QUANTIFYING PELAGE COLORATION OF SOUTHEAST ASIA SPINY RATS GENUS *Maxomys* (MURIDAE: RODENTIA) USING SPECTROPHOTOMETRIC MEASUREMENTS

KUANTIFIKASI WARNA RAMBUT TIKUS DURI ASIA TENGGARA DARI GENUS *Maxomys* (MURIDAE: RODENSIA) DENGAN PENGUKURAN SPEKTROFOTOMETRI

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ABSTRAK

Kami mendokumentasikan kajian pendahuluan tentang variasi warna rambut pada *Maxomys*, salah satu jenis tikus yang umum di Asia Tenggara. Kami menggunakan spesimen kulit yang sebagian besar disimpan di Museum Zoologicum Bogoriense, Indonesia. Pengukuran kuantitatif warna rambut yang dilakukan dengan menggunakan spektrofotometer menunjukkan tidak adanya perbedaan yang signifikan pada warna rambut bagian punggung atau dorsal, yang sebagian besar berwarna coklat tua (L* = 25-30, a* = 5-7, b* = 10-15). Warna rambut bagian perut atau ventral bervariasi pada masing-masing jenis. Kami mengklasifikasikan lima macam pola warna yang berbeda berdasarkan hasil pengukuran: abu-abu keputihan (*M. baeodon, M. whiteheadi, M. musschenbroekii, M. bartelsii*, dan *M. dollmani*), oranye coklat-gelap (*M. hylomyoides*), oranye-kastanye (*M. ochraceiventer*), coklat kekuningan (*M. alticola*) dan putih krem (*M. rajah, M. hellwaldii*, dan *M. surifer*). Karakteristik pola warna rambut ini dapat dipergunakan dalam pengenalan spesies, bersamaan dengan karakter tengkorak kepala. Selanjutnya, kajian molekuler terhadap variasi warna rambut pada *Maxomys* spp. sangat diperlukan untuk mengetahui mekanisme variasi fenotipik pada morfologi jenis ini yang dapat mempengaruhi pola penyebaran, spesiasi dan sejarah evolusi dari *Maxomys*. Kajian ini belum berhasil mendapatkan sekuens dari *Maxomys* menggunakan gen *Mc1r* (*melanocortin-1 receptor*), dan mungkin akan lebih baik jika menggunakan gen lain seperti gen *ASIP* (*agouti signaling peptide*).

Kata kunci: variasi warna rambut, pengukuran kuantitatif, *Maxomys*, spektrofotometer .

ABSTRACT

We documented preliminary study of coat color variations within *Maxomys*, one of the most common rats in the Southeast Asian region. We sampled the skin specimens that mostly deposited at Museum Zoologicum Bogoriense, Indonesia. Quantitative measurements of coat color using spectrophotometer revealed no significant difference in the dorsal pelage showing mostly dark brown (L*= 25-30, a*= 5-7, b*= 10-15). The ventral colorations were variable among the species. We classified five different color types based on the measurements: whitish grey (*M. baeodon*, *M. whiteheadi, M. musschenbroekii, M. bartelsii,* and *M. dollmani*), orange dark brown (*M. hylomyoides*), chestnut orange (*M. ochraceiventer*), yellowish brown (*M. alticola*) and creamy white (*M. rajah, M. hellwaldii, and M. surifer*). These fur color characteristics can be useful in species recognition, together with the craniometric features. Furthermore, molecular study of coat color variation within *Maxomys* spp. is needed to elucidate the mechanisms of phenotypic variation in morphology that affect the patterns of divergence, speciation and evolutionary history of *Maxomys*. Here, we failed to obtain the sequences from *Maxomys* using Mc1r (melanocortin-1 receptor) gene, and probably will be better to use other gene such as *ASIP* (agouti signaling peptide) gene.

Keywords: coat color variations, quantitative measurements, *Maxomys*, spectrophotometer.

INTRODUCTION

Mammalian pelage coloration plays important roles in crypsis, intraspecific communication, thermoregulation, predation avoidance and ultraviolet screening (Endler 1990; Caro 2005; Lai *et al*. 2008). Pelage coloration is an important phenotypic character as a result of individual adaptations to its environments and living with other animals. Adaptive significance of coloration in animals can be explained by several selective forces (Burtt 1981; Cloudsley-Thompson 1999). The color patterns of animals and their visual backgrounds may be regarded as mosaics of patches which vary in size, shape, brightness and color (Endler 1990).

Hypothetically, the different parts of the body in different mammal species are subject to several selective pressures, and pelage coloration represents as a great adaptive importance (Caro 2005).

In mammals, many of the working hypotheses regarding to the adaptive value of coat color was proposed more than 100 years ago and progressed little since then (Caro 2005). Recently, these hypotheses have attracted interest, and are again being explored and tested (e.g. Ortolani 1999; Stoner *et al*. 2003a, 2003b; Nachman 2005; Hoekstra 2006; Hoekstra *et al*. 2006). The three most important adaptive functions of pelage are concealment, communication, and thermoregulation (Cott 1940; Caro 2005; Lai *et al*. 2008). Previous studies have been conducted related to adaptive functions of pelage coloration in mammals: e.g., changing visual characteristics in order to minimize predator detection (Rowland 2009), inconspicuous or cryptic color patterns against visual background (Endler 1990; Ortolani 1999), and as thermoregulatory properties (Burtt 1981; Walsberg 1983).

Until recently, the validity of mammal pelage coloration as a diagnostic tool for species identification is still a problem. Endler (1990) stated there were five major weaknesses related to color determination on wildlife animal: 1) human subjectivity, 2) the adjacent color patches that can affect the perceived color of a patch, 3) lighting conditions, 4) the variation among normal people, and 5) the differences in a vision between humans and animals which the color patterns are directed. Despite matching with Munsell soil color chart (Lai *et al*. 2008), there is no quantitative standard color measurements in order to determine the color patterns.

Murines, one of dominant groups of small mammals represented by more than 2000 species in the world, have various kinds of pelage colorations and play an important role in ecosystem. It can be a good sample to study the variations of pelage color patterns on mammals. Previously, studies of color variations have been conducted in murines based on morphology (Hoekstra 2006; Lai *et al*. 2008; Rios and Alvarez-Castaneda 2011; Salinas *et al*. 2015) and evolutionary history or molecular phylogeny (Lovet *et al*. 1986; Montagutelli 2000; Shimada *et al*. 2009; Hubbard *et al*. 2010; Kambe *et al.* 2011; Kodama *et al*. 2015).

Within Southeast Asian murine populations, a genus *Maxomys* is known as one of the genera with widespread distributions start from mainland of SE Asia (Thailand, Vietnam, Malaysia) until Philippines and Indonesia. They also have various color variations and still there is no information about color variations based on morphology or molecular phylogeny. In this preliminary study, we documented an inventory of coat color variations within *Maxomys*, mostly from skin specimens deposited at Museum Zoologicum Bogoriense, Indonesia.

MATERIALS AND METHODS

We measured 70 skins of *Maxomys* (Appendix 1): *M. hellwaldii, M. musschenbroekii, M. dollmani, M. rajah, M. surifer, M. baeodon, M. ochraceiventer, M. whiteheadi, M. alticola, M. pagensis, M. hylomyoides,* and *M. bartelsii*. All color measurements were made on adults. Singaravelan *et al*. (2013) noted that the coloration changes during the course of ageing; pups and juveniles were lighter than fully matured adults. We measured the dorsal and ventral pelage colors using a digital colorimeter

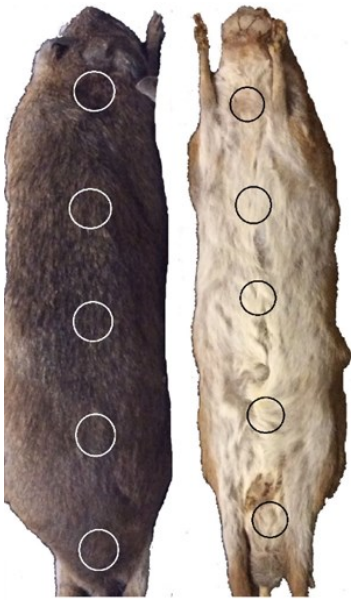

Figure 1. Photograph of a specimen of *Maxomys* sp. showing the five points over the dorsal and ventral body region, namely the neck, upper back, middle back, lower back, and rump, where we measured the pelage color.

(Spectrofotometer CM-700D, KONICA MINOLTA).

Each animal was measured at least 5 times shaping line posteriorly (Figure 1). We used the L*a*b* color space model under standard daylight illumination (Hunter 1948) to quantify different components of the measured color from both SCI and SCE techniques. We used SCI and SCE simultaneously from spectrophotometer and the color measurements based on specular reflectants (included or excluded). The color space component 'L*' represents the level of lightness in color (L* estimates equivalent to 'brown to black' eumelanin), a positive value of 'a*' was represented in red/magenta, while a negative value of 'a*' was represented in green. The positive value of 'b*' was represented by the amount of purplish-red (magenta) yellow, while the negative value of 'b*' represented by blue (a* and b* estimates were equivalent to the 'yellow to red' pheomelanin). To further characterize the coat color, principal components analysis (PCA) was used to reduce the L*a*b* color space model into a single component (PC) that represents the largest proportion of variation in coat color and lightness of the coat color using SPSS Inc.(2007). The authors also used canonical discriminant functions (DFA) to test the variables that give strong influences on the variance of variables.

RESULTS AND DISCUSSION

Results

Descriptive analysis

Mean and standard deviation from the color measurements of *Maxomys* spp. are presented in Table 1. Overall, the dorsal coat coloration depicted less variations than ventral coat color in the *Maxomys* spp. that we examined. Throughout most of their range, dorsal pelage from the specimens are mostly dark brown (ranged from L*= 25-30, a*= 5-7, b*= 10-15, see Table 1), individual hairs are banded, grey in the bases and brown to dark brown until the hair tip (Figure 2a). For ventral color, we detected five different color variations: ranged from whitish grey (ranged from L*= 60 – 70, a*= 1 – 4, b*= 13 – 15; *M. baeodon, M. whiteheadi, M. bartelsii* and *M. dollmani*), orange dark brown (ranged from L*= 40 – 58, a*= 4 – 8, b*= 12 – 25; *M. hylomyoides*), chestnut orange (ranged from L*= 44 – 60, a*= 4 – 11, b*= 14 – 26; *M. ochraceiventer*), yellowish brown (L*= 50 – 65, a*= 5 – 9, b*= 24 – 31; *M. alticola*) and creamy white (L*= 45 – 88, a*= -0.4 – 15, b*= 5 – 35; *M. rajah, M. hellwaldii* and *M. surifer*) (Figure 2b and Table 2). As typical for many rodents, individual hairs of this part were mostly uniform color on each variation.

Table 1. Descriptive analysis: mean, number of specimens, standard deviation, maximum and minimum values of dorsal color measurements.

Species		SCI			SCE		
		L*	a*	b*	L*	a*	b*
Maxomys hellwaldii	Mean	28.98	6.56	12.64	28.81	6.60	12.77
	Min	25.73	4.35	8.88	25.54	4.36	8.98
	Max	34.49	9.76	19.17	34.52	9.82	19.33
	Stdev	2.41	1.85	3.30	2.48	1.86	3.31
Maxomys musschenbroekii	Mean	26.17	4.23	9.08	26.16	4.24	9.16
	Min	20.43	2.25	4.38	21.19	2.29	4.47
	Max	33.42	7.97	18.88	33.34	7.96	18.85
	Stdev	3.08	1.31	3.36	2.86	1.31	3.34
Maxomys pagensis	Mean	28.37	6.46	11.78	28.29	6.48	11.86
	Min	21.74	2.92	5.04	21.71	2.93	5.12
	Max	36.33	11.06	20.19	36.19	11.07	20.44
	Stdev	4.19	2.25	4.38	4.19	2.27	4.39
Maxomys bartelsii	Mean	28.37	5.85	10.00	28.31	5.86	10.06
	Min	19.49	2.20	3.71	19.39	2.31	3.82
	Max	35.03	8.42	17.28	35.06	8.63	17.58
	Stdev	3.61	1.30	2.77	3.62	1.33	2.82
Maxomys dollmani	Mean	27.72	3.78	7.51	27.64	3.80	7.56
	Min	24.23	2.90	5.84	24.20	2.91	5.91
	Max	31.19	5.05	9.57	31.01	5.11	9.60
	Stdev	2.72	0.79	1.34	2.59	0.81	1.33
Maxomys baeodon	Mean	25.49	6.03	10.04	25.46	6.04	11.71
	Min	18.19	4.05	5.78	18.67	3.98	5.79
	Max	32.69	8.64	14.74	32.49	8.63	71.05
	Stdev	3.17	1.29	2.60	3.01	1.31	9.97
Maxomys alticola	Mean	26.04	6.74	11.84	25.97	6.76	11.89
	Min	22.15	5.11	8.49	22.19	5.13	8.55
	Max	33.65	8.78	18.07	33.66	8.93	18.16
	Stdev	3.61	1.13	2.93	3.58	1.16	2.95
Maxomys ochraceiventer	Mean	26.93	5.72	9.81	26.87	5.75	9.91
	Min	22.89	4.05	6.62	22.72	4.08	6.57
	Max	32.69	7.66	13.94	32.49	7.69	14.01
	Stdev	3.05	1.16	2.57	3.06	1.20	2.66
Maxomys rajah	Mean	29.67	7.31	13.12	29.59	7.33	13.18
	Min	23.45	4.23	7.49	23.42	4.21	7.71
	Max	38.10	12.37	23.36	38.03	12.35	23.33
	Stdev	3.63	1.97	3.83	3.64	1.98	3.84
Maxomys surifer	Mean	31.46	7.84	14.61	31.40	7.87	14.70
	Min	25.90	4.01	7.63	25.83	4.00	7.71
	Max	36.68	11.86	22.94	36.66	11.85	22.91
	Stdev	3.06	2.03	3.40	3.02	2.03	3.39
Maxomys whiteheadi	Mean	24.53	5.91	9.84	24.55	5.91	9.79
	Min	13.93	2.04	2.99	17.05	2.13	3.22
	Max	32.53	10.84	27.39	32.41	10.87	18.29
	Stdev	3.79	2.22	4.23	3.66	2.23	3.91

Figure 2. Representative variation in coat color (a. *dorsal pelage* and b. *ventral pelage*) among species of *Maxomys* spp.

PCA and DFA analyses

We described color variations using Principal Component Analysis (PCA) from the dependent variables (color variables) and extracted into three components in both dorsal and ventral coloration. We explained a total of 99.28 % (PC1 = 75.38%; PC2 = 23.06%; and PC3 = 0.83%) of the variance in dorsal, and 99.09 % (PC1 = 82.22%; PC2 = 14.83%; and PC3 = 2.04%) of the variance in ventral color ($F<0.05$). We run the DFA for all variables in dorsal and ventral color, and detected that in dorsal color variables L* (lightness) and a* if specular components included (SCI) give strong influence to the variations with total of 100% variance extracted from 3 discriminant functions (Function 1 = 71.2 %; Function 2 = 17.5 %; and Function 3 = 11.3 %; $P<0.001$; df = 33). For ventral color, We detected variable L* with specular component included (SCI) and b* with specular component excluded (SCE) as the main variables that give most significant influence with a total variations of 100% extracted from two functions (Function

Table 2. Descriptive analysis: mean, number of specimens, standard deviation, maximum and minimum values of ventral color measurements.

Species		SCI			SCE		
		L*	a*	b*	L*	a*	b*
Maxomys hellwaldii (n= 3)	Mean	66.99	2.48	18.95	67.10	2.45	19.10
	Min	45.81	0.01	5.43	46.23	-0.08	5.47
	Max	81.72	6.11	34.79	81.46	6.12	34.84
	Stdev	10.61	1.66	8.25	10.33	1.66	8.21
Maxomys musschenbroekii (n= 4)	Mean	67.22	5.73	28.76	67.08	5.79	28.96
	Min	55.82	1.33	19.54	55.70	1.35	19.72
	Max	82.32	11.53	39.11	82.26	11.59	39.22
	Stdev	6.33	2.33	4.49	6.40	2.39	4.60
Maxomys pagensis (n= 4)	Mean	47.40	6.46	17.71	47.39	6.46	17.81
	Min	41.06	4.41	12.09	41.35	4.41	12.18
	Max	56.21	8.17	24.46	56.16	8.18	24.61
	Stdev	4.38	1.37	3.77	4.28	1.38	3.77
Maxomys bartelsii (n= 7)	Mean	65.73	1.62	13.17	65.67	1.60	13.25
	Min	46.82	-0.77	4.06	47.40	-0.78	4.15
	Max	85.12	5.60	26.67	84.90	5.05	26.62
	Stdev	9.25	1.28	5.62	9.12	1.21	5.65
Maxomys dollmani (n= 1)	Mean	70.16	1.10	13.41	69.98	1.11	13.52
	Min	62.34	0.39	11.47	62.01	0.40	11.71
	Max	77.74	2.25	14.85	77.68	2.29	14.94
	Stdev	7.23	0.77	1.35	7.26	0.79	1.31
Maxomys baeodon (n= 6)	Mean	59.67	2.29	13.50	58.40	2.30	13.64
	Min	50.82	0.57	7.64	12.51	0.58	7.74
	Max	68.32	5.47	21.65	68.26	5.47	21.73
	Stdev	5.22	1.14	3.62	9.96	1.16	3.72
Maxomys alticola (n= 2)	Mean	57.89	7.08	29.37	57.82	7.12	29.50
	Min	50.75	5.30	24.81	50.78	5.33	24.94
	Max	64.81	9.07	30.72	64.66	9.14	30.95
	Stdev	4.23	1.16	1.81	4.18	1.17	1.82
Maxomys ochraceiventer (n= 1)	Mean	52.54	8.07	20.88	52.63	8.10	21.02
	Min	44.08	4.39	14.77	44.58	4.55	15.26
	Max	59.05	10.72	25.37	58.86	10.73	25.41
	Stdev	4.27	2.38	3.11	4.19	2.37	3.06
Maxomys rajah (n= 7)	Mean	80.68	1.20	17.40	80.67	1.20	17.50
	Min	72.12	-0.40	12.77	72.35	-0.38	12.89
	Max	87.10	2.83	25.97	86.90	2.84	26.12
	Stdev	3.35	0.81	3.47	3.20	0.80	3.46
Maxomys surifer (n= 5)	Mean	74.55	3.55	24.21	74.50	3.56	24.35
	Min	59.62	-0.09	14.60	59.76	-0.07	14.71
	Max	86.17	15.02	35.18	85.96	15.06	35.32
	Stdev	7.43	3.59	6.11	7.38	3.60	6.13
Maxomys whiteheadi (n= 23)	Mean	60.32	3.67	14.64	60.26	3.85	14.88
	Min	42.38	0.05	5.97	43.11	0.09	6.06
	Max	78.44	12.64	30.37	78.13	20.14	30.43
	Stdev	6.68	2.56	5.10	6.56	2.99	5.11

Table 3. Total variance explained for dorsal color measurements of *Maxomys* from PCA analysis using correlation matrix.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	6.03	75.38	75.38	6.03	75.38	75.38
2	1.85	23.07	98.45	1.85	23.07	98.45
3	0.07	0.83	99.28	0.07	0.83	99.28

Only cases for which Species_no = 12 are used in the analysis phase.

Table 4. Total variance explained for ventral color measurements of *Maxomys* from PCA analysis using correlation matrix.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	6.58	82.22	82.22	6.58	82.22	82.22
2	1.19	14.83	97.06	1.19	14.83	97.06
3	0.16	2.04	99.10	0.16	2.04	99.09

Only cases for which Species_no = 12 are used in the analysis phase.

Table 5. Total explained variation for dorsal color measurements on two discriminant functions (DFs) using stepwise methods.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	1.741(a)	71.2	71.2	0.797
2	.428(a)	17.5	88.7	0.548
3	.276(a)	11.3	100	0.465

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

Table 6. Total explained variation for ventral color measurements on two discriminant functions (DFs) using stepwise methods.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	4.862(a)	76.5	76.5	0.911
2	1.493(a)	23.5	100	0.774

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

1 = 76.5%; and Function 2 = 23.5%; $P<0.001$; df = 22) (Tables 3-6).

Scatter plots of PCA in dorsal color are mostly overlapped among species and supported by DFA using group centroid graph. Consistent to descriptive analysis, there is less variations on the dorsal color, even though we extracted nearly 100% variations from the dorsal color. In ventral color, from PCA and DFA scatter plots, we detected five groups that clustered close to each other and consistent to descriptive analysis. First group of *M. hellwaldii*, *M. surifer*, and *M. rajah* were clustered close to each other, and some individuals were overlapped although group centroids are separated. Second group of *M. musschenbroekii, M. baeodon*, and *M. whiteheadi* stands closer than the other group, third group of *M. pagensis* and *M. alticola*, fourth group consist of *M. bartelsii* and *M.*

dollmani, and fifth group of *M. hylomyoides* and *M. ochraceiventer*. Fifth group seems to be the most distinctive group due to ventral coloration, separated farthest from other groups (Figures 3, 4, 5, 6).

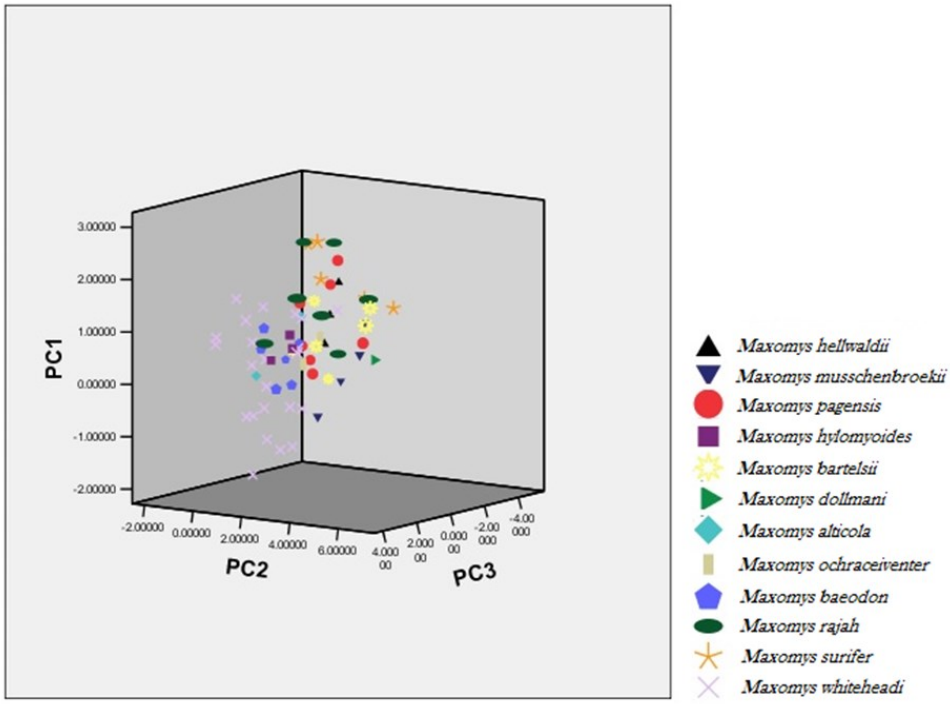

Figure 3. Three dimensional scatter plot from three components (PC1, PC2, and PC3) of PCA extracted from dorsal fur color variations among species of *Maxomys* spp.

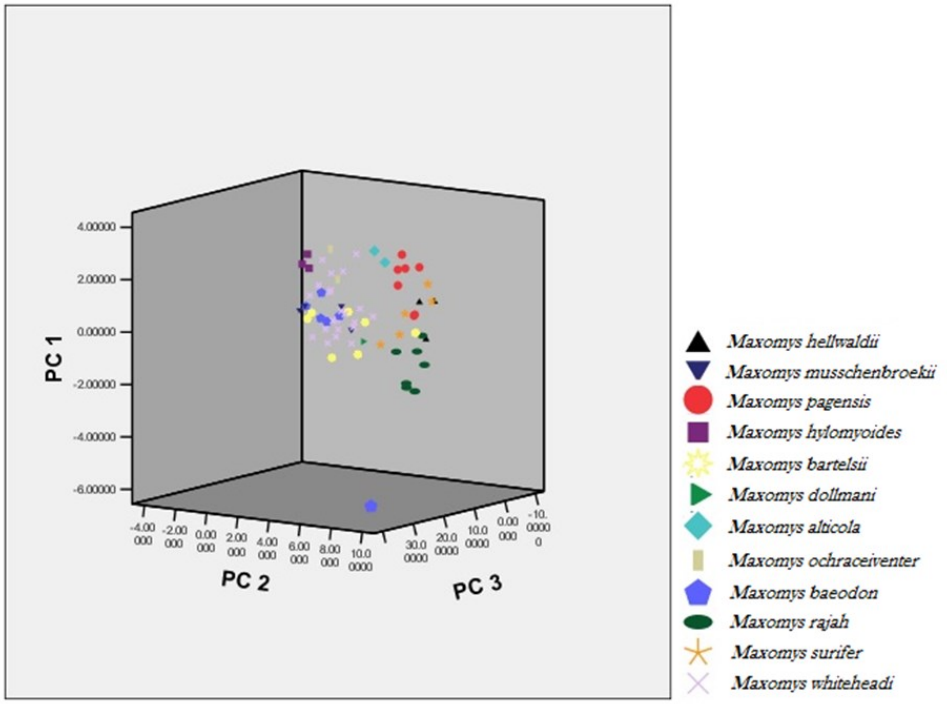

Figure 4. Three dimensional scatter plot from three components (PC1, PC2, and PC3) of PCA analysis that extracted from ventral fur color variations among species of *Maxomys* spp.

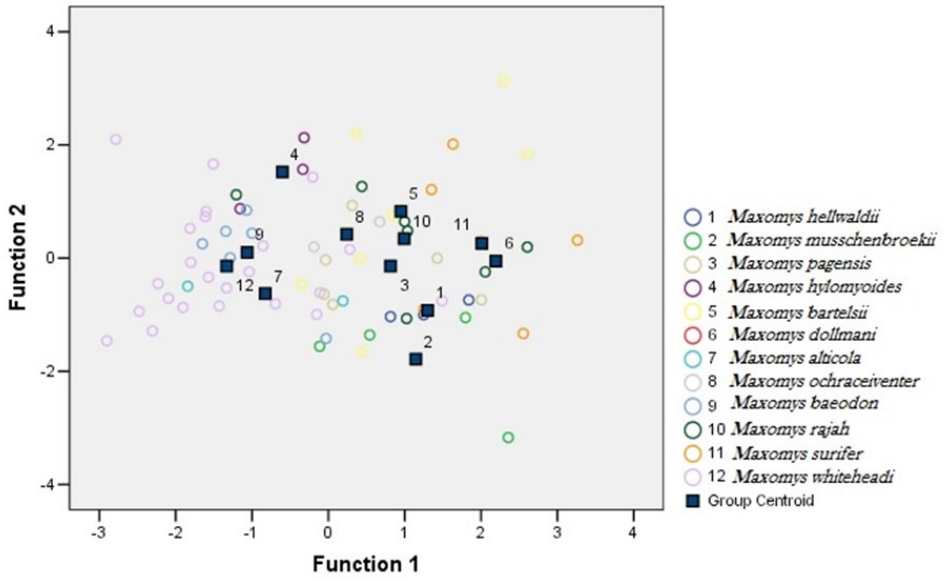

Figure 5. Plot of group centroid from DFA analysis (Function 1 and 2) among species of *Maxomys* based on dorsal coloration.

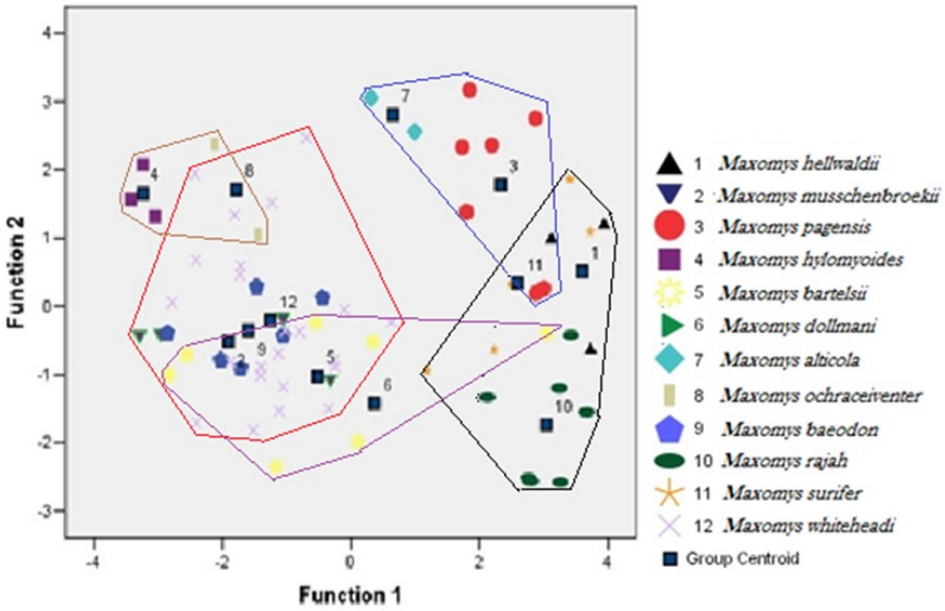

Figure 6. Plot of group centroid from DFA analysis (Function 1 and 2) among species of *Maxomys* based on ventral coloration.

Discussion

In mammals, especially murines, pelage coloration is one of the main key characters for species identification. Therefore, for some species pelage coloration used as the distinct features of the new species and descriptively determined in the monograph or in the diagnosis characters based on direct observation (Musser 1991, Pimsai *et al*. 2014). Otherwise quantitative information on color variation is very limited. In murines, few studies have been conducted to determine color variation based on quantitative analysis (Hoekstra & Nachman 2003; Lai *et al*. 2008;

Rios & Alvarez-Castaneda 2011; Salinas *et al*. 2015). Additionally, some of researchers expand the studies into molecular works (Ounpraseuth *et al*. 2009; Lamoreux *et al*. 2010; Kambe *et al*. 2011; Kodama *et al*. 2015).

Our study aimed to generate preliminary information of quantitative color measurements that presented on Tables 1-2 and Figures 3-6. As a result, it is clear that for some species, the discrete pelage coloration on ventral color can be used as distinctive character. However, for few species the resemblance of color configuration among species may cause confusion related to identify the species, though these obstacles can be support with other main characters from other external characters or skull and dental characters.

In this study, we detected that the dorsal coloration of *Maxomys* ranged uniformly from brown to dark brown. This result consistent to Caro (2005) who mentioned that the uniform coloration were found in some mammals (artiodactyls, carnivores, and lagomorphs) in certain habitat likely the closed environment, tropical forest, dense forest or swamp forest. As we know, the natural habitat of *Maxomys* spp are found in the tropical forest (lowland until montane forest), disturbed forest and swamp forest. Generally, uniform pelage coloration in rodents provides protective camouflage, which is believed to be driven by the need to avoid detection by predators with the whole pelage matching the background where animals are active (Sumner 1921; Dice 1947; Lawlor 1976; Krupa & Geluso 2000). However, we found more variations in ventral color (five significant lighter color than dorsum) from the specimens, this may because of counteract from the sun's effect (when it shines from above): lightening the dorsum and shading the ventrum (Thayer 1909, Kiltie 1988).

Recent study has demonstrating pelage color measurements using spectrophotometer to produce quantitative color variation among species of *Maxomys* spp. that can be useful for further research. Additionally, the observations of coat color variation have played an essential role in the understanding of many fundamental biological processes. Furthermore, molecular study of coat color variation within *Maxomys* spp. is needed to elucidate the mechanisms of phenotypic variation in morphology that affect the patterns of divergence, speciation and evolutionary history of *Maxomys*. We failed to obtain the sequences from *Maxomys* using *Mc1r* (melanocortin-1 receptor) gene, and probably will be better to use other gene such as *ASIP* (agouti signaling peptide) gene.

CONCLUSION

Here, we performed morphological analyses based on quantitative color measurements with specimens of *Maxomys* collected from throughout Indonesia from field works and those deposited at MZB. This quantitative measurements of coat color with a spectrophotometer revealed no significant difference in the dorsal pelage showing mostly dark brown (L*= 25-30, a*= 5-7, b*= 10-15). The ventral colorations were variable among the species. We classified five different color types based on the measurements: whitish grey (*M. baeodon, M. whiteheadi, M. musschenbroekii, M. bartelsii*, and *M. dollmani*), orange dark brown

(*M. hylomyoides*), chestnut orange (*M. ochraceiventer*), yellowish brown (*M. alticola*) and creamy white (*M. rajah*, *M. hellwaldii*, and *M. surifer*). These fur color characteristics can be useful in species recognition, together with the craniometric features.

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