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MORPHOLOGICAL VARIATION OF MOUNTAIN BLACKEYE (*Chlorocharis emiliae*) POPULATIONS IN MALAYSIAN BORNEO

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ABSTRACT

The mountain blackeye (*Chlorocharis emiliae*) is one of the few Bornean endemic birds which presents an excellent model species to illustrate evolution and speciation. Here, we use discriminant function analysis to elucidate the morphological variation on 40 specimens of mountain blackeye from four populations namely Mount Kinabalu, Mount Trus Madi, Mount Murud and Mount Mulu. The test successfully distinguished all four populations accordingly by respective nominated subspecies. Tarsus length and bill length were identified as the best predictors from nine character loadings observed which also included bill depth, bill width, head bill, wing length, wing span, tail length and total length. Along with this, the morphological patterns also revealed that solid skeletal characters such as bill length, bill depth, bill width and tarsus are genuine predictors of morphological variation and body size within species as compared to feather-based characters. The evolution of such morphological traits is more pronounced due to different ecological adaptation of the mountain blackeye populations. Several factors such as phenotypic plasticity, foraging behaviours and food availability may have influenced the morphological variation between the subspecies.

Key words: character loading, evolution, foraging behaviours, morphological variation, phenotypic plasticity, subspecies

INTRODUCTION

The study of speciation is habitually postulated from morphological evolution of populations (Larson, 1989). Since the birth of avian taxonomy, species recognition and geographical variation of Bornean birds had been exhaustively analysed based on raw external features (e.g. Banks, 1952; Mees 1955; Harrison 1955, 1956). With regards to the species studied, taxonomic subdivisions of mountain blackeye into four separate subspecies (*C. e. emiliae* of Mount Kinabalu, *C. e. trinitae* of Mount Trus Madi, *C. e. moultoni* of Mount Murud, Mount Mulu, Mount Pueh and Tama Abo Range, *C. e. fusciceps* of Mount Maga) were largely influenced by their comparative external features, although they were most heavily emphasized through plumage variation as discussed by previous authors (Mees, 1955; Harrison, 1956).

Generally, the mountain blackeye is relatively small in size (11-14 cm of total length) but comparatively bigger than their relatives of white-eyes (9-10 cm) (Smythies 1999, Myers 2009). However, previous literatures inferred that the average tail length measurement of mountain blackeye were comparatively similar to that of majority of Zosterops (Mees, 1955; Harrison, 1956). Among the subspecies, the true *emiliae* of Mount Kinabalu is slightly larger by size and relative proportions as compared to the *moultoni* populations occurring in Sarawak (Harrison, 1956). Based on the average tail-index, Mees (1955) discovered that the tail-ratio for *emiliae* is relatively larger than *moultoni* of Mount Murud and Mount Pueh, thus concluded that tail length was very pronounced in discriminating the morphological variation between both subspecies.

By comparing to Gawin (2006), the discriminant function analysis (DFA) results revealed six significant characters measured from three mountain blackeye populations which are bill length, tarsus length, total length, wing span, head bill and bill width. These findings did not coincide with Mees (1955) tail-index analysis, therefore

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depicting that classical methods were scarcely effective when dealing with complex geographical variation in species. Here, we present an extended study which further refined the subspecies characterisation of mountain blackeye by appending the population of *C. e. trinitae* from Mount Trus Madi with the other subspecies.

MATERIALS AND METHODS

Study area and sampling methods

Two sampling sites were selected in Sarawak namely Reked Meligan Church Camp, Mount Murud (N 03º 55.645', E 115º 30.676' E; 2113 m; 25 October-2 November 2008) and Camp Four, Mount Mulu (N 04º 02.694', E 114º 54.651' E; 1764 m; 3-12 February 2009), and another two sites in Sabah which are Layang-layang, Mount Kinabalu (N 06º 02.676', E 116033.795' E; 2691 m; 13-26 February 2008) and summit cabin, Mount Trus Madi (N 05º 33.199' E 116º 31.187' E; 2653 m; 8-13 July 2008) (Fig. 1). Birds were caught using conventional ground mist-nets with four shelves attached to wooden poles. Mist nets were set close to the ground at suitable foraging spots, usually along open trails and mountain edges near stunted tree canopies of 3 to 5 m high. Birds caught from the net were immediately measured before being released.

Morphological measurements

A total of 40 live specimens comprising 10 equal representatives from each population were utilized as morphological database. Nine key external traits namely; (1) bill length, (2) bill depth, (3) bill width, (4) head bill, (5) wing length, (6) wing span, (7) tail length, (8) total length and (9) tarsus length were selected from the field data log as key variables for the morphometric analysis. Accordingly, the bill measurements consist of four component characters which include bill length, bill depth, bill width and head bill. For the non-bill characters, the key measurements include wing length, wing span, tail length, total length and tarsus. All external characters were measured in millimeters unit using Mitutoyo® electronic digital caliper (Japan) and 30 cm stiff metal ruler.

Data analysis

All measurements were recorded and analyzed for mean, standard deviation (SD), minimum and maximum in Microsoft Excel 2002. Morphological data with normal distributions were used directly in the analysis while data for significant characters were computed initially by $\log_{10}$ transformation using SPSS 15 statistical package. Subsequently, every single character was tested for normality test in order to determine the uniformity of variance and SD from the dataset (Bland and Altman, 1996b). Normality test was performed based on Kolmogorov-Smirnov Test Values at significant p-value of $p<0.05$ using MINITAB 2002 v13.2 (Copyright ©2006 Minitab Inc.). After normality filtering of characters, significant character variables were subjected to log transformation to allow any multiplicative relationships of a form (for example y = a X b X c X

Fig. 1. Map showing sampling sites in Malaysian Borneo. Localities are represented as 1 = Mount Kinabalu, 2 = Mount Trus Madi, 3 = Mount Murud and 4 = Mount Mulu. Modified after Dalet (2011).

d) to become additive, thus ensuring more symmetrical and normal-distribution of data (Bland and Altman, 1996a).

Multivariate tests were conducted to generate stepwise discriminant function statistics with graphical representation from canonical variate analysis (Manly, 1994). This stepwise DFA were computed using SPSS 15 (version 15.0, SPSS Inc., 2006). Canonical variate analysis was constructed separately for three characters classification; (1) Overall external characters, (2) Bill characters and (3) Non-bill characters. For this analysis, Wilk's Lambda was applied with the probability of $0.10 < p < 0.05$. Variables were classified with the prior probabilities of equal groups and within-groups covariance matrix used.

RESULTS

Validation of external character measurements

Based on Kolmogorov-Smirnov non-parametric test, the normal probability plots showed normal distribution trends only for six external characters; tarsus, bill depth, wing length, wing span, tail and total length. All six characters were estimated within the normality range at p-value >0.15, while the remaining three external characters (bill length, bill width and head bill) were significantly different at approximately $p<0.01$. Overall measurements for total sample size (N) were summarized by mean ± SD and range in Table 1.

Classification of groupings

The accuracy rate for group classifications in overall external characters is 90% with a cross-validated accuracy of 80%. For bill characters, the grouping classifications were accurately classified by 72.5% with 67.5% cross-validated accuracy while the non-bill characters showed slightly higher accuracy rate of 75% with 70% cross-validated accuracy. These following values are fundamental for coordination of grouping classifications. For the first function of overall external characters, positive values were observed in locality 1 and 2; negative values for locality 3 and 4. In Function 2, positive values were fixed for locality 1 and 4; negative values for locality for locality 2 and 3. Finally, the group centroid for the third function revealed positive values in locality 1 and 3; negative values in locality 2 and 4 (Table 2).

By narrowing the classifications, only two functions were made available for bill characters; positive values were observed in locality 1 and 2 for Function 1 and negative values in locality 3 and 4. For the second function, positive values were represented in locality 1 and 4; negative values in locality 2 and 3 (Table 2). On the other hand, the non-bill characters consists three functions with the first function revealing positive values for locality 1 and 2; negative values in locality 3 and 4. For Function 2, positive values were fixed in locality 1, 3 and 4; negative values in locality 2. Lastly, for Function 3, positive values were drawn from locality

Table 1. Summary of mean ± SD for measurements (mm) of external characters analysed in mountain blackeye specimens**.** Values in brackets represent measurement range. Diagnostic external characters are marked with asterisk*

Characters	Kinabalu	Trus Madi	Murud	Mulu	Average
Bill length*	14.08±1.79 (11.65-16.62)	15.18±0.66 (14.13-16.06)	11.43±1.23 (10.36-14.38)	11.67±0.53 (11.09-12.56)	13.09±1.96 (10.36-16.62)
Bill depth	3.94±0.52 (3.15-4.87)	4.27±0.26 (3.91-4.72)	3.71±0.44 (3.19-4.60)	3.61±0.23 (3.23-3.93)	3.88±0.45 (3.15-4.87)
Bill width	3.83±0.43 (3.27-4.86)	4.57±0.21 (4.28-5.03)	4.61±1.63 (3.66-9.15)	4.05±0.27 (3.68-4.58)	4.26±0.89 (3.27±9.15)
Head bill	35.03±1.55 (32.62-37.95)	33.99±0.65 (33.04-34.87)	32.12±0.77 (31.01-33.33)	32.69±0.63 (31.56-33.57)	33.46±1.48 (31.01±37.95)
Wing length	67.5±3.72 (60-72)	63.00±3.92 (57-68)	63.10±5.32 (50-70)	62.3±2.16 (59-65)	63.98±4.32 (50-72)
Wing span	196.70±8.99 (190-212)	189.10±5.28 (182-198)	186.8±5.61 (176-195)	187.1±7.03 (179-196)	189.93±7.76 (176-212)
Tail length	55.9±5.07 (47-64)	57±3.65 (52-64)	51.4±1.96 (48-55)	47.5±2.8 (44-52)	52.95±5.13 (44-64)
Total length	135.5±3.75 (130-140)	133.60±7.82 (120-148)	120.3±6.52 (110-131)	125.4±7.26 (117-140)	128.70±8.84 (110-148)
Tarsus*	23.51±2.42 (20.14-26.85)	20.32±0.84 (19.22-22.02)	22±1.09 (19.96±23.72)	22.74±1.31 (20.6-24.64)	22.14±1.90 (19.22-26.85)

Table 2. Unstandardized coefficient functions at group centroid for overall external characters, bill and non-bill classifications within each locality of mountain blackeye

Characters	Localities	Function 1	Function 2	Function 3
Overall	Kinabalu	2.294	1.239	0.156
	Trus Madi	1.089	-1.801	-0.183
	Murud	-1.777	-0.126	0.665
	Mulu	-1.606	0.688	-0.638
Bill	Kinabalu	1.212	1.061	–
	Trus Madi	1.625	-0.948	–
	Murud	-1.630	-0.281	–
	Mulu	-1.208	0.169	–
Non-bill	Kinabalu	1.515	1.488	-0.003
	Trus Madi	1.066	-1.759	-0.087
	Murud	-1.144	0.024	0.774
	Mulu	-1.437	0.246	-0.684

3 while negative values from locality 1, 2 and 4 (Table 2).

Based on Wilk's Lambda test of functions, three discriminant functions were described for key external characters (Table 3). Test of Function 1 through 3 (Wilk's Lambda = 0.074) and Function 2 through 3 (Wilk's Lambda = 0.324) showed significant values at sig. = 0.000 (less than the critical value of sig. = 0.05). Subsequently, the test of Function 3 revealed a significant value of 0.020 prior to removal of Function 1 and 2. These were further depicted through percentage of variance for Function 1 (66.4%), Function 2 (28.7%) and Function 3 (4.9%) (Table 3). Likewise for bill characters, the Wilk's Lambda values explained only two functions; Function 1 through 2 (Wilk's Lambda = 0.191) and Function 2 (Wilk's Lambda = 0.628) with both valued at sig. = 0.000 (Table 3).

Additionally, three functions were observed in non-bill characters justifying test of functions for Function 1 through 3 (Wilk's Lambda = 0.107) and Function 2 through 3 (Wilk's Lambda = 0.309) at significant value of sig. = 0.000 while the third function (Wilk's Lambda = 0.770) had a value of sig. = 0.010 (Table 3). Collectively, for bill characters, both functions were explained by 79.4% and 20.6% of variance respectively. As for the non-bill characters, all three functions were represented accordingly by lower percentage of variance of 51.4%, 40.5% and 8.1%.

Character loading

Among the overall external variables, the strongest constant values for canonical discriminant functions were observed in Function 1 and Function 2. Based on the standardised coefficient values (Table 4), tarsus is the best predictor of character loading in Function 1 with 0.674, followed by bill length = 0.547, tail length = 0.546 and head bill = 0.472. For Function 2, the highest values were observed in character loading of head bill = 0.836 and the lowest is tail length = -0.145. In contrary, for bill characters, only two functions were analysed with standardised values of bill length = 0.791 and head bill = 0.321 in Function 1. Function 2 was described by head bill = 1.140 and bill length = -0.882 (Table 4).

For classification by non-bill characters, most constant values were generated by Function 1 and 2 with tarsus = 1.071 as the key predictor in Function 2 followed by wing span = 1.044, tail length = 0.836 and total length = -0.458. Subsequently in Function 1, tail length is the highest supported character with 0.864 while wing span is the least supported character with -0.173 (Table 4). The best visual presentations of each function-pairing for overall external characters were illustrated by scatterplots in Figure 2. Scatterplots of Function 2 versus 1 classified all four groupings at respective centroids with partial overlapping between locality 3 and 4. As for canonical variate analysis of bill and non-bill characters, similar scatterplots were showed in Figure 3 and 4 respectively.

DISCUSSION

Homogeneous clustering of subspecies

The discrete clustering of all sampled populations for this study corresponded expectedly with previous works on mountain blackeye, primarily of Gawin (2006) and traditional classifications by Mees (1955) and Harrison (1955). With regards to Gawin (2006), it is worth noting that previous museum specimen of *C. e. trinitae* from Gawin's work were subjected to specimen shrinkage issue. Similarly, the shrinkage in museum specimens were also reported in Tennessee warblers, *Vermivora peregrina* and trails flycatchers, *Empidonax traillii*

Table 3. Wilk's Lambda test of functions for overall external characters, bill and non-bill classifications

Characters	Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.	Variance (%)
Overall	1 through 3	0.074	91.160	12	0.000	66.4
	2 through 3	0.324	39.429	6	0.000	28.7
	3	0.799	7.870	2	0.020	4.9
Bill	1 through 2	0.191	59.575	6	0.000	79.4
	2	0.628	16.756	2	0.000	20.6
Non-bill	1 through 3	0.107	78.246	12	0.000	51.4
	2 through 3	0.309	41.098	6	0.000	40.5
	3	0.770	9.143	2	0.010	8.1

Table 4. Canonical discriminant function coefficients of overall external characters, bill and non-bill classifications. Diagnostic external characters are marked with asterisk*

Characters	Traits	Function 1	Function 2	Function 3
Overall	Tarsus*	0.674 (0.439)	0.708 (0.461)	0.241 (0.157)
	Bill length	0.547 (14.485)	-0.701 (-18.570)	-0.480 (-12.710)
	Head bill	0.472 (37.997)	0.836 (67.363)	-0.292 (-23.549)
	Tail length	0.546 (0.154)	-0.145 (-0.041)	1.007 (0.283)
	Constant	(-91.878)	(-90.067)	(31.564)
Bill	Bill length*	0.791 (20.934)	-0.882 (-23.337)	–
	Head bill	0.321 (25.840)	1.140 (91.829)	–
	Constant	(-62.665)	(-114.001)	–
Non-bill	Tarsus*	0.348 (0.227)	1.071 (0.697)	0.143 (0.093)
	Wing span	-0.173 (-0.025)	1.044 (0.152)	0.262 (0.038)
	Tail length	0.864 (0.243)	0.836 (-0.005)	0.726 (0.204)
	Total length	0.633 (0.097)	-0.458 (-0.070)	-0.950 (-0.146)
	Constant	(-25.597)	(-34.972)	(-1.368)

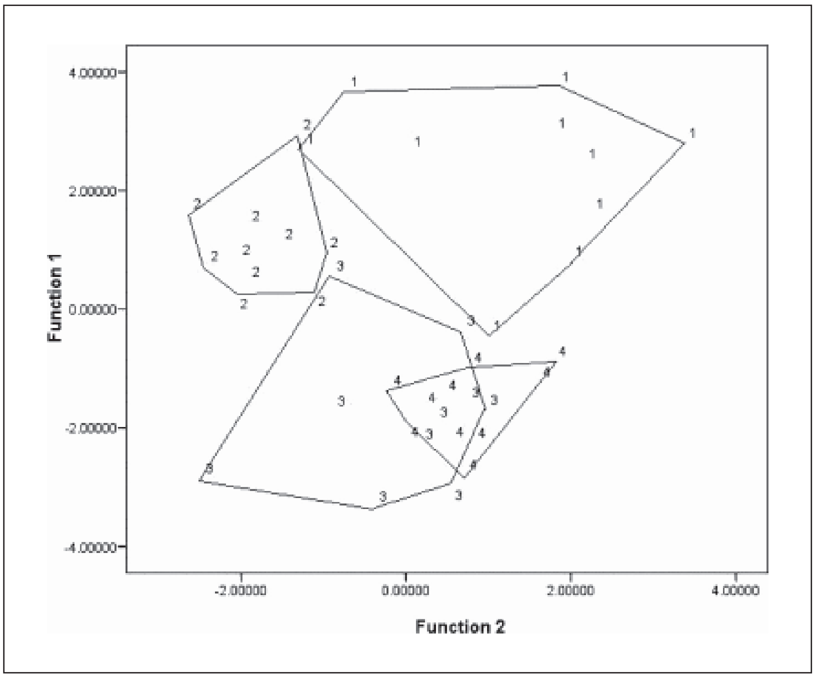

Fig. 2. Canonical discriminant analysis of Function 2 vs. Function 1 for all measured key external characters of mountain blackeye revealed clear distinctions between Sabah and Sarawak populations. *Irregular polygons are plotted as 1 = Mount Kinabalu, 2 = Mount Trus Madi, 3 = Mount Murud and 4 = Mount Mulu.

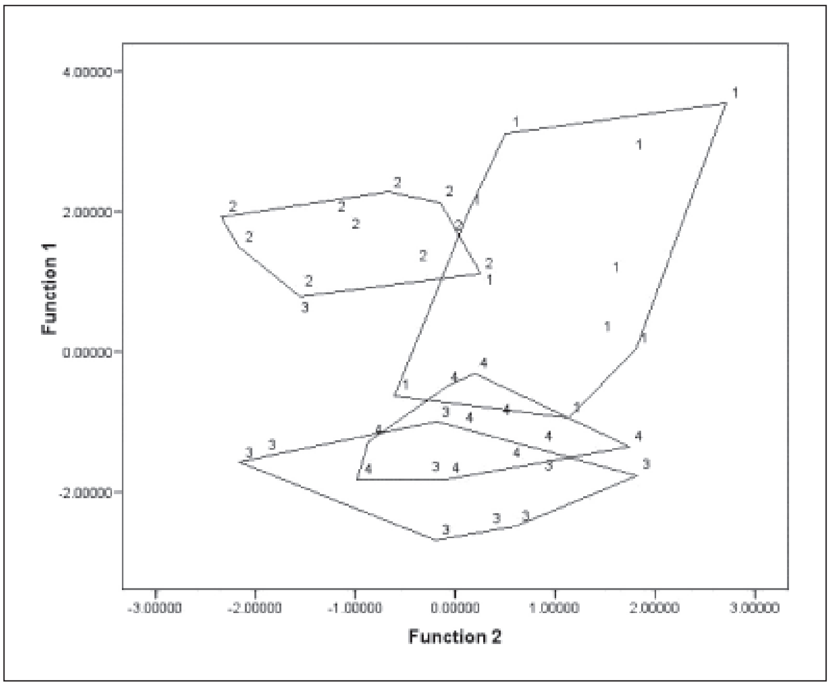

Fig. 3. Canonical discriminant analysis of Function 2 vs. Function 1 for four bill characters (bill length, bill depth, bill width and head bill) of mountain blackeye. *Irregular polygons are plotted as 1 = Mount Kinabalu, 2 = Mount Trus Madi, 3 = Mount Murud and 4 = Mount Mulu.

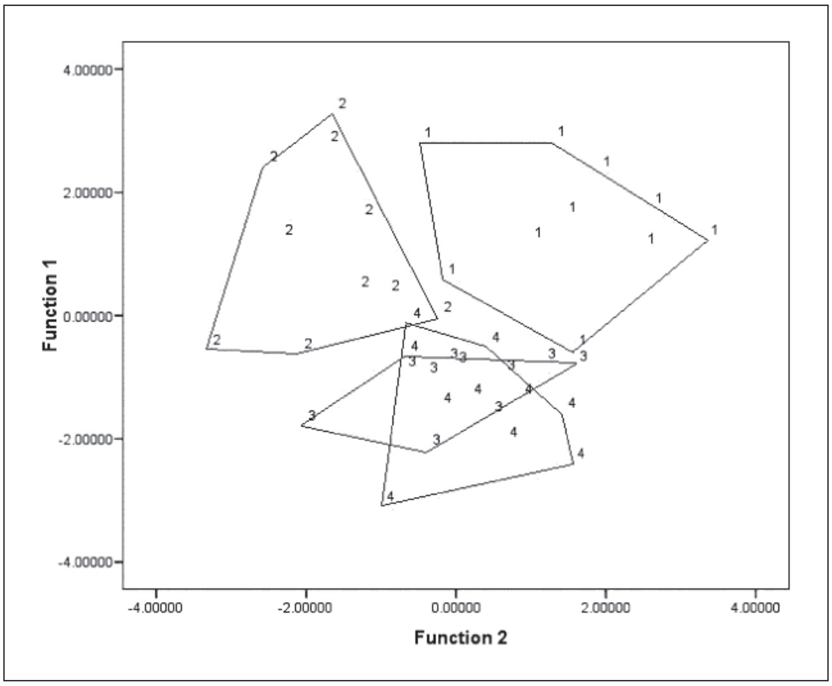

Fig. 4. Canonical discriminant analysis of Function 2 vs. Function 1 for five non-bill characters (wing length, wing span, tail, total length and tarsus) of mountain blackeye. *Irregular polygons are plotted as 1 = Mount Kinabalu, 2 = Mount Trus Madi, 3 = Mount Murud and 4 = Mount Mulu.

(Winker, 1993) and also in cinnamon teal, *Anas cyanoptera* (Wilson and McCracken, 2008). Hence, the inclusion of live specimen of *C. e. trinitae* provided broader morphological dimensions in terms of the total variables analysed.

Based on the canonical discriminant analysis for all measured external characters, it becomes clear that the clustering of morphological characters involves three separate groups; (1) Kinabalu = *C. e. emiliae*, (2) Trus Madi = *C. e. trinitae* and (3) Murud and Mulu = *C. e. moultoni*. The lineage-wide variation between presumed ancestral populations, *C. e. emiliae* and *C. e. moultoni* suggests early morphological radiations were probably distributed along the character size axis, as illustrated by Function 2 vs. Function 1 (Fig. 2). Large clustered perimeters representing *C. e. emiliae* and *C. e. moultoni* (Murud population) indicates more diversity in character sizes, therefore suggesting constraint in morphological evolution of *C. e. trinitae* and sub-populations of *moultoni* on Mount Mulu. This general pattern was also observed within the *elaenia* and tody-tyrant flycatchers (Corbin, 2002).

Character loading variation

In the present investigation, tarsus length is the key indicator for all measured characters followed by bill length, head bill and tail length. Two morphological patterns emerged from the listed predictors implies that standard character precision is more likely to be derived from solid skeletal traits than to feather-related measures (wing length, wing span, and tail length) or admixtures of both (head bill and total length). In addition, Senar and Pascual (1997) suggested that feather-based characters (for instance, tail and wing measurements) are fragile indicators of overall body size as compared to external skeletal measures. This was further supported by Winker (1998) claiming that total length and wing measurements were less concerning in recent morphometric studies except for energetic flight study.

Conversely in Gawin (2006), bill length was the first significant character, then accordingly by tarsus, total length, wing span, head bill and bill width. The slight dissimilarities were of significant character arrangements but otherwise revealed somewhat similar patterns through bill and non-bill character classifications. Both tarsus and bill length variants were also reported as significant foraging characters in the *Thamnomanes* antshrikes (Schulenberg, 1983), Serin, *Serinus serinus* (Senar and Pascual, 1997), little spiderhunter, *Arachnothera longirostra* (Rahman, 2000) and within the mountain Citril finches, *Carduelis citrinella* (Förschler and Siebenrock, 2007).

Adaptive divergence in *C. e. trinitae* and other populations

The divergence within morphological transitions of variable phenotypic and external characters shifted different evolutionary traits utilities in varying environment (Kleindorfer *et al.*, 2006). Consequently, this will lead to gradients of character change (eg. body size and feather pigmentation) or dubbed as clinal variation (Gill, 1990), as depicted primarily by subspecies *trinitae* on Mount Trus Madi. Morphological evolution which mirrors adaptive divergence and emergence of abrupt clines are modeled within numerous species, including the widely renowned Darwin's small ground finch, *Geospiza fuliginosa* (Kleindorfer *et al.*, 2006), also the rufous-collared sparrow, *Zonotrichia capensis* (Lougheed and Handford, 1993), rock pigeons, *Columba livia* (Johnston,1992), and the African little greenbul, *Andropadus virens* (Smith *et al.*, 2005).

Generally, heritable traits that have profound roles in ecological adaptation are moderately high in variety of organism, especially in birds (Keller *et al.*, 2001, Jensen, 2003). Functional morphological traits such as body size, bill size and bone dimensions are controlled by various genes, however these traits are also directly responsive to ecological selection (Corbin, 2002). With reference to the character loading analysis in mountain blackeye, tarsus and bill length are significant predictors of morphological variation among the isolated populations. Despite the relatively high rates of gene flow between subspecies *emiliae* and *trinitae* (Ramji, 2010), natural selection appeared sufficient in illuminating adaptive evolution of the acquired characters, thus supporting the divergence-with-gene-flow model (Smith *et al.*, 2005). The point to be emphasized here is rather the major question confounding the morphological pattern of the species: what factors influenced the selective evolution of these characters?

To address this issue, several studies such as Rahman (2000), Schoettle and Rochelle (2000) and Smith *et al.* (2001) demonstrated that differences in extremity size triggered phenotypic variation or phenotypic 'plasticity'. Along with this, Bokma (2004) suggest that body size dissimilarities within and among species are most likely influenced by different tempo and mode of evolution. These plastic characters are commonly appealing in tarsus and bill dimension as both had long been related to foraging behaviours in avian ecology (Carrascal *et al.*, 1990). For instance, there are numerous documentations focusing on bill adaptations with unsurprisingly abundant interest in hummingbirds (e.g. Kershaw, 2006; Chaves *et al.*, 2007), perhaps are best modeled by specialized nectar-consuming birds. In general, mountain blackeye are known to be mix-consumers of nectars, fruits and insects with clear preference on insect matters while nectars are sparingly consumed (Davison, 1992; Smythies, 1999).

An ecological observation by Steinheimer (1999) revealed several encounters with small flocks of *C. e. emiliae* foraging on blossoms of *Rhododendrons accuminatum* and *R. buxifolium* on the upper mountain scrub of Mount Kinabalu. From that, he hypothesized on the possible correlation between the relative lengths of *Rhododendrons*'s corolla tube with the premaxillae of mountain blackeye. In relation to this study, the range of bill length measurements for *C. e. emiliae* (11.65-16.62 mm) is obviously larger from *C. e. trinitae* (14.13-16.06 mm), therefore given the more diverse flowering plants (particularly *Rhododendrons*) and quite possibly with wider choices and availability of insect materials, the bill size has to adapt by developing suitable bill dimensions although by average, the bill size is longer in *trinitae* (15.18 mm ±0.66). The measurements of *C. emiliae* populations were summarized in Table 1.

It would be seemingly premature to verify these assumptions based on limited dietary information of the studied species. Nevertheless, Wiens (1989) pointed out that nectarivores are advantageous in their dietary flexibility, hence being a triplet consumer, mountain blackeye are less affected by the seasonal limiting of nectar resources. Therefore it stands to reason that *C. e. emiliae* is probably more efficient in generalizing its bill functions compared to the *moultoni* populations on Mount Murud and Mount Mulu which evidently have shorter bill lengths. Moreover, apart from *Rhododendrons* as apparent foraging stopovers, Argent *et al.* (1988) speculated that mountain blackeye also occasionally forage insects on flowering plants due to stimulations from strong nectar scents.

As for tarsus variation, the correlating factor is equally significant as bill length in developing enhanced foraging capabilities. Such behavioural modes are displayed in the antshrikes, *Thamnomanes* where longer tarsus corresponded remarkably in active-perch gleaning insectivores which aided closer-scanning of prey in dense vegetation. While in shorter tarsus, the hawking posture were best suited with longer period perch as it enhanced balance and maneuverability (Schulenberg, 1983). This is also supported by Carrascal *et al.* (1990) stating that longer tarsus permits wider radius while searching for food among the foliage in trees and bushes whereas shorter tarsus resembles birds that are prone to forage vertically. Similarly, the wide-ranging tarsus measurements (20.14-26.85 mm) in *C. e. emiliae* perhaps suggest various foraging techniques are applicable to this population and deserved comprehensive ecological attention for future studies. Elsewhere, tarsus is commonly associated with individual fitness and growth trajectories described by asymmetrical relationship with quality and quantity of food consumed (Badyaev and Martin, 2000; Grieco, 2003). It is therefore likely that different parental behaviour exists within the mountain blackeye populations reflects overall asymmetry of a trait.

CONCLUSION

This study was objectively consistent with Gawin (2006) in almost every morphological facet, only with slight differences in orientation of character loadings. With inclusion of the much genetically debated *C. e. trinitae*, the general overview on morphological distinctions between each subspecies is visually rendered by DFA and narrowed through classification of bill and non-bill characters. From these classifications, tarsus and bill length was proven as the best morphological indicators in discriminating each subspecies, particularly in addressing the adaptive features of mountain blackeye. By general classification, it can be summarized that solid skeletal characters are genuine predictors of body size and morphological variation within species as compared to feather-based characters.

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