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Morphological Variation in the Dusky Fruit Bat, *Penthetor lucasi,* in Sarawak, Malaysia

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ABSTRACT.– **Morphological analysis of 70 adult individuals of the dusky fruit bat, *Penthetor lucasi,* was performed using 15 external characters and 18 craniodental characters. Multiple regression and discriminant function analysis (DFA) were applied to test the effects of sex, location and interaction between individuals in the study, and to determine and identify characters which are efficient in differentiating individuals among populations, respectively. Most characters were significantly affected by sex, locality and their interactions. Thus, separate analyses were done for both sexes. The fourth digit metacarpal length (D4MCL) and bulla length (BL) of males, and the hind foot (HF) and dental length (DL) of females, were suggested as the best predictors for the external and craniodental characters, respectively, in differentiating *P. lucasi* from different localities. These findings establish the morphological morphological variation between three geographically separate populations of *P. lucasi* within Sarawak. It is suggested that different ecological forces between populations, such as breeding, foraging behaviour, crowding effects and resource availability, could have been the moulding factors behind the observed morphological variations in the different *P. lucasi* populations.**

KEY WORDS: ***Penthetor lucasi,* Morphological, Discriminant function analysis**

INTRODUCTION

The Indo-Malayan region is of great interest to the evolutionary biologists and systematists in terms of its high biodiversity (Maharadatunkamsi et al., 2003). Within this region, Borneo is the third largest island in the world and is well-known for both its biodiversity richness and the Pleistocene episode, making it one of the most studied areas for its flora and fauna (Abdullah, 2003; MacKinnon et al., 1996). Nevertheless, new unidentified species or subspecies are continuously emerging from the island especially for mammals (Abdullah, 2003; Achmadi, 2010; Faisal, 2008; Hasan, 2009; Jayaraj, 2008).

Borneo has at least 17 species of megachiropterans, including the dusky fruit bat, *Penthetor lucasi*. Being the only species assigned under the genus *Penthetor,* this species has gone through tentative taxonomic status from *Cynopterus* (*Ptenochirus*) *lucasi* Trouessart (1897) to *Ptenochirus lucasi* Trouessart (1904), which was later placed in the genus *Penthetor* by Andersen (1912). This bat is medium sized, with dark grey-brown upperparts and pale buffy underparts. The weight (WT) is around 30 to 40 g and they have large eyes. The forearm length (FA) ranges from between 57 to 62 mm, while its tail is eight to 13 mm in length (Payne et al., 1985). *P. lucasi* have a pair of lower incisors with the outer upper incisors shorter than the inner pair. It is widely distributed throughout southern Thailand, peninsular Malaysia, Riau Archipelago, Borneo (Abdullah et al.,

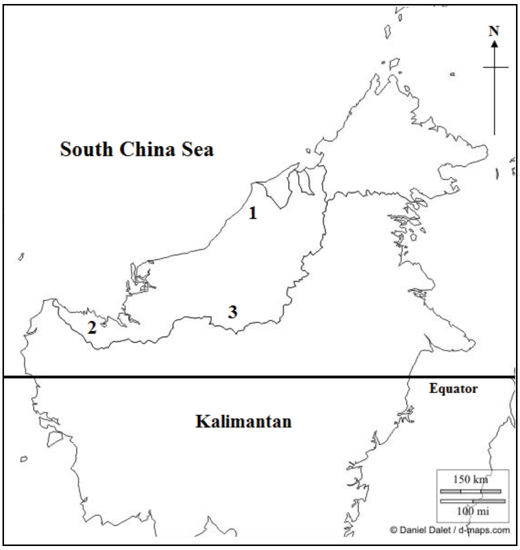

FIGURE 1. Map show the type locality of *P. lucasi* specimens used in the analyses. 1, Miri; 2, Kuching; 3, Sri Aman. Map modified from Dalet (2010).

2007; Corbet and Hill, 1992; Francis, 2008; Payne et al., 1985) and Sumatra (Maryanto, 2004). Several studies on *P. lucasi* from Borneo have investigated their reproduction, population size and sexual dimorphism (Barapoi, 2004; Kofron, 2007; Wilhelmina, 2005).

Recently, the use of morphological characters in describing species boundaries has been greatly aided by the implementation of multivariate statistics (Jayaraj, 2008). Studies on the intra- and the inter-specific morphological variation of the Indo-Malayan bats have been well-illustrated by various authors (Abdullah, 2003; Abdullah and Jayaraj, 2006; Corbet and Hill, 1992; Faisal, 2008; Hasan, 2009; Jayaraj, 2008; Kitchener and Maharadatunkamsi, 1991, 1996; Kitchener et al., 1993a, 1993b; Kitchener and Maryanto, 1993; Kitchener et al., 1995; Maharadatunkamsi and Kitchener, 1997; Sazali, 2008; Sazali et al., 2008). These studies, through morphological analysis based approaches, have successfully included descriptions of new species, subspecies and revealed cryptic species within bat populations in this region.

Indeed, Maryanto (2004) used discriminant function analysis (DFA) to differentiate two populations of *P. lucasi* from Sumatra and Kalimantan, Indonesia. Their findings confirmed that there are currently two subspecies of *P. lucasi* from Indonesia, namely *P. lucasi lucasi* (Kalimantan) and *P. lucasi suyantoi* (Sumatra). Despite this, there is no other published study focusing on morphological variation in *P. lucasi* populations, especially in Malaysia.

Thus, the aim of this study was to investigate the morphological variations that exist among populations within Sarawak with the implementation of multivariate statistics. It is hypothesised that there are no significant differences in the external, skull and dentary (craniodental) characters of *P. lucasi* from different populations within the Sarawak region.

MATERIALS AND METHODS

A total of 70 adult specimens of *P. lucasi* were used in this study that consisted of 38 individuals from Kuching (14 males and 24 females), 25 individuals from Miri (16 males and nine females) and seven individuals from Sri Aman (two males and five females) (Fig. 1; Table 1; Abdullah et al. 2010). The adult specimens were determined following Kunz (1988) by examination of the epiphyseal-diaphyseal fusion on the third, fourth and fifth metacarpals.

Skull extraction and measurements

A total of 33 body, skull and dental measurements of adults, following Kitchener et al. (1995) and Jayaraj (2008),

TABLE 1. List of the samples of *P. lucasi* used in the morphological analysis.

#	Field No.	Sex	Code	Locality	Habitat	Remark
1	MZU/M/02120	m	1	Niah NP, Miri	LF	
2	MZU/M/02121	m	1	Niah NP, Miri	LF	
3	MZU/M/02124	m	1	Niah NP, Miri	LF	
4	MZU/M/02127	m	1	Niah NP, Miri	LF	
5	MZU/M/02130	m	1	Niah NP, Miri	LF	
6	MZU/M/02153	m	1	Niah NP, Miri	LF	
7	MZU/M/02154	m	1	Niah NP, Miri	LF	
8	MZU/M/02167	m	1	Niah NP, Miri	LF	
9	MZU/M/02168	m	1	Niah NP, Miri	LF	
10	MZU/M/02169	m	1	Niah NP, Miri	LF	
11	TK152468	m	1	Niah NP, Miri	LF	
12	TK152480	m	1	Niah NP, Miri	LF	
13	TK152481	m	1	Niah NP, Miri	LF	
14	TK152484	m	1	Niah NP, Miri	LF	
15	TK152953	m	1	Niah NP, Miri	LF	
16	TK152954	m	1	Niah NP, Miri	LF	
17	MZU/M/00568	m	2	Mount Penrissen, Kuching	MF	
18	MZU/M/00570	m	2	Mount Penrissen, Kuching,	MF	
19	MZU/M/02239	m	2	Padawan, Kuching	LF	
20	MZU/M/02208	m	2	Wind Cave NR, Kuching	LF	
21	MZU/M/02209	m	2	Wind Cave NR, Kuching	SF	
22	MZU/M/02213	m	2	Wind Cave NR, Kuching	LF	
23	MZU/M/02214	m	2	Wind Cave NR, Kuching	SF	
24	MZU/M/02215	m	2	Wind Cave NR, Kuching	LF	
25	MZU/M/02216	m	2	Wind Cave NR, Kuching	LF	
26	MZU/M/02217	m	2	Wind Cave NR, Kuching	LF	
27	MZU/M/02235	m	2	Wind Cave NR, Kuching	LF	
28	MZU/M/02236	m	2	Wind Cave NR, Kuching	LF	
29	MZU/M/02237	m	2	Wind Cave NR, Kuching	LF	
30	MZU/M/02238	m	2	Wind Cave NR, Kuching	LF	
31	MZU/M/01645	m	3	Batang Ai NP, Sri Aman	LDF	
32	MZU/M/01191	m	3	Batang Ai NP, Sri Aman	LDF	Abdullah et al., 2010
33	MZU/M/01192	f	3	Batang Ai NP, Sri Aman	LDF	Abdullah et al., 2010
34	MZU/M/01193	f	3	Batang Ai NP, Sri Aman	LDF	Abdullah et al., 2010
35	MZU/M/01190	f	3	Batang Ai NP, Sri Aman	LDF	Abdullah et al., 2010
36	MZU/M/01194	f	3	Batang Ai NP, Sri Aman	LDF	Abdullah et al., 2010
37	MZU/M/01195	f	3	Batang Ai NP, Sri Aman	LDF	Abdullah et al., 2010
38	MZU/M/02245	f	2	Bako NP, Kuching	MDF	
39	MZU/M/00715	f	2	Jambusan Cave, Kuching	LF	
40	MZU/M/00714	f	2	Jambusan Cave, Kuching	LF	
41	MZU/M/01712	f	2	Kubah NP, Kuching	MDF	
42	MZU/M/01715	f	2	Kubah NP, Kuching	MDF	
43	MZU/M/01721	f	2	Kubah NP, Kuching	MDF	
44	MZU/M/01786	f	2	Kubah NP, Kuching	MDF	
45	MZU/M/01683	f	1	Lambir NP, Miri	MDF	
46	MZU/M/01684	f	1	Lambir NP, Miri	MDF	
47	MZU/M/01686	f	1	Lambir NP, Miri	MDF	
48	TK152463	f	1	Niah NP, Miri	LF	
47	TK152470	f	1	Niah NP, Miri	LF	
50	TK152473	f	1	Niah NP, Miri	LF	

TABLE 1. Continued.

#	Field No.	Sex	Code	Locality	Habitat	Remark
51	TK152478	f	1	Niah NP, Miri	LF	
52	TK152479	f	1	Niah NP, Miri	LF	
53	TK152956	f	1	Niah NP, Miri	LF	
54	MZU/M/00567	f	2	Mount Penrissen, Kuching	LF	
55	MZU/M/00569	f	2	Mount Penrissen, Kuching	LF	
56	MZU/M/02240	f	2	Padawan, Kuching	LF	
57	MZU/M/02246	f	2	Padawan, Kuching	LF	
58	MZU/M/02207	f	2	Wind Cave NR, Kuching	LF	
59	MZU/M/02210	f	2	Wind Cave NR, Kuching	LF	
60	MZU/M/02211	f	2	Wind Cave NR, Kuching	LF	
61	MZU/M/02212	f	2	Wind Cave NR, Kuching	LF	
62	MZU/M/02222	f	2	Wind Cave NR, Kuching	SF	
63	MZU/M/02223	f	2	Wind Cave NR, Kuching	SF	
64	MZU/M/02225	f	2	Wind Cave NR, Kuching	SF	
65	MZU/M/02227	f	2	Wind Cave NR, Kuching	SF	
66	MZU/M/02228	f	2	Wind Cave NR, Kuching	SF	
67	MZU/M/02232	f	2	Wind Cave NR, Kuching	SF	
68	MZU/M/02233	f	2	Wind Cave NR, Kuching	LF	
69	MZU/M/02247	f	2	Bako NP, Kuching	MDF	
70	MZU/M/02248	f	2	Bako NP, Kuching	MDF	

NP = National Park; NR = Nature Reserve; m = male; f = female; LF = limestone forest; LDF = lowland dipterocarp forest; MF = montane forest; MDF = mixed dipterocarp forest; SF = secondary forest.

were subjected for morphological analyses. Fifteen external body measurements, made using a Mitutoyo digital caliper, were recorded as follows; FA, ear length (E), tibia length (TB), hind foot length (HF), tail to ventral length (TVL), second (D2MCL) and third digit metacarpal length (D3MCL), third digit first (D3P1L) and second phalanx length (D3P2L), fourth digit metacarpal length (D4MCL), fourth digit first (D4P1L) and second phalanx length (D4P2L), fifth digit metacarpal length (D5MCL), fifth digit first (D5P1L) and second phalanx length (D5P2L) (Fig. 2).

The skulls of individuals were extracted according to Nagorsen and Peterson (1980). Twelve skull and six dental characters were measured using a Mitutoyo digital caliper. The skull characters measured were the greatest skull length (GSL), interorbital width (IOW), postorbital width (POW), cranial width (CW), mastoid width (MW), zygomatic width (ZW), post palatal length (PPL), palatal length (PL), distance between cochleae (DBC), bulla length (BL), greatest basial pit length (GBPL) and the dentary length (DL). As for the dental measurements, these were the canine tooth basal width (C1BW), breadth across both canine outside surfaces (C1C1B), breadth across both third molar teeth outside surfaces (M3M3B), canine molar length or maxillary tooth row length (C1M3L), second molar tooth crown length (M2L) and the second molar tooth crown width (M2W) (Fig. 3).

Morphological analysis

Multiple regression analysis.– Multiple regression analysis was done to test on the main effect of sex, location and their

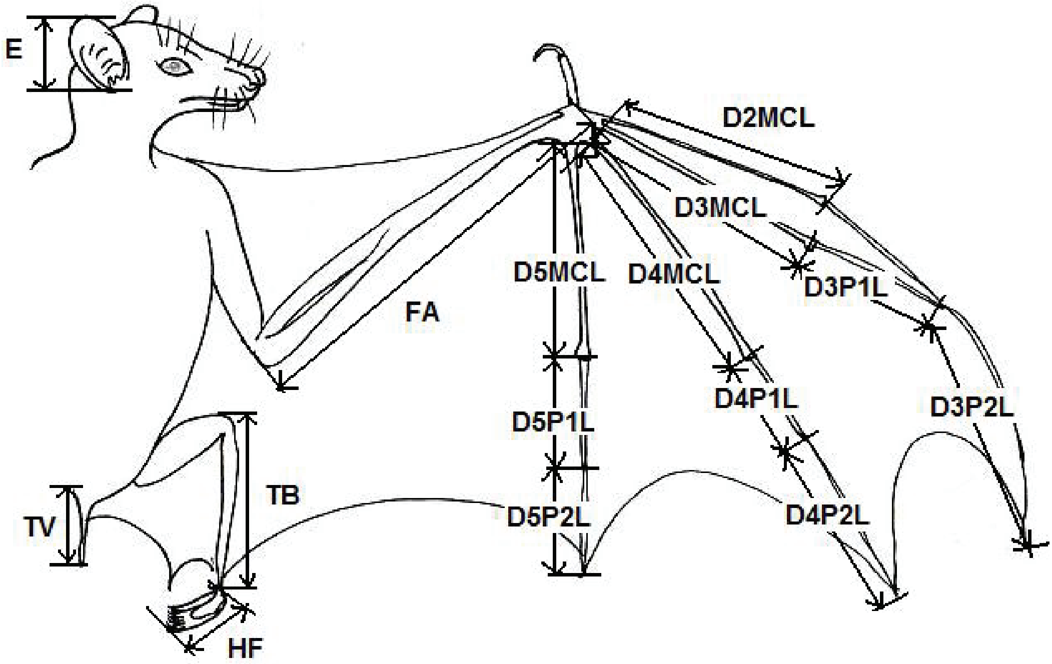

FIGURE 2. Fifteen measurements of external characters of *P. lucasi* were used. Figure is not to scale. Abbreviations are as in the text.

interaction and was performed using the Statistical Package for Social Sciences (SPSS version 15.0), utilizing a full factorial univariate model with Type III sum of squares. F values are presented for the basic effects and the interactions. Confidence intervals of 95%, and the significant value were set to reject the hypothesis that variables are not affected by sex were $0.05 > P > 0.01$, $0.01 > P > 0.001$ and $P > 0.001$ (Maryanto, 2004).

Discriminant function analysis (DFA) .– Multivariate statistics was implemented using stepwise discriminant function analysis with graphical representation from canonical variate analysis (Manly, 1994). This analysis was done to determine and identify characters that are efficient in differentiating among populations with overlapping measurements using SPSS (version 15.0). The Wilk's lambda was used with the probability of $0.10 < P < 0.05$. Variables were classified with the prior probabilities of equal groups and a within-group covariance matrix was used. The DFA analysis was run for all craniodental measurements but with males and females analyzed separately. The DFA for the external characters were also done separately from other characters. The DFA was carried out to analyze any morphological differences between the three sampled populations of Sarawak, that is from Miri (Northeastern), Sri Aman (Central) and Kuching (Southwestern).

RESULT

Descriptive statistics

The mean, standard deviation and range (minimum and maximum) of measurement values along with the samples sizes for the 15 external and 18 craniodental characters

TABLE 2. Summary of the external and craniodental character measurements (mm) of *P. lucasi* analysed in this study, shown as the mean ± standard deviation (range).

Character	Kuching		Miri		Sri Aman	
	Male (n = 14)	Female (n = 24)	Male (n = 16)	Female (n = 9)	Male (n = 2)	Female (n = 5)
External						
FA	61.04 ± 1.25 (59.09 - 63.28)	60.77 ± 1.40 (58.32 - 63.67)	61.26 ± 0.67 (60.24 - 62.85)	60.76 ± 1.57 (58.61 - 62.80)	59.63 ± 0.46 (59.30 - 59.95)	60.63 ± 1.91 (58.86 - 62.83)
E	14.24 ± 0.40 (13.46 - 14.84)	14.88 ± 0.74 (13.51 - 15.91)	14.38 ± 0.68 (13.41 -15.31)	14.21 ± 1.17 (11.77 - 15.55)	15.54 ± 0.09 (15.47 - 15.60)	15.17 ± 0.36 (14.71 - 15.51)
TB	29.21 ± 0.76 (28.1 - 30.63)	28.72 ± 1.34 (26.3 - 30.83)	29.51 ± 0.68 (28.31 - 30.70)	29.00 ± 1.26 (27.65 - 31.95)	28.28 ± 0.21 (28.13 - 28.43)	27.95 ± 1.25 (26.70 - 29.70)
HF	12.28 ± 0.72 (11.36 - 13.91)	12.39 ± 0.67 (10.98 - 13.47)	11.87 ± 0.79 (10.44 - 13.05)	12.11 ± 1.26 (10.26 - 13.75)	11.68 ± 0.16 (11.57 - 11.79)	11.49 ± 0.19 (11.36 - 11.79)
TV	12.12 ± 0.74 (10.78 - 13.52)	11.54 ± 0.85 (9.03 - 12.54)	11.57 ± 1.30 (9.71 - 13.88)	11.14 ± 1.06 (9.34 - 12.64)	10.74 ± 0.30 (10.53 - 10.95)	11.78 ± 0.79 (10.82 - 12.88)
D2MCL	37.09 ± 0.91 (35.45 - 38.29)	37.13 ± 1.41 (35.41 - 40.01)	37.63 ± 1.78 (34.69 - 40.76)	36.74 ± 1.82 (34.05 - 39.44)	37.79 ± 1.34 (36.84 - 38.74)	37.04 ± 2.29 (34.66 - 40.41)
D3MCL	41.49 ± 0.95 (40.41 - 43.64)	41.73 ± 1.27 (39.35 - 44.00)	41.81 ± 1.69 (38.72 - 44.57)	41.48 ± 1.79 (38.13 - 43.49)	39.59 ± 0.14 (39.49 - 39.69)	41.11 ± 2.39 (38.65 - 44.39)
D3P1L	26.61 ± 1.008 (24.95 - 28.57)	26.20 ± 1.314 (23.66 - 28.25)	26.72 ± 0.99 (24.57 - 28.66)	26.37 ± 1.05 (24.83 - 27.72)	25.12 ± 0.66 (24.65 - 25.59)	25.57 ± 0.63 (24.95 - 26.32)
D3P2L	36.59 ± 1.29 (34.5 - 38.88)	36.27 ± 1.729 (33.12 - 40.08)	36.42 ± 1.11 (34.68 - 38.37)	36.62 ± 1.50 (35.08 - 40.01)	35.42 ± 0.21 (35.27 - 35.57)	34.88 ± 2.11 (32.32 - 37.07)
D4MCL	39.06 ± 0.80 (38.01 - 40.61)	39.08 ± 1.318 (36.76 - 41.47)	39.71 ± 1.69 (36.61 - 42.26)	39.27 ± 1.55 (37.56 - 41.92)	37.36 ± 0.51 (37.00 - 37.72)	38.87 ± 1.96 (36.09 - 41.34)
D4P1L	21.08 ± 1.04 (19.26 - 23.01)	20.97 ± 0.97 (19.48 - 22.61)	21.39 ± 0.61 (20.38 - 23.04)	20.95 ± 0.63 (19.71 - 21.77)	19.11 ± 0.16 (18.99 - 19.22)	19.64 ± 0.31 (19.20 - 19.97)
D4P2L	24.05 ± 1.11 (22.13 - 26.15)	23.74 ± 0.97 (21.25 - 24.79)	24.20 ± 0.75 (22.52 - 25.76)	23.50 ± 1.033 (22.35 - 25.56)	23.17 ± 0.20 (23.03 - 23.31)	22.90 ± 1.88 (20.55 - 25.56)
D5MCL	39.54 ± 0.89 (37.30 - 40.68)	39.54 ± 1.25 (37.97 - 41.96)	40.15 ± 1.33 (37.94 - 43.09)	39.68 ± 1.86 (37.59 - 42.32)	38.77 ± 0.73 (38.25 - 39.28)	39.40 ± 2.24 (36.59 - 42.56)
D5P1L	17.84 ± 0.84 (16.51 - 18.84)	17.24 ± 0.87 (15.64 - 18.90)	17.80 ± 0.77 (16.15 - 19.07)	17.56 ± 0.94 (15.67 - 18.88)	16.00 ± 0.55 (15.61 - 16.39)	16.89 ± 0.77 (16.09 - 17.81)
D5P2L	19.68 ± 0.88 (18.24 - 21.12)	19.27 ± 1.15 (16.67 - 20.78)	19.96 ± 0.83 (18.61 - 21.30)	19.47 ± 1.71 (16.96 - 22.62)	19.27 ± 0.80 (18.70 - 19.83)	19.41 ± 1.76 (18.03 - 22.08)
Cranial						
GSL	29.63 ± 0.55 (28.65 - 30.45)	28.78 ± 0.62 (27.61 - 30.06)	29.18 ± 0.77 (27.97 - 30.54)	28.41 ± 0.94 (27.00 - 29.70)	29.41 ± 0.69 (28.92 - 29.89)	28.69 ± 0.39 (28.04 - 29.04)
IOW	5.79 ± 0.12 (5.65 – 6.03)	5.68 ± 0.28 (5.10 - 6.14)	5.90 ± 0.28 (5.42 - 6.30)	5.87 ± 0.44 (5.44 - 6.64)	5.61 ± 0.45 (5.29 - 5.92)	5.55 ± 0.23 (5.20 - 5.78)
POW	6.35 ± 0.32 (5.81 - 6.97)	6.45 ± 0.38 (5.69 - 7.09)	6.34 ± 0.41 (5.68 - 7.30)	6.68 ± 0.43 (6.10 - 7.53)	6.09 ± 0.01 (6.08 - 6.10)	6.15 ± 0.25 (5.80 - 6.44)
CW	12.63 ± 0.18 (12.33 - 12.88)	12.71 ± 0.32 (12.09 - 13.12)	12.85 ± 0.33 (12.29 - 13.50)	12.71 ± 0.40 (12.09 - 13.52)	12.39 ± 0.26 (12.20 - 12.57)	12.70 ± 0.15 (12.56 - 12.87)
MW	12.00 ± 0.39 (11.29 - 12.49)	11.83 ± 0.33 (11.23 - 12.31)	11.79 ± 0.46 (10.71 - 12.76)	11.76 ± 0.38 (11.20 - 12.40)	11.36 ± 0.12 (11.27 - 11.87)	11.43 ± 0.25 (11.08 - 11.77)
ZW	13.09 ± 0.27 (12.68 - 13.40)	13.06 ± 0.39 (12.28 - 13.79)	13.19 ± 0.26 (12.78 - 13.80)	13.07 ± 0.38 (12.55 - 13.92)	13.10 ± 0.43 (12.75 - 13.40)	13.51 ± 0.40 (13.07 - 13.93)
PL	14.88 ± 0.36 (14.36 - 15.51)	14.39 ± 0.49 (13.32 - 15.25)	14.71 ± 0.62 (13.37 - 15.52)	14.27 ± 0.28 (13.84 - 14.70)	14.85 ± 0.01 (14.71 - 14.86)	14.41 ± 0.23 (14.20 - 14.67)
PPL	11.37 ± 0.31 (10.98 - 12.00)	11.09 ± 0.53 (10.27 - 12.09)	11.17 ± 0.41 (10.26 - 12.10)	10.97 ± 0.57 (10.12 - 11.76)	11.11 ± 0.57 (10.70 - 11.60)	10.69 ± 0.27 (10.33 - 10.97)

TABLE 2. Continued.

DBC	5.12 ± 0.32	4.99 ± 0.25	5.07 ± 0.19	5.08 ± 0.10	5.13 ± 0.14	5.22 ± 0.08
	(4.53 - 5.56)	(4.43 - 5.40)	(4.71 - 5.37)	(4.91 - 5.20)	(4.66 - 5.23)	(5.15 - 5.31)
BL	3.22 ± 0.10	3.22 ± 0.15	3.20 ± 0.13	3.17 ± 0.13	3.38 ± 0.38	3.11 ± 0.09
	(3.05 - 3.38)	(3.00 - 3.58)	(3.01 - 3.50)	(2.98 - 3.42)	(3.11 - 3.65)	(2.98 - 3.23)
GBPL	9.14 ± 0.29	8.83 ± 0.39	8.90 ± 0.37	8.79 ± 0.48	8.29 ± 0.13	8.62 ± 0.23
	(8.68 - 9.50)	(8.02 - 9.53)	(8.20 - 9.43)	(8.00 - 9.45)	(8.20 - 9.52)	(8.41 - 8.99)
DL	20.21 ± 0.43	19.86 ± 0.47	20.11 ± 0.63	19.61 ± 0.71	19.75 ± 0.90	19.95 ± 0.35
	(19.61 - 21.05)	(19.16 - 20.64)	(19.30 - 21.36)	(18.65 - 20.63)	(19.11 - 20.38)	(19.60 - 20.42)
Dental						
C1BW	1.73 ± 0.076	1.69 ± 0.10	1.78 ± 0.096	1.70 ± 0.08	1.69 ± 0.01	1.74 ± 0.03
	(1.64 - 1.88)	(1.48 - 1.88)	(1.54 - 1.97)	(1.61 - 1.84)	(1.63 - 1.69)	(1.70 - 1.77)
C1C1B	5.53 ± 0.19	5.46 ± 0.21	5.67 ± 0.19	5.50 ± 0.27	5.47 ± 0.31	5.45 ± 0.21
	(5.16 - 5.84)	(5.00 - 5.73)	(5.32 - 5.90)	(5.18 - 5.85)	(5.25 - 5.69)	(5.24 - 5.78)
M3M3B	8.77 ± 0.32	8.75 ± 0.35	8.90 ± 0.30	8.73 ± 0.39	9.05 ± 0.30	8.70 ± 0.11
	(8.11 - 9.22)	(7.89 - 9.33)	(8.35 - 9.32)	(8.04 - 9.37)	(8.83 - 9.26)	(8.57 - 8.83)
C1M3L	7.79 ± 0.26	7.73 ± 0.24	7.77 ± 0.25	7.67 ± 0.36	7.88 ± 0.54	7.52 ± 0.24
	(7.37 - 8.10)	(7.12 - 8.19)	(7.37 - 8.21)	(7.06 - 8.29)	(7.50 - 8.26)	(7.24 - 7.79)
M2L	1.69 ± 0.13	1.60 ± 0.21	1.70 ± 0.12	1.67 ± 0.14	1.87 ± 0.11	1.71 ± 0.07
	(1.52 - 1.98)	(1.02 - 1.97)	(1.48 - 1.91)	(1.48 - 1.87)	(1.62 - 1.94)	(1.60 - 1.78)
M2W	2.08 ± 0.10	2.04 ± 0.12	2.05 ± 0.10	2.00 ± 0.17	2.13 ± 0.16	1.90 ± 0.03
	(1.78 - 2.21)	(1.76 - 2.26)	(1.88 - 2.22)	(1.66 - 2.16)	(2.01 - 2.24)	(1.87 - 1.95)

are shown in Table 2. All three populations (Miri, Kuching and Sri Aman) are separated accordingly under the multivariate analysis with very little overlap being observed between the Miri and Kuching populations. However, the Miri and Kuching populations are generally more similar to each other, but both are significantly different from the Sri Aman population. Observations from the morphological measurements suggest the specimens from the Sri Aman population are relatively small in most characters measured compared to the specimens from the Kuching and Miri populations. Individuals of the Miri population tended to have the largest external attributes, based on the mean values, in general. This is especially the case for the following characters in the male population; FA, TB, D3MCL, D3P1L, D4MCL, D4P1L, D4P2L, D5MCL and D5P2L; and for the following characters in the female population; TB, D3P1L, D3P2L, D4MCL, D5MCL and D5P2L. Meanwhile, the Kuching population generally showed the largest value for all the craniodental characters measured, namely GSL, POW, MW, PL, PPL, GBPL and DL for the male population; and GSL, MW, PPL, BL, GBPL, M3M3B, C1M3L and M2W for the female population. Thus, the Sri Aman population was the smallest of the three populations, with the male population showed larger values in several external and craniodental characters, namely E, D2MCL, DBC, DL, M3M3B, C1MCL, M2L and M2W; while the female population showed larger value in E, TV, ZW, PL, DBC, DL, C1BW and M2L characters.

Multiple regression analysis

Based on the multiple regression analysis, most characters were significantly associated with sex and locality. Eight characters (TB, D5P1L, GSL, PL, DL, C1BW and C1C1B) showed significant sexual dimorphism (Table 3), whilst eight (E, TB, HF, D4P1L, D5P1L, IOW, MW and GBPL) were significantly effected by the locality. Finally, 12 characters, namely E,

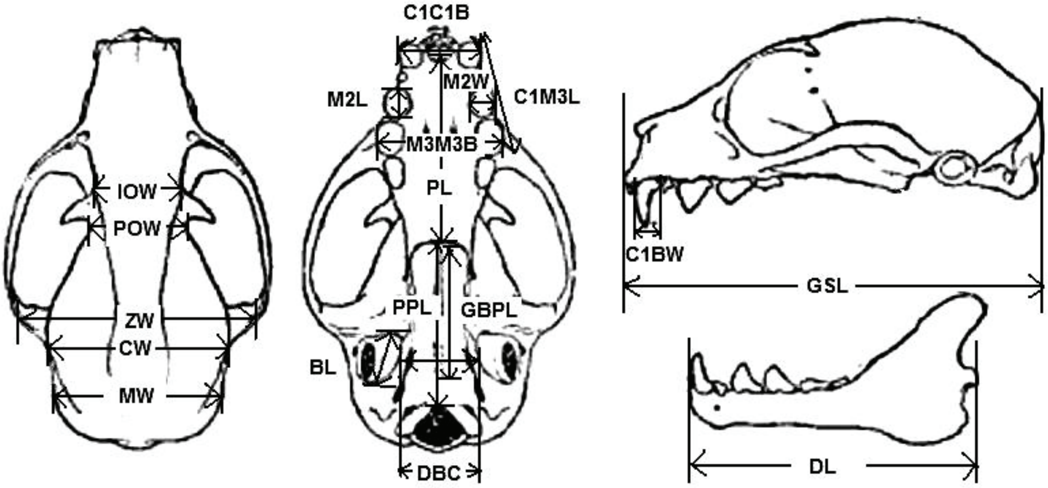

FIGURE 3. Eighteen cranial characters used for measurements and morphological analysis in *P. lucasi.* Figure was modified from Andersen (1912), and not to scale. Abbreviations are as in the text.

TB, HF, D4P1L, D5P1L, GSL, IOW, MW, PL, PPL, GBPL and C1C1B, showed a significant interaction between locality and sexual dimorphism (Table 3). Thus, the analyses for males and females were performed separately.

Discriminant function analysis

Functions at group centroid are shown in Table 4. Two discriminant functions were recognised in the analysis. Test of function 1 through 2 for the external characters of males showed a significant value (Wilk's Lambda = 0.096; *P* = 0.008), but was not significant for function 2 (Wilk's Lambda = 0.501; *P* = 0.364) (Table 5). Likewise, for the craniodental characters of males, function 1 through 2 was significant (Wilk's Lambda = 0.029; *P* = 0.000) but not for function 2 (Wilk's Lambda = 0.338; *P* = 0.175).

Female external characters showed a significant value for the test of function 1 through 2 (Wilk's Lambda = 0.211; *P* = 0.053), but not for function 2 (Wilk's Lambda = 0.686, *P* = 0.721). However, the craniodental characters showed no significance for both the test of function 1 through 2 and function 2 (Wilk's Lambda = 0.169 and 0.654; *P* = 0.102 and 0.843, respectively).

Variable D4MCL gave the highest loading for both function 1 and function 2 for the external characters of males, accounting for 81.0% and 19.0% of the variance (Table 6), respectively, with a canonical function coefficient value of 1.62 and -1.11 (Table 7). For the craniodental characters, function 1 was heavily loaded with BL and explained 84.3% of the variance with a canonical function coefficient value of -2.04. Meanwhile, function 2 was dominated by M2W, accounting for 15.7% of the variance and with a canonical function coefficient value of 1.20.

Function 1, which explained 83.1% of the variance for the female external characters was mainly dominated by HF, while function 2 (16.9% of the variance) was heavily loaded by D5P2L, with a canonical function coefficient values of 1.38

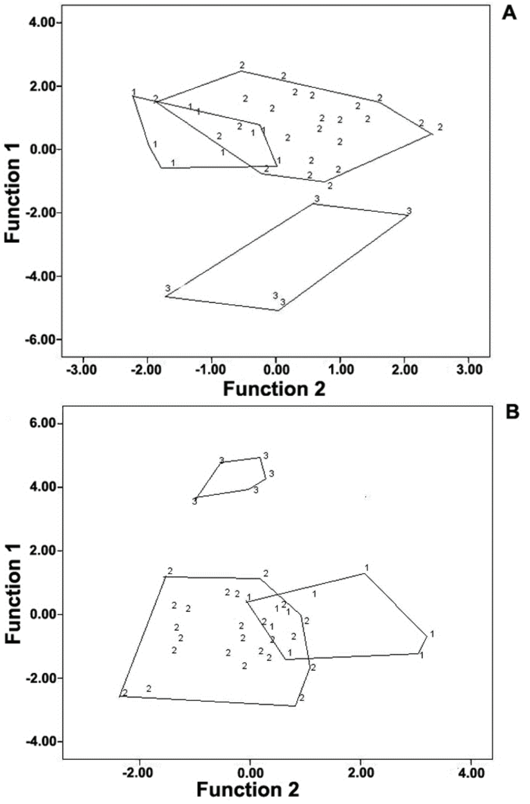

FIGURE 4. Canonical discriminant plot for (**A**) all external and (**B**) craniodental characters of male *P. lucasi* from (1) Miri, (2) Kuching and (3) Sri Aman.

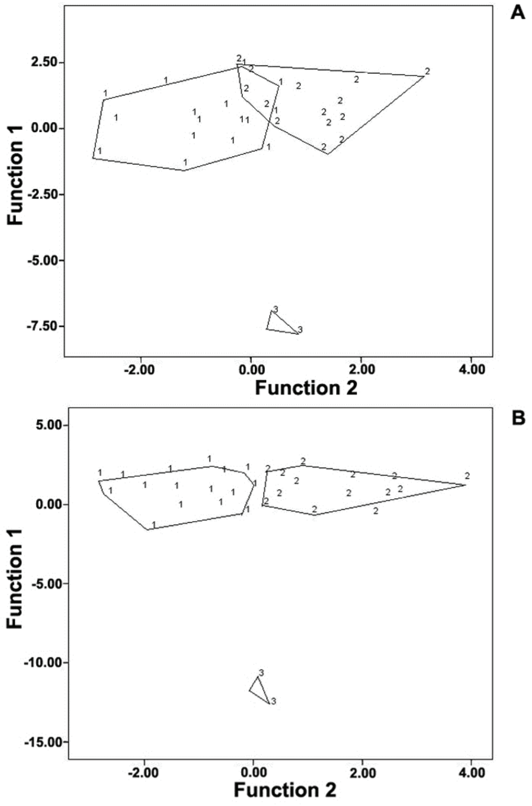

FIGURE 5. Canonical discriminant plot for all (**A**) external and (**B**) craniodental characters of female *P. lucasi* from (1) Miri, (2) Kuching and (3) Sri Aman.

and -0.97, respectively. As for the craniodental characters, both function 1 and function 2 were mainly dominated by DL with a canonical function coefficient value of 1.31 and -1.03, respectively, that explained 84.4% and 15.6% of the variance, respectively.

Four canonical discriminant plots were retrieved separately for both male and female *P. lucasi*; illustrating the variation in the external and the craniodental characters among the three populations. Function 1 for male external characters clearly separated the Sri Aman population from both the Miri and Kuching populations, while function 2 partly separated the Miri population from the Kuching population (Fig. 4A). Meanwhile, the canonical discriminant plot for the male craniodental characters clearly separated all three populations through both function 1 and function 2 (Fig. 4B).

The canonical discriminant plots for the female external characters also separated the Sri Aman population clearly from the others, and both the Miri and the Kuching populations were partially separated by function 2 (Fig. 5A). For the female craniodental canonical discriminant plot, the same pattern was also observed. The Sri Aman population was clearly separated from both the Miri and Kuching populations in function 1, while both the Miri and Kuching populations were partly separated (Fig. 5B).

TABLE 3. Multiple regression analysis on sex, locality and sex-locality interactions in *P. lucasi* external and craniodental measurements. F values are presented for the main effects with significance levels are; $0.05 > P > 0.01$*; $0.01 > P > 0.001$** and $P > 0.001$***

Character	Sex	Locality	Interaction
External			
FA	1.04	0.90	0.79
E	3.96	4.74*	3.85*
TB	5.56*	4.02*	3.88*
HF	0.80	4.26*	2.98*
TV	1.38	0.93	1.42
D2MCL	1.07	0.11	0.38
D3MCL	0.03	1.43	0.99
D3P1L	2.34	3.00	2.43
D3P2L	0.51	2.83	1.92
D4MCL	0.28	2.00	1.32
D4P1L	1.97	12.37***	8.43***
D4P2L	3.95	2.513	2.73
D5MCL	0.55	1.22	0.84
D5P1L	4.29*	4.30*	3.79*
D5P2L	2.76	0.83	0.38
Cranial			
GSL	18.63***	0.52	8.22***
IOW	2.96	4.65*	3.45*
POW	1.92	2.12	2.64
CW	0.03	1.59	1.08
MW	0.98	4.93*	3.65*
ZW	0.06	2.64	1.77
PL	15.56***	0.02	5.65**
PPL	4.85*	2.04	3.25*
DBC	1.03	134	1.29
BL	0.81	0.41	0.68
GBPL	3.48	3.60*	3.76*
DL	6.14***	0.13	2.40
Dental			
C1BW	5.35*	2.06	2.60
C1C1B	6.90*	3.09	3.53*
M3M3B	2.26	0.46	0.88
C1M3L	2.32	0.63	1.15
M2L	3.55	2.16	2.56
M2W	3.74	1.59	2.49

DISCUSSION

Sexual dimorphism

From 33 characters used in the analysis, the females of the Kuching and Sri Aman populations dominate most characters by being larger in size, in support of that mentioned by Ralls (1977) that larger females are very common in Chiroptera. However, in contrast, in the Miri population the males are larger in size compared to the females. Nevertheless, among the factors identified as contributing to sexual dimorphism within mammals, are sexual selection, fecundity selection of females, parental investment and ecological factors, such as distribution and availability of food (Brana, 1996; Ralls, 1977; Feldhamer et al., 1999).

Sexual selection would potentially favour larger males for mammals which are polygynous, since a larger male would require a more robust skeleton to support the larger muscle mass. This is important in mate-searching activities, and would be advantageous in competition between the males as the successful male would have more females (Ralls, 1977; Bonnett et al., 1998). However, sexual selection would favour larger females in terms of fecundity, since a larger female would have a higher level of gamete and offspring production (Andersson, 1994; Clutton-Brock and Harvey, 1978).

In mammals, parental investment is largely contributed by the females and so larger females are usually related to differences in the metabolism demands of pregnant females (Ralls, 1977; Findley and Traut, 1970). This is observed in the Western long-eared Myotis (*Myotis evotis*) populations, whereby the female displayed a larger body size compared to the male (Solick and Barclay, 2006). This relates to the 'big mother' hypothesis (Ralls, 1976), with the cost reduction of remaining euthermic (Williams and Findley, 1979), the increased ability for load-bearing (Myers, 1978) and larger offspring production (Fujita, 1986). Among other advantages of large females are the ability to provide more milk (Ralls, 1976), store more fat (Weber

TABLE 4. Functions at group centroids for all characters in both male and female *P. lucasi.*

	Male		Female	
Location	**Function 1**	**Function 2**	**Function 1**	**Function 2**
External				
1	0.216	-0.944	0.369	-1.153
2	0.824	1.001	0.629	0.406
3	-7.502	0.552	-3.685	0.125
Skull				
1	0.717	-1.297	-0.200	1.250
2	0.890	1.462	-0.785	-0.413
3	-11.968	0.139	4.127	-0.268

*Unstandardized canonical discriminant functions evaluated at group means

TABLE 5. Wilk's lambda test of functions for external and craniodental characters for both male and female *P. lucasi*.

Sex	Characters	Test of function(s)	Wilks' Lambda	Chi-square	df	*P*
Male	External	1 through 2	0.096	51.627	30	0.008
		2	0.501	15.210	14	0.364
	Craniodental	1 through 2	0.029	72.395	36	0.000
		2	0.338	22.250	17	0.175
Female	External	1 through 2	0.211	43.516	30	0.053
		2	0.686	10.546	14	0.721
	Craniodental	1 through 2	0.169	47.082	36	0.102
		2	0.654	11.247	17	0.843

TABLE 6. Eigenvalues for external and craniodental characters for both male and female *P. lucasi.*

Sex	Characters	Function	Eigenvalue	% of variance	Cumulative %	Canonical correlation
Male	External	1	4.235(a)	81.0	81.0	0.899
		2	0.996(a)	19.0	100.0	0.706
	Craniodental	1	10.543(a)	84.3	84.3	0.956
		2	1.961(a)	15.7	100.0	0.814
Female	External	1	2.246(a)	83.1	83.1	0.832
		2	0.457(a)	16.9	100.0	0.560
	Craniodental	1	2.866(a)	84.4	84.4	0.861
		2	0.529(a)	15.6	100.0	0.588

*First 2 canonical discriminant functions were used in the analysis.

and Findley, 1970) and hunt a wide variety of prey (Wilson, 1975).

The resource partitioning model was proposed to explain the sexual dimorphism observed in mustelids (Lynch et al., 1997). This model refers to the reduction of the intersexual food competition, whereby differences in sizes would indirectly comply the amount of food needed for each individual, adjusted accordingly with their importance and needs (Brown and Lasiewki, 1972; Lynch et al., 1997). Also, a larger body size is favourable for the gender which is responsible for feeding the young, since a larger body would allow a larger feeding area (Clutton-Brock and Harvey, 1978).

Nevertheless, body sizes usually marks the stage of maturity in most organisms, and so early maturation in females due to environment fluctuation is suggested as a cause of the reduction in female body size (Clutton-Brock and Harvey, 1978).

Male *P. lucasi* from the Kuching and Sri Aman populations might face a strong selection for large females which are productive. Since both populations are surrounded by development areas (resettlement, shifting cultivation and dam construction), habitat loss and food source depletion are likely to occur. Hence, females with a higher offspring survival rate and that are capable of providing quality parental investments are favoured as a counter-act for such a threat. On the other hand, larger males are observed in the Miri population. Resource-defense polygyny is a commonly observed in the mating pattern of bats (Altringham, 1996) that establish a harem by defending critical resources, such as food, shelter or mates (Gopukumar et al., 2005; Storz et al., 2000). This has been established to be the case in *Myotis adversus* (Dywer, 1970), *Saccopteryx bilineata* (Voigt, 2005) and *C. sphinx* (Balasingh et al., 1995; Storz et al., 2000, 2001). A polygynous mating strategy would likely favour a larger male body size so as to enhance the success rate in winning male-male combats.

Depletion of the food sources in the nearby area could also be a significant factor which in turn forces the organisms to fly farther to hunt for food, and a larger body size would likely permit a larger foraging radius (Fukuda et al., 2009). The anthropogenic changes in the environment (forest to crop plantations) have created fragmented vegetation which greatly affects the feeding behaviour as well as the abundance and diversity of forest bats. Fruit bats that largely consume forest produce might have to forage longer distances in search for suitable food (Fukuda et al., 2009). However, the unequal number of male and female individuals, sample to population size ratio and the broad ranges of sampling sites are the main factors which might contribute to the sexual dimorphism displayed by different populations of *P. lucasi* (Best, 1988).

Population size variation

The null hypothesis of no significant differences in the external and craniodental characters of *P. lucasi* from different populations within Sarawak is rejected. Significant morphological differences are detected for all three populations of *P. lucasi* in this study and are suggested to be driven by various environmental factors, exposure to relative isolation and also different selective pressures experienced by each population (Kitchener and Maryanto, 1993; Maharadatunkamsi et al., 2003).

Variations in the morphological characters displayed by organisms in different populations are usually well explained by or correlated to the geographic distance and climate differences between the two populations (Solick and Barclay, 2006). Isolation by distance would have allowed sufficient evolution of different morphological features displayed by both populations (Solick and Barclay, 2006). Extremities in the sizes of organisms are also commonly related to thermoregulatory advantages. For example, a smaller body size is well adapted to colder environments (Allens' rule) (Allen, 1877; Lindsay, 1987; Johnston and Selander, 1971; Wathen et al., 1971). However, Bergmann's rule states that a larger body size is more suited to cooler environment (Bergmann, 1847; Meiri and Dayan, 2003). Size reduction is suitable

TABLE 7. Canonical variate function coefficient of external and craniodental characters of both female and male *P. lucasi* from Kuching, Miri and Sri Aman. The standardized value is followed by the unstandardized value in brackets.

Character	**Male**		**Female**	
	Function 1	**Function 2**	**Function 1**	**Function 2**
External				
FA	-0.31 (-0.32)	-0.58 (-0.60)	-0.28 (-0.19)	0.73 (0.49)
E	-0.93 (-1.67)	0.10 (0.19)	-0.53 (-0.64)	0.59 (0.71)
TB	-0.12 (-0.16)	0.20 (0.28)	0.54 (0.41)	-0.29 (0.22)
HF	0.50 (0.67)	0.89 (1.20)	*1.38 (1.69)	-0.00 (-0.00)
TV	0.19 (0.17)	0.52 (0.50)	-0.56 (-0.62)	0.37 (0.41)
D2MCL	-1.12 (-0.78)	-0.06 (-0.04)	-0.93 (-0.57)	0.58 (0.36)
D3MCL	-0.17 (-0.13)	0.64 (0.46)	0.92 (0.59)	0.19 (0.12)
D3P1L	0.15 (0.15)	0.65 (0.66)	-0.18 (-0.15)	-0.60 (-0.50)
D3P2L	-0.55 (-0.46)	0.78 (0.66)	-0.29 (-0.17)	-0.21 (-0.12)
D4MCL	*1.62 (1.22)	*-1.11 (-0.83)	-0.69 (-0.48)	-0.46 (-0.32)
D4P1L	0.77 (0.93)	-0.77 (-0.93)	0.85 (1.00)	0.32 (0.38)
D4P2L	0.44 (0.48)	0.18 (0.20)	1.32 (1.17)	0.93 (0.82)
D5MCL	-0.62 (-0.54)	-0.64 (-0.56)	-0.76 (-0.49)	-0.29 (-0.19)
D5P1L	1.17 (1.47)	0.37 (0.47)	-0.10 (-0.11)	-0.34 (-0.39)
D5P2L	-0.92 (-1.08)	-0.26 (-0.31)	-0.46 (-0.34)	*-0.97 (-0.70)
Constant	**23.75**	**13.89**	**0.09**	**-26.43**
Variation explained (%)	**81.0**	**19.0**	**83.1**	**16.9**
Cranial				
GSL	-0.06 (-0.08)	1.09 (1.61)	-0.47 (-0.68)	-0.26 (-0.38)
IOW	0.53 (2.27)	0.04 (0.19)	-0.09 (-0.30)	0.50 (1.57)
POW	-0.57 (-1.54)	0.36 (0.99)	-0.13 (-0.34)	0.55 (1.45)
CW	1.40 (5.22)	-0.99 (-3.70)	-0.09 (-0.30)	0.14 (0.42)
MW	1.78 (4.20)	0.46 (1.09)	-1.28 (-3.84)	-0.36 (-1.08)
ZW	-1.45 (-5.36)	0.02 (0.06)	0.96 (2.43)	0.02 (0.05)
PL	-1.20 (-2.37)	-0.70 (-1.39)	-0.05 (-0.11)	0.24 (0.55)
PPL	-0.67 (-1.77)	0.55 (1.45)	-0.82 (-1.59)	0.05 (0.10)
DBC	0.56 (2.20)	0.12 (0.48)	0.59 (2.75)	-0.05 (-0.22)
BL	*-2.04 (-15.32)	-0.12 (-0.89)	-0.56 (-4.06)	0.04 (0.27)
GBPL	1.35 (4.12)	0.27 (0.83)	0.72 (1.81)	0.27 (0.68)
DL	1.14 (2.03)	-0.61 (-1.09)	*1.31 (2.51)	*-1.03 (-1.98)
Dental				
C1BW	0.64 (7.40)	-0.02 (-0.19)	0.01 (0.13)	-0.13 (-1.35)
C1C1B	0.53 (2.75)	-0.09 (-0.48)	-0.24 (-1.05)	0.42 (1.86)
M3M3B	-1.12 (-3.66)	-1.00 (-3.29)	-0.12 (-0.34)	0.21 (0.60)
C1M3L	-0.06 (-0.20)	-0.12 (-0.43)	-0.08 (-0.21)	-0.13 (-0.47)
M2L	-0.93 (-7.56)	0.144 (1.175)	0.79 (4.30)	0.77 (4.21)
M2W	0.59 (5.60)	*1.20 (11.52)	-0.01 (-0.11)	-0.28 (-2.24)
Constant	**-24.60**	**7.36**	**-3.30**	**11.77**
Variation explained (%)	**84.3**	**15.7**	**84.4**	**15.6**

in flight membranes in dry and warm environments (Solick and Barclay, 2006), but differences in the foraging ecology could also be a potential contributor to the morphological variation since this species can inhabit many different types of forest (Francis, 2008; Solick and Barclay, 2006; Payne et al., 1985).

Furthermore, the effect of constant crowding could lead to changes in body size due to competition for space and food resources. According to Debinski and Holt (2000), when a population is isolated by fragmentation into smaller patches, its local concentration is likely to be high as time progresses, leading to overcrowding in the population in the isolated patches. Such fragmentation may then stunt developmental processes that usually promote the symmetrical growth of an organism (Floate and Fox, 2000; Lens et al., 2002). In small habitat fragments, restricted food availability or low habitat quality may result in smaller individuals (Bancroft and Smith, 2005) or perhaps in food sources of a low nutritous value for development. Such a phenomenon is especially dominant in small-mammals and has also been observed in bird and insect communities (Debinski and Holt, 2000).

The Sri Aman population differs significantly from the Miri and Kuching populations by displaying relatively smaller body sizes compared to the others. According to Raia and Meiri (2006), a small body size would result from the adjustment taken to cope for space and resource shortage. Meanwhile, in the presence of predators, a small body size is to counteract the predator, giving a greater manoeuverability and quick escape (Karr and James, 1975).

The Miri population is characterised by large external attributes, especially the wing characters. In bats, large external characters are mainly related to their ecomorphology (Norberg, 1981; Norberg and Rayner, 1987). Larger wings and body shapes are known to give powerful flight which is needed for long distance foraging activities and to avoid predators (and thus increased survivorship) (Abdullah, 2003). Among other advantages of a large body are the provisions of a better adaptation to maintaining body constancy in variable conditions and to facilitate in effective digestion (Begon et al., 1990; Raia and Meiri, 2006). Differences in the foraging behaviour could have been a major issue for the Miri population of *P. lucasi*. Food resources have become scarce and patchy, and so the foraging radius has likely had to become wider and demands a longer flight for food. Thus, the population is suggested to have undergone adaptive radiation by favouring larger external characters which would allow the robust musculature development to endure long flight.

Generally, morphological characters correlate to the dietary adaptation of organisms. The degree of food hardness is viewed as a mechanism of resource partitioning in vertebrate communities, and is reflected in variations in their morphology (Dumont, 2007). The higher the degree of food hardness, the greater the biting loads that have to be born by the skull and jaws (Aguirre et al., 2003). Thus, a greater bite force develops in parallel with an increase in body size in bats (Dumont, 2007). The Kuching population is identified to have large craniodental characters, namely the skull size and dental sizes.

The dental characters are mainly associated with the dietary aspects of the species (Dechmann et al., 2006). A narrow post-orbital constriction (POW) would allow a larger temporalis muscle, and so greater biting forces. For example, the anterior part of the temporalis muscle is largely responsible for canine teeth actions (Wiig, 1989). A stronger bite-force is important in handling harder food (Lynch and O'Sullivan, 1993). The Kuching population had the widest POW compared to the other two populations, thus suggesting the lowest biting forces of the three populations in this study.

CONCLUSION

Morphological analysis of the three populations of *P. lucasi* in Sarawak established the existence of distinct morphological variation between the three populations of *P. lucasi* such that *P. lucasi* from the three different localities could be distinguished accordingly by morphological characters. The D4MCL and BL of males and the HF and DL of females are the best predictors for the external and craniodental characters, respectively, in differentiating *P. lucasi* from the three different localities. Different ecological factors, such as breeding, crowding effect, foraging behaviour, resource availability and selective pressure, could have been the factors driving the morphological variation among these *P. lucasi* populations. Among other factors for this to occur, is the absence, or minimum number of migrations between the different *P. lucasi* populations leading to genetic isolation (Rahman, 2010). Thus, slowly each population have adapted to their ecological environments and as such the data support the hypothesis of high site fidelity of *P. lucasi* in this region.

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