



Morphometric variability of *Praomys misonnei* (Rodentia: Muridae) in west central African forests reveals complex relationships between populations

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Abstract

This study addresses the morphological biometrics of *Praomys misonnei* and the signatures of its population history through a survey of external morphological characters measured on 133 individuals from eight West Central African (Gabon and Cameroon) localities. Four standard external characters were measured: head + body length, tail length, hindfoot length, and ear length. Using univariate and multivariate statistics, we inferred inter-population relationships from these morphometric characteristics and tested hypotheses of historical patterns of local adaptation (phylogenetic relationships) or of association with ecological gradients. We also tested the influence of sex on morphometric parameters. Our results support the existence of two morphometrically distinct groups of *P. misonnei*. The first one includes individuals from northern, central, and southern Gabon, while the second one includes individuals from southern Cameroon and one locality in southern Gabon (Mbaya). This result could be explained by the fact that the first group inhabits an area mainly covered by dense rainforest (about 90% of Gabon), while the second group is found in degraded forest or mosaics of forest-savanna habitats (Cameroon and southeastern Gabon). Another reason could be seasonal reversal, which has been postulated right at border between Gabon and Cameroon. The pattern of morphometric variation was correlated with local environmental factors. No sexual dimorphism was recorded.

Keywords: Morphometrics, external characters; Biometric measurements; *Praomys misonnei*; Geographic variation; Central Africa

1 Introduction

Muroid rodents (Muridae family) represent a highly diversified mammalian clade that inhabits in nearly all habitat types [1]. Biometric body data on this taxon in Central African rainforest remain relatively sparse. Recent studies have emphasized the role of habitat gradients in lineage diversification. Most authors have focused on cranial measurements from small rodents (Lavrenchenko et al. (2007) [2]; Nicolas et al. (2008) [3]; Lalis et al. (2009) 4; Katy et al. (2020) [5]) because they are usually supposed to be less affected by adaptive evolution [1]. However, the entire body size itself may play an important role in the adaptive profile of a species and is sometimes subject to rapid evolutionary changes, as clearly demonstrated by the phenomenon of island gigantism repeatedly reported in other murids, e.g. *Apodemus*; [5] recently analysed the cranial morphometry of West Central African *Praomys misonnei* populations, and found that rainfall gradients and vegetation structure were associated with craniometric variation. Nicolas et al. (2011) [6] also showed a strong phylogeographical structure of *P. misonnei* (four clades) in tropical Africa, with one clade from West Central Africa clearly defined. This author detected signs of population expansion in most *P. misonnei* clades or subclades. This paper focuses on *P. misonnei* which is widely distributed from eastern Ghana to western Kenya (Nicolas

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et al. (2011) [6]). It is also a commonly found strict forest rodent, not associated with human activities. Like most small terrestrial mammals, it probably has low dispersal abilities. This latter property, together with narrow habitat requirements, makes this species a good material for evolutionary biogeographical studies [7].

West Central Africa is mainly covered by rainforest. The current forest expansion and fragmentation has not obliterated the genetic pattern of the latest episode of large expansion of species in this continuous forest landscape [8]. In the present case, the history of the geographical distribution of *P. misonnei* is expected to be closely related to the forest landscape in West Central Africa, which underwent vegetation changes over the last 150,000 years (summarised by Dupont et al. (2000) [9] and more detailed for the last 70,000 years by [10,8]. Rainforests are characterised by seasonal changes in several ecological parameters, including rainfall, relative humidity, leaf fall, leaf litter, fruit fall, and insect and earthworm abundance [11]. At the regional scale, the rainforests of Gabon and Cameroon are associated with different temperature and rainfall gradients. For example, the time of the small dry season in Gabon (mid-December to mid-March) corresponds to the great dry season in Cameroon (December to February). Correlated with this seasonal reversal, many rainforest animals – notably small rodents – can show changes, especially in the size of the specimens that colonise these environments. For instance, Nicolas et al. (2011) [6] identified two subclades in West Central Africa; one was limited to one locality from southern Cameroon, while the other had a broader geographical distribution in West Central Africa. Following this phylogeographic structure of *P. misonnei* populations in Central Africa, we wanted to know if these populations also had a morphometric pattern in link with their geographical range at the regional or local scales. We used body measurements of individuals from five localities from central, northern, and eastern Gabon and three from southern Cameroon to study their morphometric variability. The localities differ in their vegetation, soils, animal species, climate and degree of geographic isolation ([12]; Goodman et al. (2001) [13]; Ayissi et al. (2013) [14]; 2018 [15]; Dadem Gueguim et al. (2018) [16]; Temgoua et al. (2018) [17]). While determining if morphometric variation of *P. misonnei* populations is associated with ecological gradients – in other words, if their morphometrical patterns are influenced by habitat type –, we expected to find (1) a size difference between individuals from Gabon and those from Cameroon (regional scale); (2) a size difference between specimens from spatially distant populations within a same country (local scale); (3) size similarity between individuals from northern Gabon and those from southern Cameroon (regional scale) due to their geographic proximity. This could contribute to identify the body parameters that best describe morphological variability of this species in West Central Africa.

2 Material and methods

2.1 Study sites

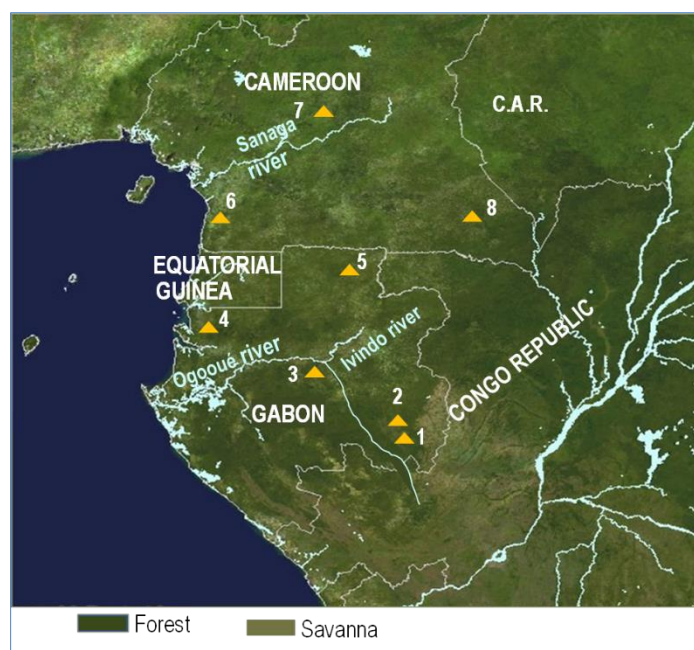


Figure 1 Map (www.globalforestwatch.org; modified by Mboumba et al.) showing the geographical localities from which the populations of *P. misonnei* were collected in Gabon (1: Kessala (KS), 2: Mbaya (MB), 3: Lopé (LOP), 4: Monts de Cristal (MC) and 5: Minkébé (MKB) and Cameroon (6: Campo-Ma'an, (CPM), 7: Mbam-Djerem (MD) and 8: Lobéké (LBK)

This study took place from May to July 2013 and from May to July 2014 in five localities in Gabon and three localities in Cameroon. Gabon and Cameroon are known for their natural habitat heterogeneity, with savanna areas interspersed with strips of gallery forest and forest islands often located near continuous forest.

In Gabon and Cameroon, the climate has four seasons, i.e., two humid seasons alternating with two dry seasons. More specifically, seasons are as follows in Gabon: the great dry season (June-September), the small rainy season (March-June), the small dry season (December-March), and the great rainy season (September-December). In Cameroon, seasons are as follows: the great dry season (December-February), the small rainy season (March-June), the small dry season (July-August) and the great rainy season (September-November). We sampled animals across different forest habitats, including primary forest, secondary forest and periodically flooded secondary forest, all present in Gabonese and Cameroonian localities. This study was carried out in the buffer zones of four National parks (NPs) in Gabon and three NPs in Cameroon, but also in one other forest-savanna mosaic locality (Mbaya: MB) in Gabon (Figure 1).

In Gabon, the sites were as follows:

Lopé NP (LNP; Central Gabon) is a lowland forest in the center of Gabon (Mboumba et al. (2020) [18]). Most of the park is covered by a semi-evergreen lowland rainforest and forest-savanna mosaics corresponding to the Congolian mosaic of lowland rainforest, and secondary grassland [19]. The consensus about the origins of these savannas is that they are natural relicts of a drier period [20], and have persisted for thousands of years. Several types of forests have been described [21] according to their structure and species composition: forest groves in savannas, gallery forest, Marantaceae forest, and mature forest. LNP is enclosed in the African equatorial moist forest [21]. Temperatures vary little over the year, but mean monthly minima and maxima are lowest during the major dry season (20-23°C and 26-33°C, respectively) (Mboumba et al., 2020[18]). The area receives about 1,500 mm annual rainfall, substantially less than in its surroundings, with a long dry season lasting about three months from mid-June to mid-September (Bremond et al. (2021) [22]). The climate is an equatorial transition type (hot and humid). Our study was conducted in Lopé NP buffer zone (00°07' S, 011°42.3' E)

Minkébé NP (Northwestern Gabon) is an area of mixed heterogeneous forest, Marantaceae forest, swampy flooded forests and inselberg forests (Gooman et al. (2001) [13]); Larson & Breda, 2018) with an equatorial climate. The average annual rainfall is 1,800-2,000 mm/year, and the temperature is 24 °C (Huijbregts et al. (2003) [23]). Minkébé is also the largest of all Gabonese NPs and is part of the Northwest Congolian Lowland Forest ecoregion. Our study site was conducted in Minkébé NP buffer zone (01°09.436' N, 12°41.849' E).

Mont de Cristal NP (Mons de Cristal region, Northwest Gabon,) is characterised by upland forest and lowland swamp forest. The natural vegetation of this region is globally dense humid evergreen rainforest (Medjibe et al., (2011) [24]), and the climate is of the transition equatorial type, with an average annual average rainfall of 2,000-2,400 mm, and average temperatures of 24-26 °C. The study was conducted in the periphery of Mons de Cristal NP (00°51.613' N, 10°31.744' E).

Kessala and Mbaya are located in the Batéké Plateaux region (south-eastern Gabon). Mbaya (a neighbourhood of Franceville, 01°40 S, 13° 31'E) and Kessala (located 2 km north of the northern border of the Batéké Plateau NP buffer zone; 01°51.907' S, 013°51.120'E), are crossed by the Mpassa River, 50 km from Franceville. These two localities are characterised by lowland forest made up of a mosaic of forests and savannas. The mean annual rainfall is 1,800-2,000 mm minimum and 2,000-2,500 mm maximum, and the climate is a transition equatorial type.

In Cameroon, the sites were as follows: the coastal forests in Campo-Ma'an (CM) NP, in southwestern Cameroon. The Campo Ma'an rainforest (Bekhuis et al. (2008) [25]) is unique at the species level, and its fauna and flora differ from those of Lobéké forest. The climate is equatorial with about 2,800 mm average annual rainfall, and the mean annual temperature is about 25 °C. Part of the area around the park acts as a buffer zone, making the forest contiguous with that of Equatorial Guinea and Gabon (Bekhuis et al. (2008) [25]). The site is located at the southern periphery of CM NP (02°20.52' N; 10°12.634' E).

Lobéké is located in the northwest of the Congolese basin slope (Zapfack et al. (2013) [26]), and characterised by the presence of clearings on hydromorphic soil. Its vegetation is very important for large and medium-sized herbivores. The climate is typically equatorial, and rainfall occurs throughout the year. The maximum rainfall is approximately 1,500 mm/year. Mean temperature is 25.4 °C, with a slight seasonal variation. From a phytogeographic viewpoint, Lobéké is a transitional forest between the evergreen forest of Dja and semi-deciduous forest of Malvaceae and Ulmaceae). The site is located at the southern periphery of Lobéké NP (' 02° 16.940' N, 15° 40.428' E)

Mbam-Djerem is situated in the central part of Cameroon (Figure 1) at the northern limits of the Guineo-Congolian forest, where the rainforest fades into savannah (Chifu Nchanji & Fotso, 2006 [27]). This region harbours an exceptionally rich diversity of habitats, including closed-canopy rainforest, woodland savannah, riverine forest, gallery forest, tree and bush savannah and flood savannah ([27]). The climate is Sudano-Guinean type (Dadem et al. (2018) [28]), average annual rainfall is 1,900 mm, and average annual temperature is 24 °C (Bobo et al. (2006) [29]). The site is located at the southern periphery of Mbam-Djerem NP ('Open forest, riparian forest: 06° 09.213' N, 12° 51.106' E)

2.2 Sampling method and species identification

We caught the animals alive using baited Sherman traps (7.5 × 9 × 23 cm) (see sampling protocol details in Mboumba et al. (2019) [30]). The specimens were collected by the authors during field studies in different localities of Gabon and Cameroon. The traps were checked twice a day in the early morning and late afternoon, and fresh bait was supplied when necessary. Most of the studied *P. misonnei* specimens were determined using an identification key based on external morphological characteristics, morphometric measurements, and cranio-dental examinations (Denys et al. (2012) [31]; [32]). Then, individuals were sexed, weighed, and measured. For the specimens whose species identity was difficult to determine using morphological characters only, genetic analyses were performed to confirm the identification. All specimens were identified on the spot and released straight away.

2.3 Morphometric analysis

The skeletal elements of mammals grow at different times in different species. This may further complicate the interpretation of correlations among traits [1]. We avoided this potential problem by including only fully grown individuals in our analyses, with sufficient tooth wear and fully developed gonads. Therefore, adult *P. misonnei* specimens were used to compare several body parameters of different populations. We performed a classical morphometric analysis on external parameter distances, focused on parameters of body size. For each individual specimen, four standard external measurements (in millimeters) were made using calipers: head and body length with head (HBL; length from the tip of the nose to the root of the tail); tail length (TL; length from the root of the tail to the tip of the first caudal vertebra); hindfoot length (HFL; length of the hindfoot, claws included); ear length (EL; length from the base of the auditory meatus to the farthest tip of the pinna, measured laterally). All these measurements were made by the same collectors. We excluded weight measurements because gravid females can cause a bias.

2.4 Statistical analyses

Morphometric characters were investigated for geographic variability in the size of individuals among different regions of Gabon and Cameroon.

The body variability in each population was first calculated using descriptive statistics: mean, minimum, maximum, standard deviation. Standard univariate and multivariate statistics were calculated from external measurements. Sexual dimorphism was statistically evaluated by a one-way analysis of variance analysis (ANOVA). An ANOVA was also used to assess differences between body parameters (see above). The normality of the data was checked beforehand using a Shapiro-Wilk test. In the absence of data normality, a non-parametric Kruskal–Wallis (KW) test was performed to compare the averages of each morphometric parameter among populations. *Post-hoc* comparisons were carried out using Tukey's HSD test to identify the significant differences. A principal component analysis (PCA; Hotelling, 1933) was performed to highlight the overall divergence between samples and visualise intra-species variability within each locality. The influence of growth on external measurements was analysed. Males and females were considered together since preliminary analyses did not show any sexual dimorphism. A total of 122 individuals was used for this last analysis (PCA). All analyses were performed with R software (version 4.1.2; [33], <http://www.r-project.org>).

3 Results

A total of 133 individual adult specimens were sampled from Gabon and Cameroon May to July 2013 and from May to July 2014, and morphometric measurements were performed on them (Table 1).

Table 1 Standard body measurement (HBL: Head-Body length; TL: Tail length; HFL: Hindfoot length; EL: Ear length) in mm from *P. misonnei* studied from Gabon and Cameroon localities. m: mean; s: standard deviation; min-max: minimum and maximum

Species	Country	Locality	Number	Head and Body (HBL)			Tail (TL)			Hind-foot (HFL)			Ear (EL)		
				m	s	min-max	m	s	min-max	m	s	min-max	m	s	min-max
<i>Praomys misonnei</i> (Van der Straeten & Dieterlen, 1987)	Cameroon	Campo-Ma'an	11	109,6	4,19	105 - 119	133,6	5,34	127,1 - 143,3	21,9	0,62	21,2 - 22,8	15,9	0,77	14,9 - 17
	Cameroon	Lobéké	16	106,1	5,79	95,5 - 114,7	136,9	8,89	123,7 - 157,9	21,6	0,51	21 - 22,6	16,9	0,43	16,3 - 17,6
	Cameroon	Mbam-Djerem	22	109,8	8,62	92,4 - 128,4	137,5	8,72	125,2 - 153,6	22,6	0,93	21 - 23,9	17,3	0,75	15,8 - 18,4
	Gabon	Kessala	13	102,9	13,95	86,11-138,5	129	16,9	83,2 - 150	23,2	1,35	21 - 25	16	1,75	12-17,3
	Gabon	Lopé	21	107,2	6,87	97,2 - 120,8	134	7,67	119,9 - 149,3	21,7	1,07	19,9 - 24,4	0	0	0
	Gabon	Minkébé	21	109,9	12,29	74,2 - 123	126,9	13,73	99,4 - 146,8	23,3	1,67	21,5 - 24,6	16	2,27	10,3-18,6
	Gabon	Mbaya	7	113,8	17,45	75,5- 125	139,7	25,79	83-156	22,5	1,12	20-23	16,3	1,6	13-18
	Gabon	Mt Cristal	22	105,2	8,64	92 - 123,8	128,6	10,64	96 - 149,7	22,6	1,25	21,1 - 25,9	16,9	1,13	15,2-19,2

3.1 Morphometric comparisons of sexes and sites

Among the 133 individuals, xx were males, xx were females, the greatest number of specimens was collected in Mont de Cristal, Mbam and Djerem (n = 22 at each site), while the lowest number was collected in Mbaya (n = 7; Table 1). There was no significant difference between males and females for HBL (F = 3.06, df = 1, p-value = 0.0864).

The absence of sexual dimorphism implied that sex had no influence on the size of individuals. Therefore, male and female individuals were pooled for further analyses. Kruskal-Wallis test globally showed significant differences between regional or local parameters: HBL, TL, EL and HFL were significantly different at the regional or local scales (p-value < 0.05); EL was not significantly different at the regional scale (F= 2.88, df = 1, p-value = 0.089).

3.2 Principal component analysis (PCA)

The first two axes PC1 and PC2 represented 45.20% and 27.01% of the total variance, respectively (Figure 2).

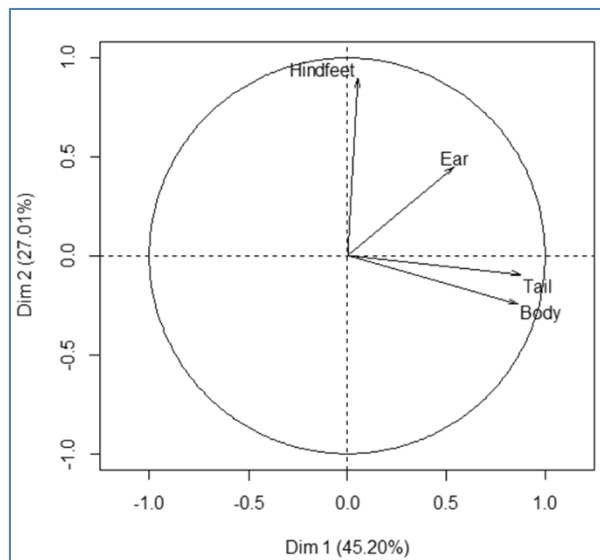


Figure 2 Principal component analysis (PCA) of external size variables from 122 individuals. Plot of the first (PC1) and second (PC2) principal components in *P. misonnei* explaining, respectively, 45,20% and 27,01% of the total variance

The projection of the four body variables on the PC1 x PC2 planes showed that the PC1 axis was positively correlated with all variables. On the other hand, two variables (HL and EL) were positively correlated with the PC2 axis. The variable most positively correlated with the PC2 axis was HL, with a correlation value of 0.90. The scatter plot of the individual PCAs according to region and locality showed different distinct groups (Figure 3 A and B).

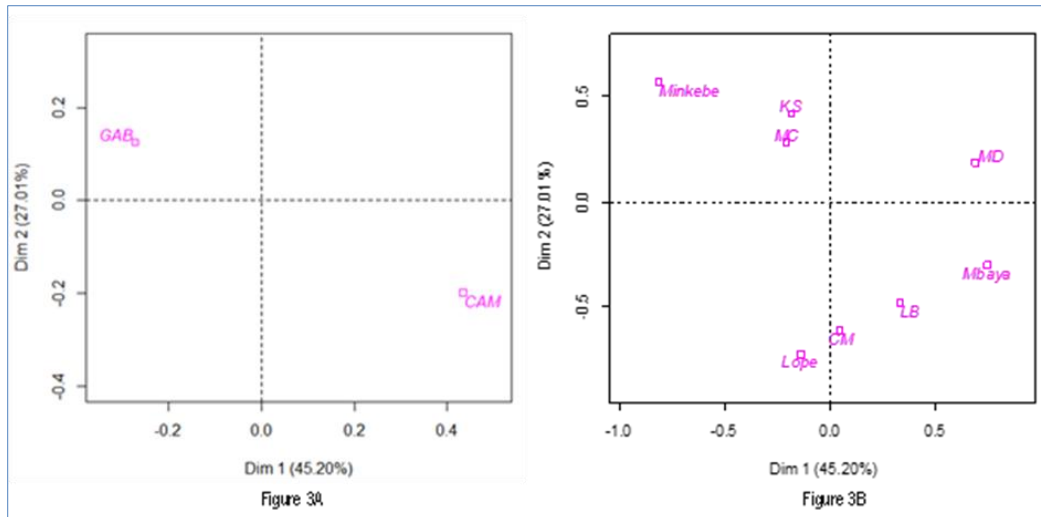


Figure 3 Principal component analysis (PCA) of external size variables from 122 individuals. Plot of the first (PC1) and second (PC2) principal components in *P. misonnei* explaining, respectively, 45,20% and 27,01% of the total variance based on regions (Figure 3A) and localities (Figure 3B). GAB= Gabon and CAM= Cameroon

All specimens from Cameroon were located on the positive side of the PC1 axis. Conversely, specimens from localities in Gabon were mainly located on the negative side of the PC1, except Mbaya. Most specimens from Gabon (KS, Minkébé, MC and Lobé: Figure 3B) were smaller, while those from Cameroon (CM, LB and MD: Figure 3B) were larger. In Gabon, only individuals from Mbaya were larger and similar in size to those from Cameroon. The populations from Cameroon exhibited the greatest morphometric variability on this positive axis and at the local scale: Mbam-Djerem populations were characterised by relatively long hindfeet and ears, while Lobéké and Campo-Ma'an populations were characterised by relatively long bodies and tails (Table 1).

4 Discussion

The analysis of *P. misonnei* sexual dimorphism data did not reveal any sex-related discrimination of morphological characters. This result is in accordance with Nicolas et al. (2003) [34]; Lalis et al. (2009) [4]; Kouakou Bohoussou et al. (2014) [35]. This suggests that males and females followed the same growth pattern, at least during one period of their development.

The morphometric study results revealed significant morphological variability among *P. misonnei* populations from Gabon and Cameroon. The greatest differences were observed in the hind foot, body, and tail lengths. This morphometric structuring could be explained by the wide distribution of this species in West Central Africa and the vast landscape and environmental diversity of this region.

The PCA revealed great variability in the morphology of individuals within a same forest region or among forest regions. The analysis also revealed a distinct differentiation between Gabon and Cameroon at the regional scale. The *P. misonnei* specimens from Gabon clustered together and differed from those from Cameroon. This result could be explained by biogeographical conditions: the first group inhabits an area mainly covered by dense rainforest (about 90% of Gabon), while the second group is found in degraded forest or mosaics of forest-savanna habitats (Cameroon and southeastern Gabon). Another reason could seasonal inversion, which has been postulated right at the border between Gabon and Cameroon (Katy et al. (2020) [5]). The parameters that most contributed to this clustering were body and tail lengths. The morphometric results of the populations from northern Gabon and those from southern Cameroon differed significantly. These populations are located in diverse bioclimates: equatorial climate for Campo-Ma'an, Lobéké and Minkébé; subequatorial climate for Mbam-Djerem; equatorial transition climate for MC. This result is in line with those of Nicolas et al. (2011) [6] who showed that these geographically close populations do not share common haplotypes despite several genetically identified subclades. These authors also highlighted that potential forest refugia may have been localised in southwestern Cameroon and northern Gabon. Our results show that these forest refugia (southwestern Cameroon vs. northern Gabon) have not come into contact. A certain biogeographical barrier, likely a large area of savanna or a river, must have persisted in this region, and impeded a general expansion of austral populations (*P. misonnei*) from Cameroon to the northern parts of the Gabonese forest block. However, we remain cautious about this hypothesis.

Other biogeographical patterns were more surprising, such as the clustering of three populations from south Cameroon with one from south-eastern Gabon (Mbaya): the latter population dwells in lowland forest, whereas the sites of the Cameroon regions are at higher elevations. The populations from these localities showed no significant difference in size despite their geographical remoteness. This result suggests that i) an ancient contact that existed between the southeastern Gabon and south Cameroon forests during the savanna expansion did not disappear, or ii) the forests of southeastern Gabon and south Cameroon have a common history, notably during the forest reconquest (Holocene). This may also be due to i) the persistence of a forest corridor during the forest fragmentation periods (forests were strongly reduced 145,000-130,000, 70,000-40,000- and 30,000-12,000-years BP), but also during a short forest destruction period (2,500 years BP) that is still going on today and promotes a recent colonisation by *Praomys* individuals in the study area, ii) the biogeographical history of *Praomys* in West Central Africa. The present and relatively recent forest expansion and savanna fragmentation would not have obliterated the genetic pattern of the latest episode of large expansion of the species in a continuous forest landscape. This last result is in line with Nicolas et al. (2011) [6] who showed that *P. misonnei* populations from southern Cameroon and from southern Gabon share common haplotypes.

In addition, these authors identified forest refugia localised in southern Gabon. Our results show that despite the successive phases of savanna expansion in West Central Africa (Cameroon and Gabon), these forest refugia (southwestern Cameroon vs. northern Gabon) have been in contact and so have their faunas. Another unexpected result was that the populations of KS (Gabon) differed from those of MB (Gabon), although MB and KS appeared to be more similar in terms of environment (lowland forest) and geographic proximity in contrast to the forests of south Cameroon. However, at a local scale (Batéké Plateaux region), KS and MB individuals showed no similarity in the measured parameters, suggesting an influence of local ecological factors on their external morphological parameters. Ours results show that the morphometric differences between *Praomys misonnei* populations are not tightly linked to climate/vegetation type or geographical distance between populations.

5 Conclusion

The study of *P. misonnei* populations in Gabon and Cameroon shows that the variation of certain body parameters is not a function of geographic distance (or site proximity). Local and regional factors could influence the size of individuals just as historical events (including past forest fragmentation) may have influenced current morphological models. However, it would be interesting to test other strict forest murids to further confirm this hypothesis.

Compliance with ethical standards

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Disclosure of conflict of interest

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