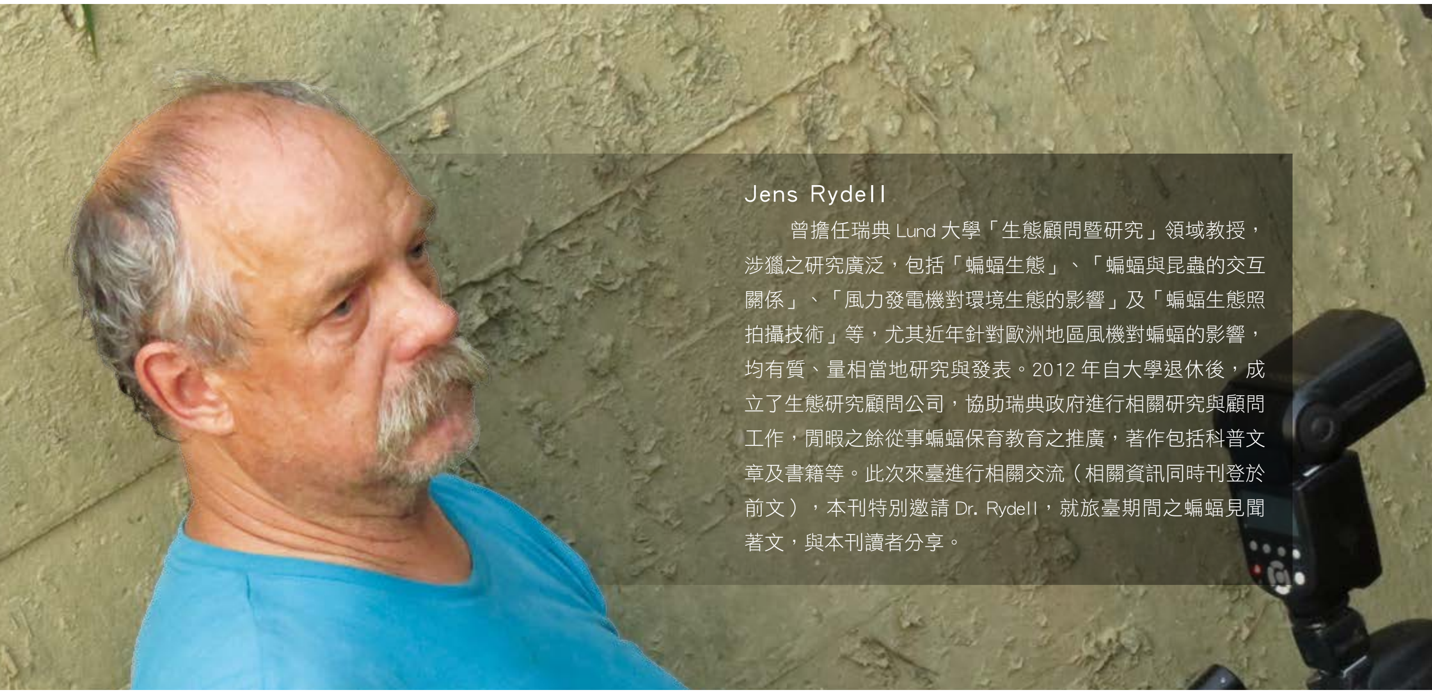
Bats in the tunnel
隧道中的蝙蝠

Jens Rydell / 瑞典Lund大學退休教授

陳宏彰(譯) / 行政院農業委員會特有生物研究保育中心研究助理
Hung-Chang Chen



Jens Rydell

曾擔任瑞典 Lund 大學「生態顧問暨研究」領域教授，涉獵之研究廣泛，包括「蝙蝠生態」、「蝙蝠與昆蟲的交互關係」、「風力發電機對環境生態的影響」及「蝙蝠生態照拍攝技術」等，尤其近年針對歐洲地區風機對蝙蝠的影響，均有質、量相當地研究與發表。2012 年自大學退休後，成立了生態研究顧問公司，協助瑞典政府進行相關研究與顧問工作，閒暇之餘從事蝙蝠保育教育之推廣，著作包括科普文章及書籍等。此次來臺進行相關交流（相關資訊同時刊登於前文），本刊特別邀請 Dr. Rydell，就旅臺期間之蝙蝠見聞著文，與本刊讀者分享。

（陳宏彰 攝）

Little horseshoe bats light-sampling
臺灣小蹄鼻蝠藉由評估光線亮度決定外出覓食時機。（Jens Rydell 攝）

Evening emergence

Hundreds of female little horseshoe bats *Rhinolophus monoceros* congregate at the tunnel entrance just before the evening emergence, flying back and forth in a left hand loop. Their maternity roost, now with the newborn young left behind, is located almost a kilometer away, at the far end of the tunnel. By approaching the entrance from the inside several times, the bats do what is called "light sampling", checking that the ambient light level is appropriate for safe departure from the tunnel and towards the hunting grounds. Particularly at roosts with many bats, birds of prey often wait outside, ready to catch any careless bat. Therefore, leaving the safety of the tunnel while the light is still bright outside is extremely dangerous, since it would make the bat vulnerable to attacks from birds of prey, which hunt by vision. To minimize the risk even further, the bats emerge in large coherent groups, each individual trying to stay in the middle of the flock, so that other individuals are caught first. Once the bats are outside the tunnel, they are careful not to expose themselves in the open air before it is fully dark, while they may still be vulnerable to attacks from birds. They always start to hunt in the shade near the ground or among the leaves and branches of trees, where they would be hard to spot and follow even for the sharpest eyes.

Compared to birds of prey, bats are slow flying and have poor vision, and so are always at a disadvantage, as long as the birds can see properly. The necessary avoidance of hawks, falcons and other birds is in fact the principal reason why bats nearly always are strictly nocturnal. At night, the bats have the advantage, thanks to their ability of echolocation.

傍晚湧現

傍晚時分，數百隻的雌性臺灣小蹄鼻蝠(*Rhinolophus monoceros*)在隧道開口處盤旋，等待著飛離的契機。此時，在近 1km 深處的隧道底，有一群暫時被留下的新生小蹄鼻蝠寶寶，顯然這隧道是臺灣小蹄鼻蝠用來生殖育幼的棲所。這些正準備離開隧道棲所的蝙蝠媽媽們，透過數次來回逼近隧道口的方式，藉由評估光線亮度(light sampling)以決定外出覓食的時機。由於在許多蝙蝠棲息的洞穴或隧道外，常有猛禽出沒，準備隨機捕抓警覺度不高的蝙蝠。因此，蝙蝠如果在外界仍然太亮時飛離隧道，很容易受到依靠視覺狩獵的猛禽攻擊。為了將被捕食的機率降到最小，蝙蝠常大量、緊密成群地飛出洞穴，而且每隻個體都試圖擠進飛行團隊中間，避免身處外圍而被猛禽捕獲。如飛離隧道時天色未全暗，蝙蝠也會小心地不要暴露在空曠處，以降低受到來自猛禽的傷害。因此，常可見蝙蝠傍晚開始覓食時，總是貼近地面或圍繞著樹叢飛行。如此一來，即便是最銳利的猛禽眼睛，都難以發現牠們的蹤跡。

相較於猛禽，蝙蝠的飛行速度與視覺能力都屈居於劣勢，為了躲避來自鷹、隼或其他鳥類的攻擊，也是促使蝙蝠成為夜行動物的主因之一。然而，蝙蝠在夜間活動能具有優勢，這就得感謝牠們所擁有的回聲定位(echolocation)能力了。

Jamming

To find the way in the darkness of the tunnel and to avoid colliding with each other, the bats have to rely on ultrasonic echolocation or sonar (short for SOund NAvigation and Ranging). They use the time delay between the emitted echolocation call and the return of the echo to estimate the distance to the wall of the tunnel. But how can they separate the echoes from their own calls from the echoes resulting from

干擾

蝙蝠依賴超越人類可聽音頻的回聲定位或聲納(sonar：聲音導航與測距 Sound Navigation and Ranging)，才能在黑暗的隧道中找到飛行路線或避免碰撞到其他個體。牠們利用發出回聲定位叫聲與收到反射音之間的時間差，估算出與隧道牆壁之間的距離，但牠們究竟如何區別自己與其他附

the calls of other bats flying nearby? Attention to the wrong echoes may result in a miscalculation of the position and it may even result in a fatal crash into the water. Bats flying in groups always have to deal with this issue, called jamming avoidance, and they seem to handle it easily and without problems. But exactly how they do it is not clear at all to anyone except the bats themselves.

Research into jamming avoidance and other aspects of bat echolocation is an expensive high tech business, but it helps to develop similar systems for the use by man, for example in radar and sonar technology, ultrasonic diagnostics and for the aid of blind people.

Long-fingered bats

As the light level drops further, the Taiwanese long-fingered bats *Miniopterus schreibersii fuliginosus*, a large colony of which shares the tunnel with the little horseshoe bats, also start to depart. In some contrast to the little horseshoes, they arrive at the entrance at high speed in straight flight on their long narrow wings, and fly directly towards the sky, where they will spread out in search of small arthropods, "aerial plankton" high among the clouds. Their food includes small flies, aphids, and sometimes even spiders and small caterpillars, the latter having been carried aloft by the wind, hanging in their silk threads. These bats occur in large colonies in tunnels, sometimes counting tens of thousands, all over Taiwan. The colonies are highly valuable resources, because they deliver important ecosystem services by feeding on agricultural pest insects in enormous numbers. But because so many bats are concentrated in relatively few roosts, they are highly vulnerable to disturbance in their roosts and, because they feed partly on pest insects, they may perhaps also accumulate high levels of pesticides.

近飛行個體的聲音呢?若錯聽了回聲,將導致自我位置判斷錯誤,進而造成碰撞或墜入水中等致命結果。因此,當蝙蝠群體飛舞時,總需要面對這被稱為「干擾迴避(jamming avoidance)」的問題。顯然地,牠們處理得相當好,完全沒有因為判斷錯誤而造成「飛行意外」的狀況,但是這究竟是如何辦到的?除了蝙蝠自己,我們仍然一知半解。

儘管進行干擾迴避及蝙蝠回聲定位等研究所費不貲,但是相關研究確有助於人類發展類似的系統,包括雷達與聲納技術、超音波診斷學,以及輔助盲人的器材等。

長指蝠(摺翅蝠)

當夜幕更加低垂,一大群與臺灣小蹄鼻蝠共棲於隧道中的東亞摺翅蝠(*Miniopterus schreibersii fuliginosus*)也陸續飛出。不同於臺灣小蹄鼻蝠,摺翅蝠擁有較長且窄的翅形,牠們快速穿越隧道口並直接朝天際飛去。在空中各自分散後,覓食一些出現在雲端高處的小型空中浮游節肢動物,包括蚊子、牙蟲、蜘蛛與毛毛蟲等,後兩者常因懸掛著絲並被風帶往高空中。以臺灣整體狀況來說,摺翅蝠常在隧道中群聚成大群集,數量有時甚至可達上萬隻。這些摺翅蝠群集具有非常高的價值,因為牠們可以吃掉相當大量的農業害蟲,提供了非常重要的生態服務功能。儘管牠們可消滅大量農業害蟲,但也可能因此導致體內殘留、累積了高濃度的殺蟲劑(農藥);另外,大量的蝙蝠卻只集聚在相對少數的棲所,若這些棲所面臨干擾,將對牠們造成極大的傷害。


Long-fingered bat and horseshoe bats emerging from tunnel 東亞摺翅蝠與臺灣小蹄鼻蝠由隧道內蜂擁而出。(Jens Rydell 攝)

Approaches to echolocation

Most bats, including the long-fingered bats, normally search for insects in the open air space, above the trees, where there is no background except air and where any returning echo is likely to come from a flying insect (or perhaps from a fellow bat). When searching for insects, these bats constantly emit short calls at high frequencies (50 kHz), and listen for echoes in the time interval between the calls. The calls originate in the larynx, just as the sounds of other mammals including humans, and they are emitted through the open mouth, using the lips to form an acoustic beam. The bats call about ten times per second, and the echoes reveal the presence of an insect. But after the detection of an insect the call rate increases to about 200 calls per second, as the insect is zoomed in and finally captured.

Keeping the emitted call and the returning echoes separate in time in this way, is the most simple and straight-forward approach to echolocation, as used by bats. But this technique has some limitations. For example, it restricts the bats' hunting efforts to more or less open places, where there are no background echoes masking the echoes from insects. Such background echoes, which are

回聲定位的途徑

包括摺翅蝠在內的多種蝙蝠,通常會在開闊的空域或樹冠層上搜尋昆蟲,此時會反射其回聲定位聲波的僅有飛行中的昆蟲或其他的蝙蝠個體。當蝙蝠偵測到昆蟲,會持續發出較短且高頻(約50kHz)的叫聲,同時在每個叫聲間接收回音。與其他哺乳類(包括人類)的發音方式相同,這些聲音源自喉頭,張嘴以發出聲音且利用嘴唇形成音束。蝙蝠在搜尋時發出的音波頻度大約每秒10次,當偵測到昆蟲時,蝙蝠會提高叫聲頻度達每秒200次,目的在於以更高的解析力鎖定昆蟲,直到捕獲昆蟲為止。

蝙蝠運用回聲定位最簡單且直接的方式,是藉由不斷發出叫聲並即時監聽反射回聲,但這方法卻有些限制。舉例來說,當小昆蟲位於空曠環境,在沒有背景回聲(background echoes)遮掩時,蝙蝠利用上述發音、接收方式,或可減少獵食努力量。在此,背景回音聲亦可稱為雜訊(clutter),其強度大過小昆蟲反射的回音,當反射超音波的物體表面過大,將導致蝙蝠無法偵測到小昆蟲。

Little horseshoe catching moth
臺灣小蹄鼻蝠正在捕抓蛾類。(Jens Rydell 攝)

臺灣小蹄鼻蝠利用超音波鎖定飛蟲。(周政翰 攝)

called clutter, are always much stronger than echoes from small insects, simply because the reflecting surface is larger, and would make it hard to detect the insects. This problem is emphasized when insect are really close to the background, so that the echoes from the insect and the background arrive more or less at the same time. Indeed, the threat from hunting bats is one of the reasons why many insects prefer the relative safety close to vegetation. For insects, as well as for the bats, a venture out in the open space usually means exposure to danger.

The little horseshoe bats, most of which have already left the tunnel before the long-fingered bats, have a different approach to echolocation. They use a technique that allows them to filter off the clutter, enabling them to search for insects even in the close vicinity of vegetation, among leaves and branches, and without facing the problem of background echoes masking the echoes of insects. In these bats the sound is emitted through the nose, which has an extremely elaborate form with a largely unknown function. The sonar technique of the horseshoe bats relies on the

這樣的問題在昆蟲非常接近背景時更為凸顯，因為反射自背景與昆蟲的音波幾乎同時到達蝙蝠耳朵，背景回音會掩蓋掉昆蟲的訊號。事實上，來自掠食蝙蝠的威脅是很多昆蟲偏好在相對安全的植被(大背景)附近活動的原因之一。如同蝙蝠躲避猛禽一樣，對昆蟲而言，現身於空曠區域意謂著暴露於危險之中。

比摺翅蝠提早離開隧道的臺灣小蹄鼻蝠，則採用不同的回聲定位途徑。牠們運用了過濾雜訊的技巧，讓牠們可以靠近植物並沿著樹葉或枝條搜尋昆蟲，且完全不受背景回聲掩蓋住昆蟲回聲的問題影響。蹄鼻蝠運用鼻子發出超音波，其鼻葉結構相當精細，但運作功能目前仍所知不多。蹄鼻蝠運用的聲納技巧是藉由發出定頻(constant-frequency)的音波並監聽反射自昆蟲的已變頻回聲，其原理類似警察使用的測速

emission of constant-frequency calls and the shift in frequency of the echo caused by the movement of the insect. Like the police with their speed radar, the bats make use of what is called Doppler-shifts, which is the apparent change in frequency resulting from movement. The horseshoe bats can then separate the emitted sound from the returning echoes in frequency rather than in time. Moving insect wings reflect Doppler-shifted echoes, which return to the bat's ear at a slightly different frequency than the emitted sound, and this particular frequency is emphasized in the bat's ear, while the opposite is true of the emitted frequency. Hence, the horseshoe bats are practically deaf to their own calls, but extremely sensitive to the returning echoes that may arrive at the same time! The Doppler-shifted echoes would tell the bat not only of the presence of a moving insect, it would also reveal the speed and direction of movement in relation to that of the bat itself and the background. This elegant technique, discovered by the horseshoe bats nearly 50 million years ago, relies on the same principle as modern radars, although the latter use radio waves instead of sound waves.

雷達，蝙蝠運用所謂的「都卜勒頻移」(Doppler-shifts)效應，這是頻率在移動過程造成的明顯變化。蹄鼻蝠可由反射的回聲分辨出自己所發的聲音頻率，而不是利用時間差來區分。因為，移動中的昆蟲翅膀會反射「都卜勒頻移」回聲，這些昆蟲反射回聲與蝙蝠發射出的音波有些微的差異，聽在蝙蝠的耳中，這些微差異會被放大。因此，蹄鼻蝠若同時間聽見自己發出的聲音與變頻後的回音，其聽覺對變頻後的回聲會格外敏銳，但原發音波則會被忽略(過濾掉)。「都卜勒頻移」回聲不僅可以告訴蝙蝠移動中昆蟲的存在，更能讓蝙蝠清楚自身速度、方向與背景之間的關聯性。蹄鼻蝠早在5,000萬年前就已發展出這樣優雅的聲納技巧。現今人類使用的雷達也是依據相同的原理，差別只在以電磁波取代了音波而已。

Ultra-high ultrasound

The horseshoe bats use higher frequencies than other bats, in our case about 110 kHz, more than twice that of Miniopterus, and this is yet another interesting but poorly understood feature of horseshoe bat sonar. Why the bats use such high frequencies is a very good question, particularly since sound of high frequencies travels very poorly through the air and thus provide echoes of objects only at very close range, about a meter at best. Indeed, one might think that the bats would do better by using lower frequencies that travel much further, thus providing more and stronger echoes.

However, high frequencies do have their advantages. First, high frequency sound gives higher resolution than lower frequencies, and therefore permits detection of smaller insects, of which there usually are many more. Second, the ultra-high frequencies used by horseshoe bats bypass the hearing of most insects, so that the bats can approach them undetected. Many nocturnal insects including moths, for example, have ultrasonic ears or bat detectors, with the primary function of providing the insect with an early warning of approaching bats, so that the insect can take evasive action. However, insect ears are very sensitive to the frequencies used by Miniopterus but not to those of the horseshoe bats. Third, by using very high frequencies, the magnitude of the Doppler-shifts would increase, so that echoes of insects would be easier to separate from background echoes.

Which of these explanations is the most important is not known but remains the subject for future research on bat sonar. In any case, it is clear that the horseshoe bats catch hearing insects such as moths to a much higher extent than other bats, so the ultra-high frequencies help them somehow.

Spiders

The gem among the Taiwanese bats may be the tiny tail-less leaf-nosed bat *Coelops frithii formosanus*, a distant relative to the horseshoe bats. Like the horseshoe bats the tail-less bat emits the sonar signals through the nose, which is formed like a flexible megaphone. The sonar receivers, the ears, are two parabolas directed forwards. However, in contrast to the horse-shoes the sound of the tail-less is not of constant frequency and the bat does not rely on Doppler-shifted echoes. As recently

超高頻的超音波

相較於其他蝙蝠，蹄鼻蝠發出更高頻率的超音波，在臺灣小蹄鼻蝠的例子中，甚至可高達110 kHz，這樣的音頻幾乎是摺翅蝠超音波的兩倍高。為什麼蹄鼻蝠要使用如此高頻的超音波？這是一個非常好、有趣且尚未被深入瞭解的議題。因為依據聲音傳播原理，音頻越高能量衰減越快，且傳播距離越短。因此，蹄鼻蝠的高頻超音波在空氣中的最佳解析回聲距離，莫約僅有1m。確實，依此邏輯蝙蝠理當採用可傳更遠的較低音波，以確保有更大及足夠的回聲才對。

然而，高音頻卻仍有其優勢。首先，高音頻比低音頻具有更高的解析力，可偵測到相對數量更多的小型昆蟲。再者，蹄鼻蝠的超高音頻已超出蛾類昆蟲聽覺的範圍，蝙蝠可以無聲無息地接近蛾而不被發覺。事實上，許多夜行性昆蟲（包括蛾類）擁有可聽超音波的耳朵或偵測蝙蝠 超音波的器官，主要功能在於讓昆蟲可以提早注意到逼近中的蝙蝠，並進行閃躲，但昆蟲耳朵較敏銳的聽覺範圍，卻落在摺翅蝠的音頻（約50 kHz）附近，可惜並無法預先聽到這些來襲的蹄鼻蝠。最後一點，使用極高的音頻有助於增強「都卜勒頻移」效應，可更容易區分來自昆蟲與背景的回聲之間的差異。

我們還不知道上述解釋哪一點是最重要的，這也是未來蝙蝠聲納研究可以著墨的地方。不過在許多案例中可見，蹄鼻蝠明顯地比其他蝙蝠捕食更多的蛾類，所以超高頻超音波或應有助於蹄鼻蝠的捕食效率。

蜘蛛

小型的臺灣無尾葉鼻蝠（*Coelops frithii formosanus*）或許是臺灣蝙蝠物種中最耀眼的一顆寶石。這種與臺灣小蹄蝠有遠親關係的蝙蝠，一樣是透過鼻子發射聲納訊號，其鼻形就像一部彎曲皺摺的擴音器，聲納的接受器則是那方向朝前的圓盤狀雙耳。然而，與臺灣小蹄鼻蝠不同的是，無尾葉鼻蝠並非使用定頻音波，也不依靠「都卜勒頻移」回聲。近期臺灣研究者揭露了這個現象（Ho *et al.* 2013），

Taiwanese tail-less leaf-nosed bat
臺灣無尾葉鼻蝠。（Jens Rydell 攝）

Leaf-nosed bat in tunnel
隧道中的臺灣葉鼻蝠。（Jens Rydell 攝）

Colony of leaf-nosed bats in tunnel
隧道中的臺灣葉鼻蝠群集。（Jens Rydell 攝）

人工開鑿之隧道常成為蝙蝠的棲所。（陳宏彰 攝）

引水涵道常是蝙蝠棲息之地。（陳宏彰 攝）

群聚於日治時期開鑿引水涵道中的東亞摺翅蝠（右）及臺灣小蹄鼻蝠（左）。（陳宏彰 攝）

demonstrated by Taiwanese researchers, the tail-less sonar has been modified drastically during the course of evolution and is now of a very special kind, unlike anything else, although it still relies on very high frequencies (150 kHz). The bat eats spiders, which are caught in their webs. Since spiders are largely non-moving and usually occur in places with clutter, their detection would not be facilitated by using any of the sonar techniques just described for the other bats.

But how the sonar of the tail-less bat functions and in particular how it facilitates the detection of spiders is not known. Research on this interesting topic is continuing in Taiwan and elsewhere.

儘管無尾葉鼻蝠仍使用超高音頻（約150 kHz）的聲納，但在演化過程中卻徹底地改變了策略，已與其他類群蝙蝠不同，如今被歸類在相當特殊的聲納種類。這種主食蜘蛛的蝙蝠，可由蜘蛛網上直接抓取獵物，由於蜘蛛多半停滯於網上不動，而且常結網或出沒在背景複雜之處，顯然地，無尾葉鼻蝠並非利用前述其他蝙蝠類群的聲納技巧來捕食蜘蛛。

但有關無尾葉鼻蝠的聲納功能，以及如何協助其偵測到蜘蛛，目前卻仍未有確切的答案。因此，在臺灣或世界其他地區的研究者仍持續鑽研著這個非常有趣的議題。

Tunnels

Drain pipes, old railway tunnels, bunkers and mines occur all over Taiwan, some of them were built already during Japanese occupation and are currently part of Taiwan's rich technological and natural heritage. In the absence of natural caves, many or even most of these artificial caves serve as roosts for bats, and there is no doubt that there would have been much fewer bats without them. The magnificent Taiwanese leaf-nosed bat *Hipposideros armiger terasensis* is a particularly good example. This species is a distant relative of the little horseshoe bat, although much larger, and uses a similar echolocation system of constant

隧道

排水涵管、舊火車隧道、地下碉堡（防空洞）及礦坑遍布在臺灣各地，有些結構是日治時期所遺留下來，現在已成為臺灣豐富的工藝技術及自然遺產。在缺乏天然洞穴的地方，這些人工建物幾乎都可提供成為蝙蝠的棲所。無庸置疑，蝙蝠也相當地捧場，壯碩的臺灣葉鼻蝠（*Hipposideros armiger terasensis*）就是絕佳的例子。這種蝙蝠也是臺灣小蹄鼻蝠的遠親，儘管體型相對巨大很多，但卻利用同樣的定頻叫聲方式及「都卜勒頻移」效應。臺灣葉鼻蝠普遍分布於臺灣中、低海拔區域且會聚集形成

臺灣小蹄鼻蝠（左）使用鼻子發定頻音波，東亞摺翅蝠（右）則利用嘴巴發變頻音波。（周政翰 攝）

偶而可拍到雄性飛行個體的外生殖器，可作為性別辨識。（周政翰 攝）

飛行技巧高超的臺灣無尾葉鼻蝠，由鼻子發出超音波。（張鈞翔 攝）

frequency calls and Doppler-shifts. The leaf-nosed bat forms large colonies and is common throughout the lowlands and mid-altitudes in Taiwan. Like the little horseshoe bats and the long-fingered bats, they nearly always roost in tunnels, artificial "caves".

Indeed, the tunnels are extremely important as bat roosts and hopefully they receive adequate protection, so that the magnificent bat populations of Taiwan will persist, to be studied by future generations of students, young and old alike.

Impressions

Taiwan has a rich natural heritage and despite a dense human population there is still much intact forest, thanks partly to the rugged hills and mountains that occupy about half the country. The bats on the island are mostly endemic, which means that they occur nowhere else, and this means that Taiwan has the full responsibility of these populations, shared by nobody. Fortunately, there are several highly devoted bat scientists that guarantee that the bats get their much needed attention and share of resources for research and conservation.

Finally, I would like to thank the colleagues at the Endemic Species Research Institute in Ji-Ji for a fantastic journey through Taiwanese bat habitats, to old railway tunnels, drain pipes and bamboo forests, and for the unique opportunity to photograph this great natural heritage in great surroundings. The hospitality during my stay was just fantastic!

大群集。如同臺灣小蹄鼻蝠與東亞摺翅蝠，牠們幾乎總是棲息在隧道（亦即人工洞穴）中。

確實，隧道除了可以成為蝙蝠的棲所外，更能保護其安全，這也是壯碩臺灣葉鼻蝠族群得以持續存在臺灣的原因。也因此，未來新一代的學生（無論老或少學生）都得以延續研究這些蝙蝠。

印象

臺灣擁有豐富的自然資產，即使人口密集卻仍保有多數的原始森林，這得感謝國家有一半面積以上是高低起伏的丘陵或高山。臺灣島上的蝙蝠多數是特有種，意味著牠們只專屬於這座島嶼，也代表著每個臺灣人對於這些蝙蝠都具有絕對的責任與義務。所幸地，已有數位蝙蝠科學研究者全身投入、扛起提醒大眾關注蝙蝠的工作，且他（她）們非常願意與大家分享研究成果及保育資源。

最後，我要感謝集集特有生物研究保育中心的同仁們，他們帶我經歷了絕妙的蝙蝠棲地之旅，包括參訪舊廢棄火車隧道、排水涵道與竹林等，並感謝讓我有獨一無二的機會，在這非常好的環境中拍攝到這些非常棒的自然遺產，並謝謝在我旅臺期間絕妙的款待。