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Evidence of predation on butterflies in the cave-roosting Formosan tailless leaf-nosed bat

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ABSTRACT: The Formosan tailless leaf-nosed bat (*Coelops frithii formosanus*) is an endemic subspecies in Taiwan and is classified as a nationally vulnerable small insectivorous bat. In 2010, many discarded lepidopteran wings, particularly butterfly wings, were discovered in a roosting cave in Beinan, Taitung. Therefore, this study conducted a long-term survey (2010–2012 and 2015–2018) to investigate the species composition, abundance, and temporal distribution of prey transported back to the roost by this bat. A total of 1,283 discarded wings were collected, representing at least 68 species from 12 lepidopteran families. Butterflies (41 species) clearly exceeded moths (27 species) in both abundance and species richness; in the standardized 2015–2018 dataset, the butterfly-to-moth ratio was approximately 4.9:1. The most frequently recorded prey species was *Badamia exclamationis* (Hesperiidae), accounting for 47.5% of all discarded wings. The occurrence of discarded wings showed a distinct temporal pattern, mainly from November to May of the following year, with high abundance typically observed between February and March. In addition, interannual variation in species composition was observed. The dominance of diurnal butterflies, which are generally inactive at night, suggests that *C. f. formosanus* may employ a gleaning strategy for certain lepidopteran taxa. This study provides the first documentation of lepidopteran utilization by the Formosan tailless leaf-nosed bat based on discarded-wing remains and offers foundational data for future studies on its foraging ecology and life history.

KEY WORDS: Butterfly, *Coelops frithii formosanus*, discarded wing, insectivorous bat, moth.

INTRODUCTION

Bats are predominantly insectivorous and commonly consume a wide range of arthropods (Kasso and Balakrishnan, 2013), including Lepidoptera. While the evolutionary interactions between moths and bats have attracted considerable attention (e.g., Ter Hofstede and Ratcliffe, 2016; Kawahara *et al*., 2019), records of bat predation on butterflies have been documented, but remain relatively limited.

Records of bat predation on butterflies can be traced back to the 1920s and 1930s. The brown long-eared bat (*Plecotus auritus*), which is well known for its gleaning foraging strategy (Swift, 1998), was among the earliest species reported to prey on butterflies across Europe. Gould (1955) compiled earlier literature (Poulton, 1929; Buckhurst, 1930; Nicholson, 1937; Manwaring, 1939) and listed two nymphalid butterflies, *Pyronia tithonus* and *Vanessa atalanta*, among its prey. In addition, two other common European nymphalids, *Aglais urticae* and *A. io*, have also been recorded as prey of *P. auritus* (Hanson, 1950; Natuschke, 1960; Roer, 1969). Roer (1969) further noted that these butterflies constituted winter prey, as they entered diapause while hiding in attics or mines, making them susceptible to predation during winter.

Similarly, Jones (1990) reported that the greater horseshoe bat (*Rhinolophus ferrumequinum*) in the United Kingdom also preyed upon butterflies aggregating in preparation for overwintering, including *A. urticae* and *A. io*. This suggests that overwintering aggregations of butterflies may represent accessible prey for different bat species. However, records of butterfly predation are not restricted to the overwintering season. In the Czech Republic, the serotine bat (*Eptesicus serotinus*) was recorded feeding on *A. urticae*, *Vanessa cardui*, *Coenonympha arcania* (Nymphalidae), and *Pieris napi* (Pieridae) during summer, when butterflies were normally active (Mikula and Čmoková, 2012). That study, which was based on discarded wings, documented a relatively higher number of butterfly species; however, both the species richness and abundance of moth prey remained substantially greater. Furthermore, evidence of butterfly predation is not limited to direct observations or discarded-wing records. A molecular study reported relatively high frequencies (up to 30.5%) of butterfly taxa (Nymphalidae and Hesperiidae) in the feces of two aerial-hawking bat species, the little free-tailed bat (*Chaerephon pumilus*) and the Angolan free-tailed bat (*Mops condylurus*), although species-level identifications were not mentioned (Bohmann *et al*., 2011). These cases suggest that bat predation on butterflies may be influenced by multiple factors, including season, prey aggregation behavior, and foraging strategy.

In Taiwan, the Formosan tailless leaf-nosed bat (*Coelops frithii formosanus*) has been found to leave large numbers of discarded butterfly wings in its roosting caves (Fang and Cheng, 2011). This endemic subspecies is a small, cave-dwelling insectivorous bat (body length: 40–52 mm; forearm length: 36–43 mm; Cheng *et al*., 2022). Due to its specific habitat requirements, restricted

distribution, and small population size, it was designated as a protected species in 2008 and classified as Nationally Vulnerable under the IUCN Red List criteria (Lin *et al*., 2009; Cheng *et al*., 2024). Ecological studies on this subspecies remain few. Previous research has focused on wing morphology (Lai, 2000), phylogenetics (Li *et al*., 2007), population genetics (Chu, 2006; Fang and Cheng, 2011), and echolocation calls (Ho *et al*., 2013); however, information regarding its foraging ecology remains scarce.

The aforementioned observations of discarded butterfly wings originated from the first life-history monitoring study of this species across Taiwan, initiated by Fang and Cheng (2011) in 2009. During that study, this phenomenon was discovered in roosting caves at one of the study sites in Taitung County, Taiwan. Infrared camera footage also documented individuals returning to their roost with lepidopteran prey in their mouths (see Supplementary Material Fig. S1). However, the species composition and temporal patterns of these discarded wings have not yet been described. This study provides the first documentation of the species composition, abundance, and temporal distribution of discarded lepidopteran wings in the roosting cave of *C. f. formosanus*, providing foundational data for future studies on the foraging ecology of this subspecies.

MATERIALS AND METHODS

Study area

The study site is in Dongxing Village (Beinan Township, Taitung County, Taiwan). The roosting cave was situated at the foothills beside the Lijia River (altitude: 183 m). The study area is primarily covered by evergreen broad-leaved forests interspersed with patches of bamboo forest. The population size of the Formosan tailless leaf-nosed bat (*Coelops frithii formosanus*) in the cave varies seasonally, with a peak in winter (maximum recorded count: approximately 300 individuals), representing a relatively large population among the caves inhabited by this subspecies in Taiwan (Fang and Cheng, 2011).

The site contained numerous abandoned artificial caves. According to long-term monitoring by Fang and Cheng (2011), *C. f. formosanus* primarily uses Cave B2 as its diurnal roost and was the dominant occupant of this cave. Other bat species were only occasionally observed in Cave B2 and in low numbers. Moreover, *C. f. formosanus* generally did not form mixed-species roosts, and occupied areas clearly separated from those used by other bats within the cave (Fig. S2). Accumulations of feces, together with discarded butterfly and moth wings, were observed on the ground directly beneath the roosting sites. The internal environment of the cave is relatively stable, with temperatures ranging from 20.6–23.0 °C and relative humidity ranging from 95.1–100% throughout the year (Fang and Cheng, 2011).

Survey and sampling

Discarded-wing data were obtained from two separate study periods. The first period (February 2010–February 2012) was part of a life-history study of *C. f. formosanus* and involved monthly surveys (Fang and Cheng, 2011). During this period, sampling was conducted on a single survey day per month (except in February 2011 and 2012, when surveys extended over two days), and representative discarded wings of each species encountered were collected (Fig. 1). Therefore, the species composition and abundance of discarded wings recorded during this period were not comprehensive.

The second period (February 2015–May 2018) adopted a discontinuous but standardized and exhaustive collection approach (Fig. 1). Each survey generally lasted three consecutive days (except for the February and March 2015 surveys, which lasted two days). On the first day of each survey, several white plastic sheets (approximately 35 cm × 25 cm) were placed on the ground directly beneath the roosting sites of *C. f. formosanus* to facilitate the detection of newly discarded wings on the following day (Fig. 2). On the second and third days, we entered the cave in the morning after sunrise to collect wings newly appeared during the preceding night, which were then placed in paper triangles and transported to the laboratory for identification. During each survey, we collected all non-degraded lepidopteran wings observable within the cave to the extent possible (i.e., wings with intact wing membranes, regardless of whether scales were present or had been lost), thereby providing a standardized assessment of wing composition for each survey. In 2017 and 2018, additional efforts were made to ensure relatively even sampling across the four seasons (winter: December–February; spring: March–May; summer: June–August; autumn: September–November). This sampling design represented a compromise of standardized collection because of limitations in manpower and funding, particularly during 2015–2016, while the surveys conducted during 2010–2012 had already provided a preliminary understanding of the overall distribution patterns of discarded wings.

Identification and data processing

Butterfly identification primarily referred to *The Butterflies of Taiwan* series (Hsu, 2013a,b, c), while moth identification relied on *Guide Book to Insects in Taiwan* series (Wang, 1994, 1995a,b,c,d,e, 1996a, b; Wang *et al*., 2000; Wang and Stange, 2000) and the websites "DearLep" (http://dearlep.tw/) and "Taiwan Moth Information Center" (https://twmoth.tw/peo/MothQuery).

We used binary logistic regression (implemented in R version 4.3.1; R Core Team, 2023) to analyze the relationship between the body size of butterfly species and whether each species had ever been recorded among the discarded wings in the cave (present/absent). The

Table 1. Abundance and composition of discarded wings from butterflies and moths collected within Cave B2 during 2010–2012 and 2015–2018.

	2010-2012		2015-2018	
Butterfly	141	85.5%	925	82.7%
Moth	24	14.5%	187	16.7%
Unidentified	0	0.0%	6	0.5%
Total	**165**	**100%**	**1,118**	**100%**

Table 2. Numbers of discarded wings collected on days 1–3 of each survey trip to Cave B2.

Survey month	Day 1 (N=14)	Day 2 (N=14)	Day 3 (N=12)
2015.02	59	12	-
2015.03	8	1	-
2015.09	0	0	0
2015.11	0	0	0
2016.03	398	17	1
2016.09	0	0	0
2016.12	13	5	1
2017.02	133	20	36
2017.05	16	0	0
2017.07	0	0	0
2017.09	0	0	0
2017.11	10	0	1
2018.02	264	57	49
2018.05	17	0	0
Mean	**65.6**	**8.0**	**7.3**

present/absent designation for each species indicated only whether the species had been recorded during at least one survey and did not involve quantitative calculations of its occurrence frequency or abundance. Therefore, all records from the two survey periods between 2010 and 2018 (i.e., representative sampling during 2010–2012 and comprehensive collection during 2015–2018) were included in this designation. Background data on butterfly species were derived from faunal surveys conducted by Chao and Tang (2001) and Yang and Li (2005) in the neighboring Li-jia Major Wildlife Habitat, located approximately 5–6 km from our sampling site with an elevation difference of about 900 m. Papilionidae were excluded from the analysis as they have never been recorded in the caves. Moths were also excluded due to the lack of local data.

RESULTS

Patterns of occurrence

According to the monthly surveys conducted during 2010–2012, discarded wings of butterflies and moths began to appear in December and persisted until April of the following year. Based on the discontinuous surveys conducted between 2015 and 2018, discarded wings were first observed as early as November and could persist until May (Fig. 1). In addition, a few remains of other invertebrates (e.g., Odonata and spiders) were also observed within the cave.

We collected a total of 1,283 discarded wings from Cave B2, of which 165 were from 2010–2012 and 1,118 were from 2015–2018 (Table 1). Based on the quantitative data collected during 2015–2018, large numbers of discarded wings were typically recorded in February–March. However, interannual variation was observed, with relatively low numbers recorded in 2015 and 2017 (Fig. 1).

During the 14 surveys conducted between 2015 and 2018, the highest number of discarded lepidopteran wings was collected on the first day of each survey (mean = 65.6). During months with large numbers of discarded wings, accumulated wings that had persisted for extended periods and showed signs of degradation (e.g., mould growth) were commonly observed on feces, most of which belonged to *Badamia exclamationis* (Hesperiidae). The number of discarded wings collected on the second day usually decreased markedly (mean = 8.0), whereas the number collected on the third day showed no consistent trend, either increasing, remaining similar to, or decreasing relative to the second day (mean = 7.3) (Table 2).

Species composition

The number of discarded butterfly wings was consistently greater than that of moths in each sampled month, with a clear difference between the two groups (Fig. 1). Of the 1,283 discarded wings collected, 1,066 were from butterflies, 211 were from moths, and 6 were unidentified. Based on the quantitative data from 2015–2018 (n = 1,118), the ratio of butterfly to moth wings was approximately 4.9 to 1 (925 vs. 187) (Table 1).

At least 68 species of Lepidoptera from 12 families were identified, including 41 species of butterflies from four families and 27 species of moths from eight families (Table 3). Among the discarded wings, 1,039 of 1,066 butterfly wings (97.5%) and 135 of 211 moth wings (64.0%) were identified to species level. The butterflies belonged to Nymphalidae (21 species), Hesperiidae (14 species), Pieridae (3 species), and Lycaenidae (3 species). The most abundant species was *B. exclamationis* (Hesperiidae), accounting for 610 discarded wings (47.5%) (Table 3). No discarded wings of Papilionidae were recorded. The moths belonged to Erebidae (14 species), Geometridae (5 species), Noctuidae (3 species), Uraniidae (2 species), Drepanidae (1 species), Crambidae (1 species), and Callidulidae (1 species), while Notodontidae was identified only to family level (Table 3). The most abundant moth species was *Eumelea ludovicata ludovicata* (Geometridae), accounting for 45 discarded wings (3.5%) (Table 3).

Among butterfly families, Hesperiidae (55.3%) and Nymphalidae (25.2%) were the most abundant; and among the moth families Geometridae (5.1%) and Erebidae (4.0%) were the most abundant. Although the methods used to collect discarded wings differed between the two survey periods (2010–2012 and 2015–2018), the overall compositional patterns of discarded wings among families were broadly similar among years within each survey period (Fig. 3). During 2010–2012, the proportion

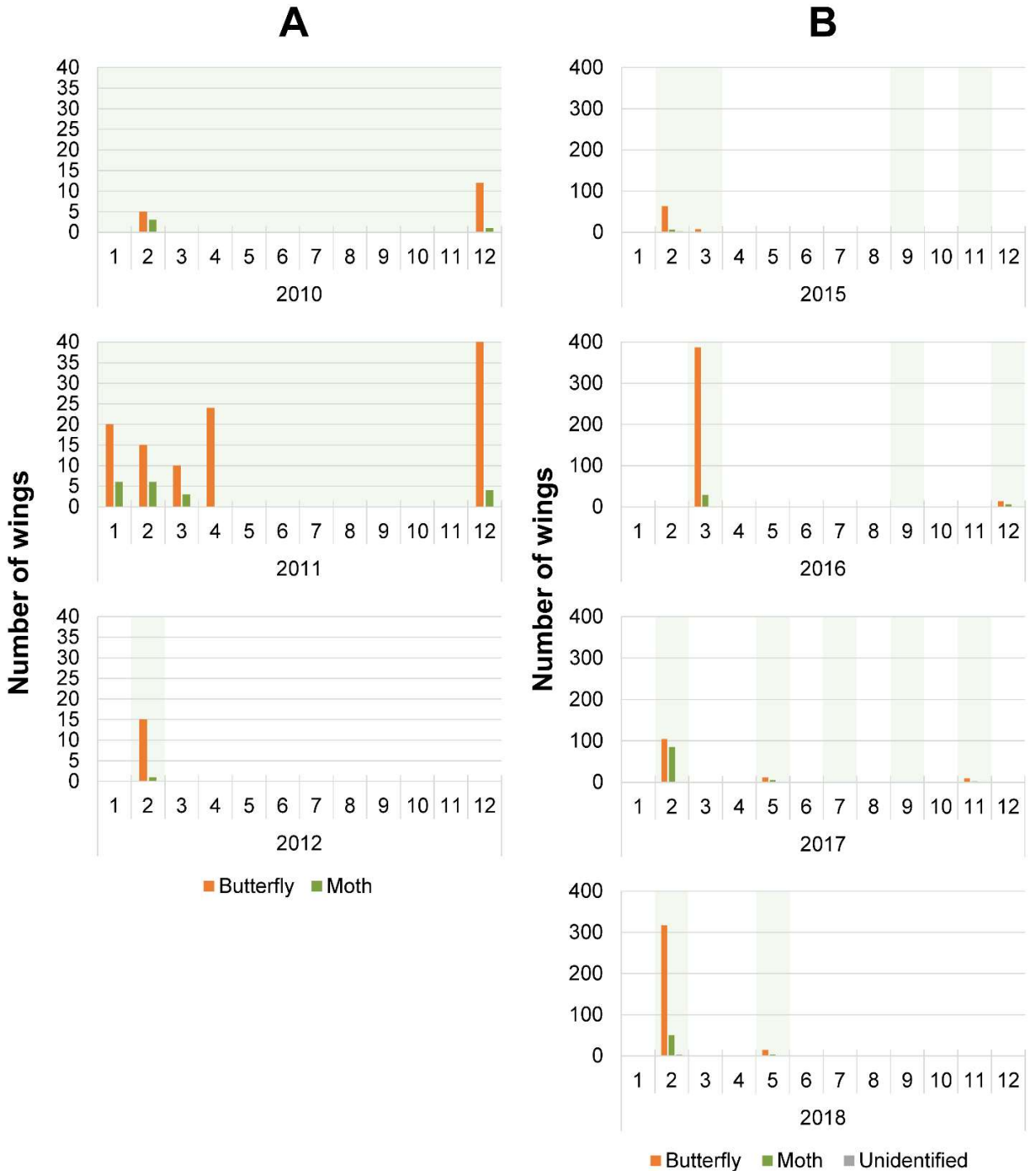

Fig. 1. Monthly distribution of discarded lepidopteran wings collected in Cave B2 from 2010 to 2018. **A.** Collection data for 2010–2012 and **B.** for 2015–2018. Months with a light green background indicate that a survey was conducted, while those with a white background indicate no survey was performed.

of Nymphalidae was higher than or comparable to that of Hesperiidae. In contrast, during 2015–2018, Hesperiidae consistently dominated, except in 2017 when its proportion declined markedly. In the same year, numbers of discarded wings of Geometridae and Erebidae increased (Figs. 1 and 3).

Morphological and ecological traits

In terms of body size, the forewing length of the 41 butterfly species ranged from 14.2 to 36.9 mm, with *Parnara guttata* (Hesperiidae) being the smallest and *Melanitis leda* (Nymphalidae) the largest. The most abundant butterfly species, *B. exclamationis* (Hesperiidae),

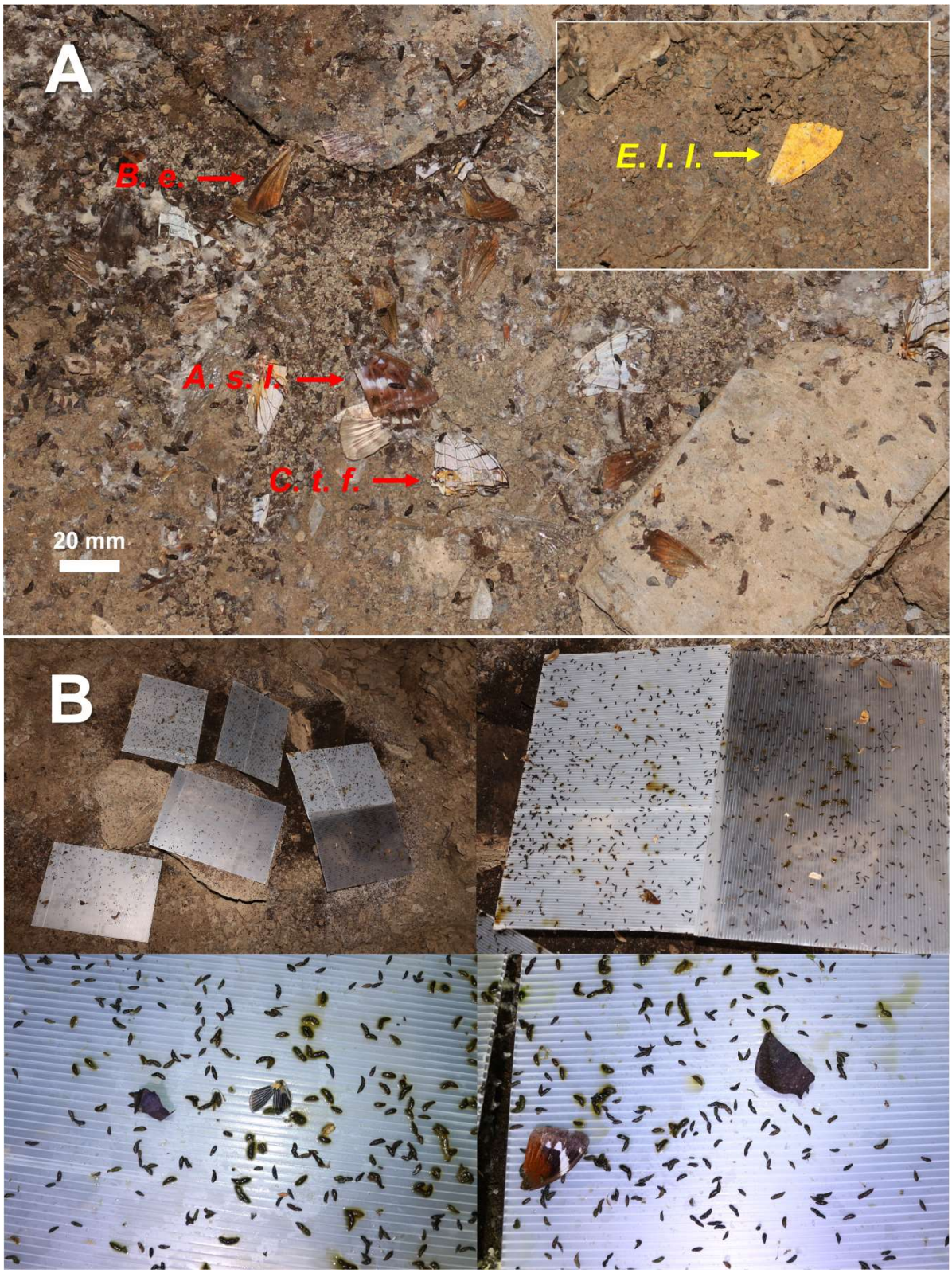

Fig. 2. Discarded lepidopteran wings brought back to Cave B2 by the Formosan tailless leaf-nosed bat (***Coelops frithii formosanus***). **A.** Discarded wings as found on the cave floor. Labeled species include ***Badamia exclamationis*** (*B. e.*), ***Cyrestis thyodamas formosana*** (*C. t. f.*), ***Athyma selenophora laela*** (*A. s. l.*), and ***Eumelea ludovicata ludovicata*** (*E. l. l.*). **B.** Experimental collection using white plastic sheets placed beneath bat roosting sites. Observations the following morning revealed the sheets covered with bat guano and freshly discarded wings from the preceding night's prey.

Table 3. Species list and abundance of discarded lepidopteran wings inside the roosting cave of the Formosan tailless leaf-nosed bat (***Coelops frithii formosanus***). Cave B2 recorded 41 butterfly and 27 moth species.

Family	Subfamily	Species	Cave B2		Forewing length (mm)	Hearing organ
			n	%		
Butterfly						
Hesperiidae	Coeliadinae	*Badamia exclamationis*	610	47.5%	24.8	
		Burara jaina formosana	1	0.1%	22.1	
		Hasora badra	10	0.8%	20.5	
		Hasora chromus	8	0.6%	20.3	
		Hasora taminatus vairacana	48	3.7%	18.8	
	Hesperiinae	*Caltoris ranrunna*	7	0.5%	18.2	
		Notocrypta curvifascia	1	0.1%	19.9	
		Parnara guttata	1	0.1%	14.2	
		Pelopidas agna	3	0.2%	16.9	
		Telicota bambusae horisha	2	0.2%	14.8	
		Telicota ohara formosana	6	0.5%	14.8	
		Telicota sp.	1	0.1%	-	
	Pyrginae	*Seseria formosana*	3	0.2%	18.5	
		Tagiades tethys moori	1	0.1%	17.6	
		Tagiades trebellius martinus	5	0.4%	16.9	
	(Unidentified)	Hesperiidae sp.	2	0.2%	-	
Lycaenidae	Theclinae	*Arhopala bazalus turbata*	1	0.1%	19.4	
		Deudorix epijarbas menesicles	1	0.1%	19.0	
		Mahathala ameria hainani	4	0.3%	18.2	
	(Unidentified)	Lycaenidae sp.	1	0.1%	-	
Nymphalidae	Apaturinae	*Chitoria chrysolora*	10	0.8%	32.7	+
	Cyrestinae	*Cyrestis thyodamas formosana*	75	5.8%	29.6	
	Heliconiinae	*Cupha erymanthis*	5	0.4%	31.5	
	Limenitidinae	*Athyma cama zoroastres*	3	0.2%	30.9	
		Athyma selenophora laela	72	5.6%	31.0	
		Athyma sp.	1	0.1%	-	
		Limenitis asura baelia	2	0.2%	34.3	
		Neptis nata lutatia	5	0.4%	28.5	
		Neptis taiwana	1	0.1%	34.5	
		Neptis sp.	1	0.1%	-	
	Nymphalinae	*Kaniska canace drilon*	4	0.3%	33.3	
		Symbrenthia formosanus	9	0.7%	24.7	
	Satyrinae	*Elymnias hypermnestra hainana*	18	1.4%	36.1	+
		Lethe chandica ratnacri	23	1.8%	33.4	+
		Lethe europa pavida	7	0.5%	34.1	+
		Lethe verma cintamani	1	0.1%	29.2	+
		Melanitis leda	6	0.5%	36.9	+
		Melanitis phedima polishana	42	3.3%	35.9	+
		Melanitis sp.	2	0.2%	-	+
		Mycalesis francisca formosana	13	1.0%	26.1	+
		Mycalesis mucianus zonatus	10	0.8%	25.0	+
		Mycalesis sp.	2	0.2%	-	+
		Neope muirheadii nagasawae	5	0.4%	36.1	+
		Telinga mara	4	0.3%	22.8	+
		Ypthima angustipennis	1	0.1%	26.9	+
		Ypthima sp.	1	0.1%	-	+
Pieridae	Coliadinae	*Eurema blanda arsakia*	7	0.5%	23.1	
		Eurema sp.	16	1.2%	-	
	Pierinae	*Appias albina semperi*	1	0.1%	28.3	
		Leptosia nina niobe	3	0.2%	22.3	
Moth						
Callidulidae	Callidulinae	*Callidula attenuata*	8	0.6%	18.2	
Crambidae	Pyraustinae	*Nevrina procopia*	8	0.6%	18.9	+
	Spilomelinae	*Pleuroptya* sp.	1	0.1%	-	+
	(Unidentified)	Crambidae sp.	1	0.1%	-	+
Drepanidae	Drepaninae	*Neoreta purpureofascia*	2	0.2%	16.6	+
Erebidae	Aganainae	*Mecodina praecipua*	1	0.1%	26.2	+
	Calpinae	*Rusicada* sp.	1	0.1%	-	+
	Erebinae	*Bastilla absentimacula*	3	0.2%	24.9	+
		Bastilla acuta acuta	1	0.1%	25.2	+
		Bastilla arcuata	1	0.1%	24.1	+
		Bastilla simillima	1	0.1%	21.4	+
		Bastilla sp.	1	0.1%	-	+
		Ercheia cyllaria	10	0.8%	25.8	+

		Erebus ephesperis	1	0.1%	50.2	+
		Ericeia inangulata inangulata	5	0.4%	22.6	+
		Ommatophora luminosa	2	0.2%	27.1	+
		Oxyodes scrobiculata	10	0.8%	27.4	+
		Sympis rufibasis	1	0.1%	23.5	+
	Herminiinae	*Bertula parallela*	2	0.2%	22.2	+
		Simplicia bimarginata	1	0.1%	21.1	+
	Hypeninae	*Itmaharela basalis*	6	0.5%	25.2	+
	(Unidentified)	Erebidae sp.	4	0.3%	-	+
Geometridae	Desmobathrinae	*Eumelea ludovicata ludovicata*	45	3.5%	30.9	+
	Ennominae	*Borbacha pardaria*	6	0.5%	23.0	+
		Nothomiza flavicosta	2	0.2%	20.0	+
	Geometrinae	Geometrinae sp.	2	0.2%	-	+
		Hemistola sp.	1	0.1%	-	+
		Herochroma baibarana	2	0.2%	21.5	+
		Herochroma sp.	1	0.1%	-	+
	Larentiinae	*Ecliptopera benigna*	3	0.2%	22.5	+
	(Unidentified)	Geometridae sp.	3	0.2%	-	+
Noctuidae	Noctuinae	*Euplexidia pallidivirens*	5	0.4%	19.6	+
		Mythimna sinuosa	1	0.1%	18.1	+
		Tiracola plagiata	5	0.4%	26.8	+
	(Unidentified)	Noctuidae sp.	1	0.1%	-	+
Notodontidae	(Unidentified)	Notodontidae sp.	7	0.5%	-	+
Uraniidae	Microniinae	*Acropteris leptaliata*	1	0.1%	21.4	+
		Micronia aculeata	2	0.2%	22.8	+
Unidentified moth			53	4.1%	-	
Unidentified Lepidoptera			6	0.5%	-	
Total			**1,283**	**100%**		

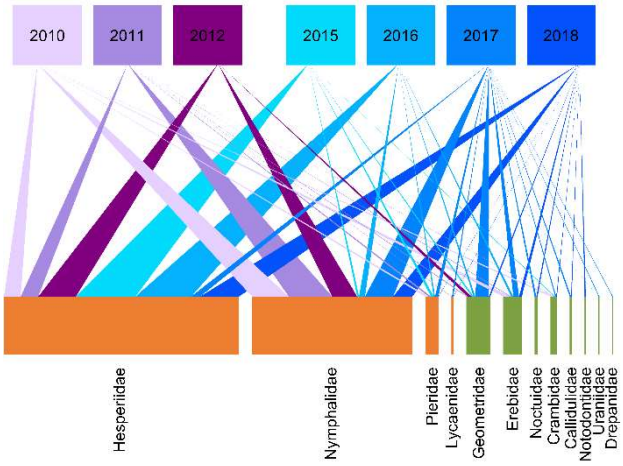

Fig. 3. Bipartite network of discarded lepidopteran wings collected in Cave B2 across different years. The top nodes represent the collection years, categorized by study periods (purple shades: 2010–2012; blue shades: 2015–2018). The bottom nodes represent different families, color-coded by group (orange: butterflies; green: moths). The width of the links indicates the relative proportion of discarded wings for each family in a given year.

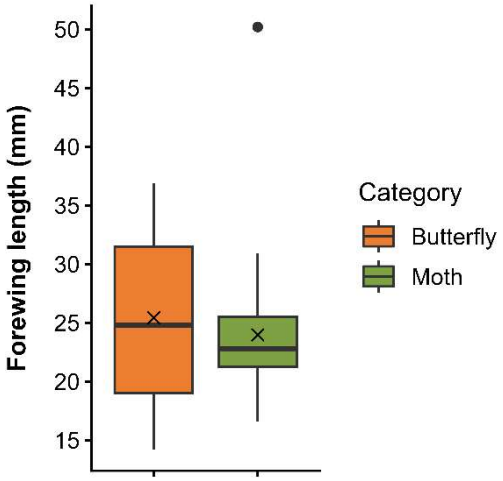

Fig. 4. Boxplots of forewing length distributions based on species list for butterfly and moth wings collected in Cave B2. The y-axis represents forewing length (mm). Orange boxes represent butterflies, and green boxes represent moths. In the plots, "x" denotes the mean, the horizontal line denotes the median, and dots represent outliers.

had a forewing length of 24.8 mm. For moths, the forewing length of the 27 species ranged from 16.6 to 50.2 mm, with *Neoreta purpureofascia* (Drepanidae) being the smallest and *Erebus ephesperis* (Erebidae) the largest. According to the boxplot, *E. ephesperis* represented an extreme outlier, with only a single discarded wing recorded. The species with the second largest forewing length was *E. ludovicata ludovicata* (Geometridae) at 30.9 mm, which was also the most abundant moth species. The range of forewing lengths in butterflies encompassed that of moths (excluding the extreme moth outlier) (Fig. 4).

Regarding auditory traits, all identifiable moth families, except Callidulidae (i.e., *Callidula attenuata*), possess hearing organs. In butterflies, the auditory organ is known as Vogel's organ (VO); species with VO among the discarded wings were restricted to 12 species within the subfamilies Apaturinae and Satyrinae (Nymphalidae) (Table 3).

In terms of ecological traits, most species represented by discarded wings in the cave were diurnal, as no nocturnal butterflies occur in Taiwan. Although moths

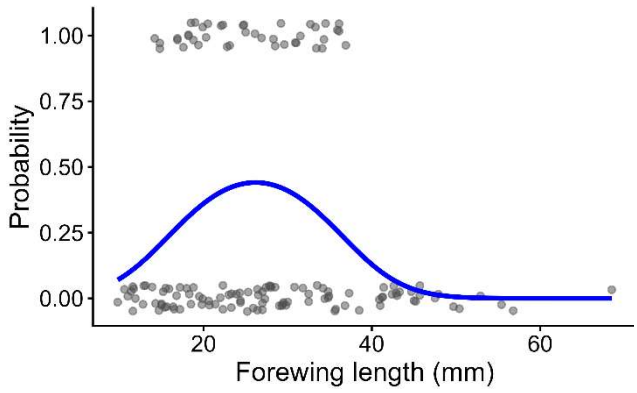

Fig. 5. Effect of butterfly forewing length on the probability of being brought into the cave, fitted with a binary logistic regression model. Gray points represent the original binary data (Y = 1: brought into the cave; Y = 0: not brought). The blue curve shows the predicted probability. The relationship was modeled using a quadratic term.

are predominantly nocturnal, *Eumelea ludovicata ludovicata* (Geometridae) and *Callidula attenuata* (Callidulidae) are diurnal species.

Potential size preference

The binary logistic regression revealed a quadratic relationship between butterfly size and the probability of being brought back to Cave B2, with the probability initially increasing with forewing length before declining beyond an optimal size (forewing length: $B = 0.458 \pm 0.152$ (SE), Wald $\chi^2 = 9.077$, $P = 0.003$; forewing length squared: $B = -0.009 \pm 0.003$ (SE), Wald $\chi^2 = 9.373$, $P = 0.002$) (Fig. 5).

DISCUSSION

The Formosan tailless leaf-nosed bat (*Coelops frithii formosanus*) is to date the first and only bat in Taiwan recorded to prey on diurnal butterflies. Moreover, discarded butterfly wings were clearly more abundant and diverse than those of moths. Based on the discarded-wing data, the extent of butterfly predation by *C. f. formosanus* appears exceptional among bats known to consume butterflies. Long-term observations in the caves of Dongxing Village, Taitung, confirmed that this feeding behavior occurs consistently rather than occasionally. Notably, this foraging behavior has only been recorded in this local population and has not yet been observed elsewhere (Fang and Cheng, 2011), and the underlying causes remain to be investigated.

The occurrence of discarded lepidopteran wings in the cave exhibited a temporal pattern, with discarded wings observed from November to May of the following year, and large numbers recorded in February–March. This pattern indicates that the exploitation of butterflies by *C. f. formosanus* exhibits seasonal characteristics. In addition, limited fecal analyses suggest that this species may also consume a considerable proportion of spiders (Cheng and Tsai, 2009; Fang and Cheng, 2011; Chou *et al*., 2012), indicating that our understanding of its overall diet and ecological requirements remains incomplete.

Although butterflies and spiders differ greatly in taxonomy and ecological habits, both share vulnerability to predation while immobile: butterflies are inactive and roosting at night, whereas spiders are inherently non-volant. Gleaning may have been one of the strategies used to capture lepidopteran prey, particularly diurnal butterflies, as stationary or flightless prey have been interpreted as evidence supporting bat gleaning (e.g., Arlettaz *et al*., 1995; Schulz and Wainer, 1997; Schulz, 2000; Johnston and Fenton, 2001; Chiang, 2006; Geipel *et al*., 2013). However, further evidence is required to understand how *C. f. formosanus* captures nocturnal moths, as nocturnal prey may be taken either at rest or in flight, and bats may employ flexible foraging strategies (Dey and Balakrishnan, 2024).

The interaction between moths' hearing organs and predation pressure from bats is often a major focus of research. Lu (2011) used molecular methods to analyze the lepidopteran diet of the Formosan lesser horseshoe bat (*Rhinolophus monoceros*) and found that 95% of the moth species consumed possessed hearing organs, with 72% belonging to the superfamilies Noctuoidea and Geometroidea. This pattern is comparable to the moth species brought back to the cave by *C. f. formosanus*. The first harmonic of *C. f. formosanus*'s echolocation calls is 90.6 ± 2.0 kHz, and the second harmonic is frequency-modulated from 194 to 113 kHz (Ho *et al*., 2013), frequencies that may exceed the auditory range of many moths (Ter Hofstede and Ratcliffe, 2016).

Echolocation and wing morphology jointly shape the foraging abilities of bats. In addition to producing high-frequency broadband calls, *C. f. formosanus* emits echolocation calls with intensities so low that they are difficult to detect even at close range (<50 cm) (Ho *et al*., 2013). In terms of wing morphology, *C. f. formosanus* exhibits low wing loading and a low aspect ratio (Lai, 2000). High-frequency broadband calls are considered advantageous for detecting small objects and surface textures, whereas low-intensity calls reduce detection range and may require bats to search for objects at close distances (Schnitzler and Kalko, 2001). Bats with low wing loading and low aspect ratio generally fly more slowly but exhibit excellent maneuverability in cluttered environments (Norberg and Rayner, 1987). From the perspectives of echolocation and wing morphology, *C. f. formosanus* exhibits traits consistent with a gleaning foraging strategy; however, the link between these traits and the predation of nocturnal moths remains insufficiently understood.

In addition, passive listening is considered one of the direct lines of evidence for gleaning behavior (Neuweiler, 1990; Holderied *et al*., 2011; Raghuram *et al*., 2015; Dey

and Balakrishnan, 2024), although not all gleaning bat species employ this strategy (Swift, 1998). Bats that use passive listening are generally sensitive to low-frequency sounds produced by prey (Neuweiler, 1990) and often possess large external ears. Whether *C. f. formosanus*, which emits extremely high-frequency echolocation calls, also employs passive listening remains to be investigated.

Based on multiple years of observations of discarded wings, *Badamia exclamationis* (Hesperiidae) was the most abundant species overall. Although discarded wings cannot directly reflect the complete diet composition, *B. exclamationis* appears to be the most representative species in the cave. During 2010–2012, the dominance of Hesperiidae was not evident due to incomplete collection of discarded wings; however, surveys from 2015–2018 showed that, although Hesperiidae generally accounted for a high proportion of discarded wings in most years, interannual variation in overall wing composition was still observed. For example, the total number of discarded wings was relatively low in 2015 and 2017, whereas in 2017 the proportion of Hesperiidae decreased and that of moths increased. These variations may reflect shifts in prey use, although the underlying causes remain unclear.

Bats may preferentially carry larger prey back to their roosts for handling and consumption, and the size of consumed prey may differ from the average availability of resources in the environment (Burford and Lacki, 1998; Lacki and Ladeur, 2001; Dodd and Lacki, 2007; Lacki and Dodd, 2011; Dodd *et al*., 2015). From an energy-gain perspective (Emlen, 1966), selecting larger prey can ensure that the energetic returns from consumption compensate for the costs of flight and searching (Vesterinen *et al*., 2016; Dey and Balakrishnan, 2024). The range of prey body sizes represented in the discarded-wing assemblage in this study may reflect the outcome of *C. f. formosanus* balancing prey size against the associated costs and benefits. Whether factors other than prey size also influence the bats' decisions to carry prey back to the cave remains to be investigated in future studies. In this context, no Papilionidae wings were recorded in this study, which may be related to their relatively large adult body size and reduced vulnerability to predation. In addition, small-sized Papilionidae species in Taiwan, such as *Papilio epycides melanoleucus*, *Graphium eurous asakurae*, and *G. mullah mullah*, have no documented distributions in local survey records from the Taiwan Biodiversity Network (TBN) or in surveys conducted in adjacent regions (Chao and Tang, 2001; Yang and Li, 2005). The butterfly survey data reported by Chao and Tang (2001) and Yang and Li (2005) were used as a regional comparative baseline in this study. Although differences in elevation between their survey sites and our study site introduce some uncertainty, we considered these data appropriate because no butterfly surveys were conducted as part of the present study and these studies represent some of the few sources of data from the surrounding area based on relatively rigorous surveys. Furthermore, these three papilionid species typically overwinter as pupae (Hsu, 2013a), making overlap between adult emergence and the season of discarded wings unlikely.

The discarded wings in the Dongxing Village cave mainly were recorded during colder months, a pattern somewhat similar to the timing of butterfly predation by the brown long-eared bat (*Plecotus auritus*) and the greater horseshoe bat (*Rhinolophus ferrumequinum*) (Roer, 1969; Jones, 1990). The bat cave was located in a forest near a stream valley and may therefore support abundant butterfly resources. Based on informal field observations, considerable numbers of butterflies could still be seen flying during daytime in winter, and a single instance of danaine butterflies clustering on trees was observed during cold weather. The area may therefore provide suitable overwintering conditions for butterflies. We tentatively observed that the number of wings collected each day seemed to vary inversely with the preceding night's temperature. Gleaning bats exhibit lower temperature dependence in their foraging activity (Swift, 1998; Andreas *et al*., 2012; Hope *et al*., 2014); this is because they can still exploit insects that are unable to fly at low temperatures (Rydell, 1989). Because butterflies are inactive at night, their availability is theoretically independent of ambient temperature. As for moths, their response to ambient temperature in Taiwan's tropical and subtropical climate remains to be explored and may differ from the patterns in temperate regions. However, with respect to the bats themselves, *C. f. formosanus* does not hibernate or enter torpor (Fang and Cheng, 2011) and will even continue to forage during cold waves. Due to the limited number of consecutive days of collection, whether temperature influences the behavior of carrying prey back to the cave remains unclear, and more intensive survey effort would be needed to address this question.

Overall, this study shows that *C. f. formosanus* consistently exploits diurnal butterflies, revealing a pattern of use in terms of temporal distribution and species composition. However, these conclusions are based mainly on discarded wings from the cave, which may not fully represent the species' use of lepidopteran resources. Discrepancies may exist between the composition of discarded wings and actual diet (Dodd *et al*., 2015), and the relationship between diet composition and environmental resources requires rigorous verification. In addition, this behavior has only been observed in a single local population, and whether it exhibits regional or population-level variation remains to be clarified. With advances in molecular techniques, species identification from feces has become feasible (Zeale *et al*., 2011), and future studies combining molecular diet analysis will help provide a more complete understanding of *C. f. formosanus*'s use of lepidopteran resources.

CONCLUSIONS

This study provides the first evidence that the Formosan tailless leaf-nosed bat (*Coelops frithii formosanus*) consistently brings a highly diverse assemblage of diurnal butterflies back to the cave. Both the species richness and abundance of butterflies were greater than those of moths, suggesting that *C. f. formosanus* may employ a gleaning strategy for certain lepidopteran taxa. Discarded lepidopteran wings in the cave occurred primarily during winter, suggesting that the diet of *C. f. formosanus* population in this area may exhibit seasonal variation.

Because caves are limited resources for cave-roosting bats, lepidopteran prey available in this area may represent an important food resource for *C. f. formosanus*. Furthermore, because the unique behavior of butterfly predation by *C. f. formosanus* has so far been documented only in this single population, comprehensive dietary studies, particularly those using molecular approaches, are needed. Dietary analyses can not only provide a more complete understanding of lepidopteran resource use by the Formosan tailless leaf-nosed bat but also provide essential ecological information for the conservation of this endemic and nationally vulnerable bat species in Taiwan.

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