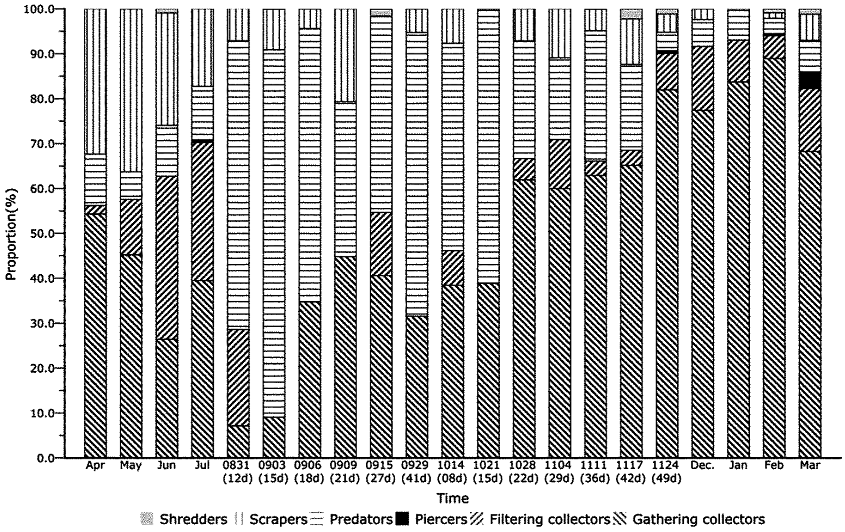

Fig. 7. Proportion of functional feeding groups abundance at site 1 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 0831 (12d) indicates 31st August and 12 days after typhoon.

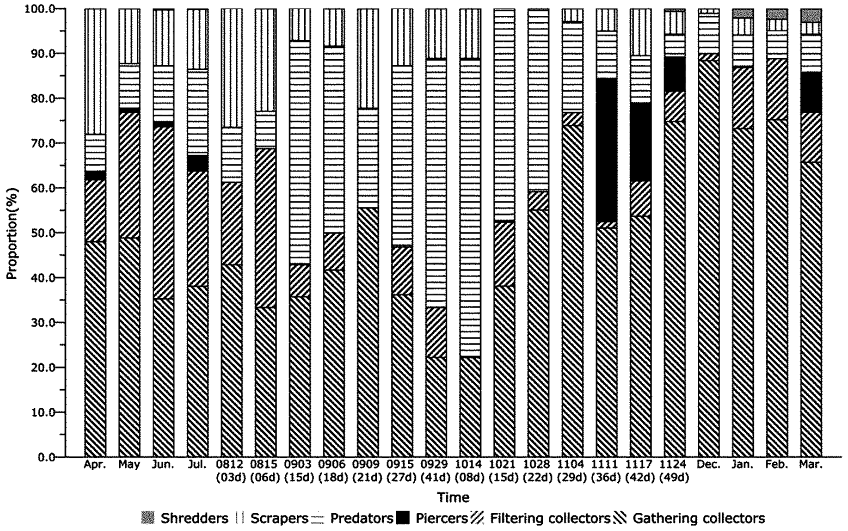

Fig. 8. Proportion of functional feeding groups abundance at site 2 in the Shakadang Stream from April 2007 to March 2008.

Conclusion

Aquatic insect community structure drastically changed and shifted toward the pre-typhoon structure pattern before typhoon hit. The dominant taxa *Baetis* spp. and *Ecdyonurus* spp. were replaced by *Pseudocloeon* spp., and *Rhithrogena* spp. *Pseudocloeon* spp. had better crawling ability, thus could endure a higher velocity than *Baetis* spp. During the higher current velocity, *Epeorus erratus* and *Rhithrogena* spp. was relatively more abundant than *Ecdyonurus* spp. Both *Epeorus erratus* and *Rhithrogena* spp. are collectors and thus had better population recovery potential. *Rhithrogena* spp. dominated over *Epeorus erratus* and it was found to out-number *Epeorus erratus*.

Investigation by the stream-bank showed that *Baetis* spp. and chironomids preferred areas with slower running velocity. *Hydroptila* sp. at the bank showed a scattered distribution associated with filamentous algae. Perlids (Perlidae) and gomphids (Gomphidae) were most abundant during the early stage of colonization after typhoon attack, resulting in a high relative abundance of predators. *Pseudocloeon* spp. started to colonize when attached algae became more abundant and resulted in a decrease in ratio of predators and increase in relative abundance of scrapers, which was followed by gradual colonization of *Rhithrogena* spp., *Epeorus erratus*, and *Baetis* spp. Subsequently, collector-gatherers became more abundant and scrapers less so. Population density of collector-filterers was also found to be lower than in the pre-flood period while the ratio of piercers increased.

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Dactylophorella muricata (Gottsche) R. M. Schust. (Marchantiophyta, Family Lejeuneaceae), a Genus and Species Record New to Liverwort Flora of Taiwan

棘鱗蘚(地錢門，細鱗蘚科)，臺灣蘚類植物誌新紀錄屬、種

Jia-Dong Yang[1, 2] and Shan-Hsiung Lin[2,*]

楊嘉棟[1,2] 林善雄[2,*]

[1] Endemic Species Research Institute, Jiji, Nantou,Taiwan
[2] Department of Life Science, Tunghai University, Taichung, Taiwan

[1] 行政院農業委員會特有生物研究保育中心 南投縣集集鎮民生東路 1 號
[2] 東海大學生命科學系 臺中市臺中港路三段 181 號

*Corresponding author: slin@thu.edu.tw

*通訊作者：slin@thu.edu.tw

Abstract

Dactylophorella muricata (Gottsche) R. M. Schust. is reported as a genus and species record new to liverwort flora of Taiwan. *Dactylophorella* R. M. Schuster is a monotypic genus, with *D. muricata* known from Sumatra, Java, Celebes, Sabah and the Philippines. The previously known northernmost locality for the genus *Dactylophorella* and for *D. muricata* were Luzon, the Philippines. As for the locality recorded here in Taiwan, Orchid Island (22°04'39" N, 121°30'36" E) is the northernmost locality for this genus and species. A morphological description, illustration, habitat and specimens examination of *D. muricata* are provided in this study.

摘　要

棘鱗蘚(新擬中名)爲臺灣蘚類植物誌新紀錄屬、種。棘鱗蘚屬(新擬中名)爲一單種屬，只有棘鱗蘚，分布於蘇門答臘、爪哇、西里伯斯、沙巴及菲律賓等地區。過去已知棘鱗蘚屬及棘鱗蘚最北的分布地點爲菲律賓的呂宋島。棘鱗蘚在臺灣的分布地點蘭嶼(北緯 22°04'39", 東經 121°30'36")爲本屬之最北分布地點。文中提供形態描述、圖版、棲地及引證標本等。

Key words : *Dactylophorella*, Lejeuneaceae, liverwort, Taiwan

關鍵詞：棘鱗蘚屬、細鱗蘚科、蘚類、臺灣。

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Introduction

Dactylophorella R. M. Schuster is a monotypic genus, with *D. muricata* (Gottsche) R. M. Schust. known from Southeast Asia (Schuster 1980). Our recent studies on the Lejeuneaceae of Taiwan have shown that *D. muricata* is a genus and species record new to liverwort flora of Taiwan.

Taxonomic Treatment

Dactylophorella R. M. Schust. in Phytologia 45: 427. 1980. 棘鱗蘚屬

Plant minute, vigorous, creeping on substrate. Stems irregularly branched, cross-section of the stem with 7 cortical cells and 5–8 medullary cells, cell walls ± leptodermous. Leaves contiguous to loosely imbricate, lobes lobulate, triangular-ovate, margin densely muricate-spinous toothed; lobule inflated, free margin involute, apical tooth unicellular, straight or slightly curved. Ocelli absent. Underleaves bi-lobed, lobes erect, sinus U-shaped, strongly muricate-spinous toothed, margin recurved. Dioecious. Androecea briefly spiked, on short lateral branches, male bracts up to 7 pairs. Gynoecia on lateral branches; bracts, bract lobules and bracteole all with ciliolate-spinose margins; perianth obovate, with 5 keels, keels densely muricate-spinous toothed at margin (Herzog 1934; Schuster 1980).

A monotipic genus, represented by *D. muricata*.

Dactylophorella muricata (Gottsche) R. M. Schust. in Phytologia 45: 427. 1980.

Lejeunea muricata Gottsche in Gott., Lindenb. & Nees, Syn. Hepat. 348. 1845.

Drepanolejeunea muricata (Gottsche) Schiffn. In Engler & Plantl, Nat. Pfl.-fam. I, 3:126. 1895.

棘鱗蘚 Fig. 1

Descriptions:

Plant minute, yellowish brown in herbaria. Stems 3–5 mm long, 39–60 μm in diameter, with leaves 0.2–0.3 mm wide, irregularly branched; cross-section of the stem with 7 cortical cells and 5–8 medullary cells, cell walls leptodermous. Leaves contiguous to loosely imbricate, obliquely spreading, ovate-triangular in outline, ca. 0.3 mm long, and ca. 0.1 mm wide; margin densely muricate-spinous toothed; marginal cells 19–30 × 9–11 μm; median cells 19–22 × 15–22 μm; basal cells 32–45 × 17–26 μm, thin walled, without trigone and intermediate thickening; cuticle smooth. Ocelli absent. Leaf-lobule ovate, inflated, 2/5–1/2 as long as the lobe; free margin involute; apex constricted; apical tooth unicellular, obtuse, straight or slightly curved; keel arched. Underleaves distant, subtransversely inserted, 0.11–0.15 mm long, 0.12–0.14 mm wide; lobes erect, with strongly muricate-spinous teeth, sinus U-shaped, margin recurved. Sexual reproductive organs not seen.

Habitats:

Epiphyte in hardwoods forests, growing on boulders, rocks, tree roots, trunks, branches, or creeping on other bryophytes in the filtered or shade environment (Herzog 1934; Mizutani 1970, 1977).

Distribution:

Sumatra, Java, Celebes, Sabah and the Philippines (Herzog 1934; Mizutani 1970, 1977). New to Taiwan.

Specimens examined :

Taitung County: Hsiaotienchih (小天池) , Orchid Island, on rocks with thin layer of soil, mixed with *Fissdens* sp., at 150 m in elevation, 22°04'39" N, 121°30'36" E, 23 Jul. 1997, *Chi-Da Wu et al. 1897a* (**TAIE**, **TUNG**).

Remarks:

Genus *Dactylophorella* was separated from genus *Drepanolejeunea* by Schuster in 1980. It is different from *Drepanolejeunea* in (a) lobulate dorsal lobes; (b) leptodermous stem cells, the medullary in 5–8 rows; (c) under-leaves with erect, strongly spinulose lobes, the sinus U-shaped with reflexed margins; (d) apparent lack of ocelli (Schuster 1980). *Drepanolejeunea dactylophora* (Nees) Schiffn., with densely toothed leaf margins, is easily confused with *Dactylophorella muricata*, which differs in its bifid underleaves with entire margin and leaf lobe usually with 3–4 ocelli.

Based on woody plants, Orchid Island has a closer relationship with the Philippines than with Taiwan proper (Chang 1986). In accordance with Takhtajan’s global floristic system, Orchid Island is assigned to the Philippinean Province of the Paleotropical Kingdom, and an analysis of vescular plants from Orchid Island shows that roughly 56% of the species are tropical elements (Hsieh 2002). The new record of this species well supports the phytogeographic affinity of the flora between the Orchid Island and the Philippines.

The previously known northernmost locality for the genus *Dactylophorella* and for *D.*

muricata were Luzon, the Philippines (Mizutani 1977). The locality recorded here in Taiwan, Hsiaotienchih (22°04'39" N, 121°30'36" E), Orchid Island, is the northernmost locality for this genus and species.

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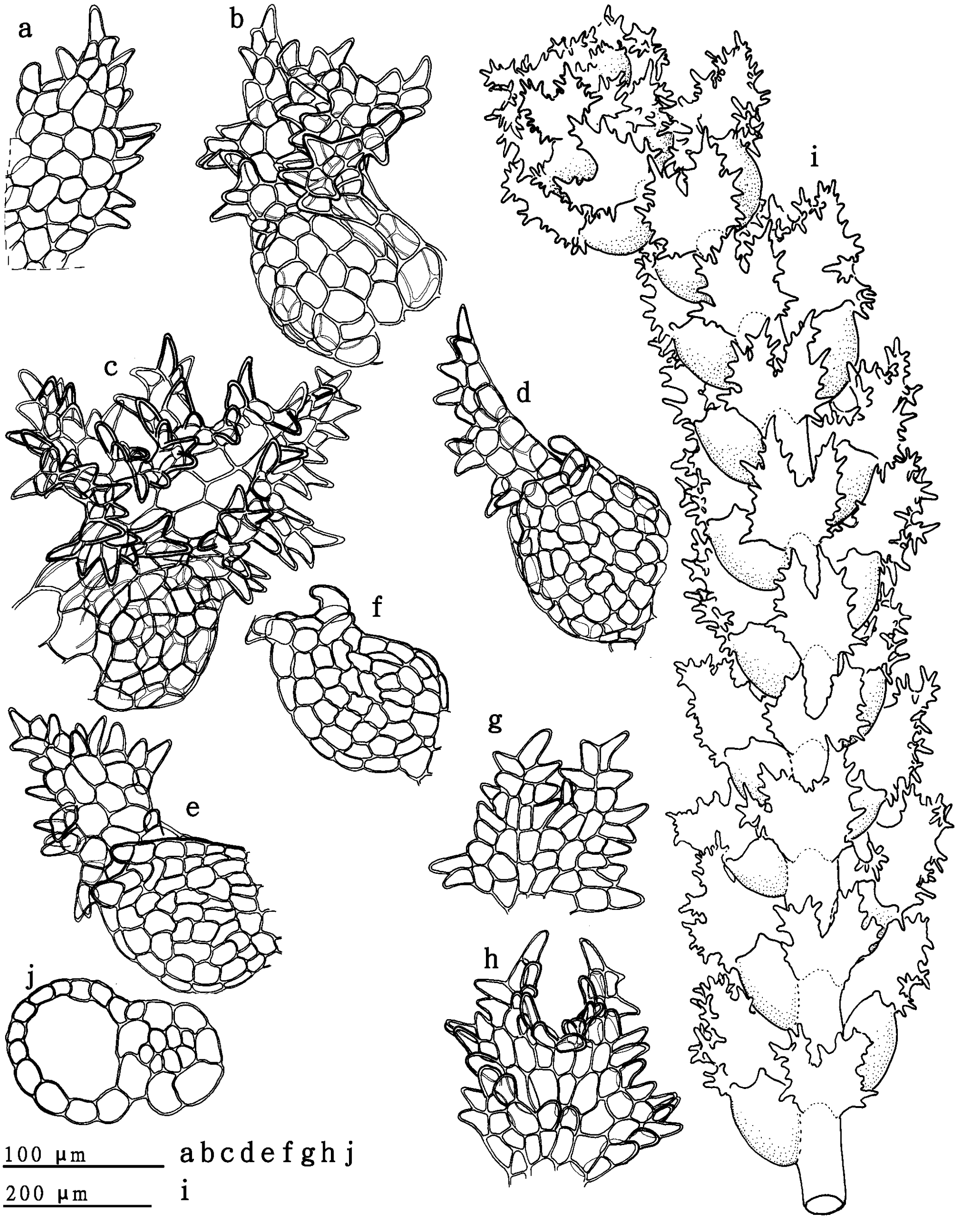

Fig. 1. ***Dactylophorella muricata*** (Gottsche) R. M. Schust. a. Cells of leaf lobe, dorsal view. b–e. Leaves, ventral view. f. Leaf lobule. g, h. Underleaves. i. Portion of sterile plant, ventral view. j. Transverse section of stem. (All drawn from *Chi-Da Wu et al. 1897a*).

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8. Table should be typed on a separate sheet and be headed by a title of dual languages (Chinese and English). It consists of only horizontal lines and typed with English terms (if possible) and Arabic numerals. If foot notes are required, mark with superscripts ^{1}, ^{2}, *, $^\#$, etc.
9. Figure should be drawn with black ink on a separate white tracing paper with a figure legend of the dual languages below. Computer graph made from laser printer is acceptable.
10. Photograph should be a glossy black and white shot with sufficient resolution to be clearly legible after reduction. When multiple photos are employed, the author should arrange them in plates. Micrographs should include bars indicating scales of magnification. Photos should be pasted on white A4 paper loosely with the figure legend below.