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Full Length Research Article

Mesowear Pattern of the Fourth Upper Premolar in Tropical Raccoons (*Procyon cancrivorus)* From Three Nigerian Ecologic Zones: Intra-specific Dietary Resource Partitioning

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Summary: Tooth-wear signatures obtained from maxillary carnassial fourth premolar teeth of raccoons in three ecologic regions in Nigeria testified to segregations in diet of the species with more abrasive diet in specimens from coastal south-western areas compared to more vegetal diet content of those from middle belt and northern areas. Endoloph assessments showed sexually dimorphic mesowear signals between and within locations suggestive that males are more exposed to dental wears compared to females; Male and female specimens from rainforest zone had 40.2% and 34.2% respectively, Sudan Savanna zone had 46.8% and 40.6% for females and males while 67.6% and 44.3% for Sahel zone specimens in similar order. We investigated dietary resource use for sustained survivability within limits of interspecific spatial overlaps using seasonal rainfall indices between two years. There was 86% per high dental occlusal surface relief in the specimens from the savannas while 32% per low relief was observed in South-Western badgers teeth samples. This study observed a change in habitat use as a predisposing factor to sub-regional dental wear differences among age groups as well as sexes of species from three geographic climatic areas. The richness of the eco-habitat/life expectancy found in the rain forest can be ascribed to diet availability which is reduced in the savanna areas. The study suggests minimal change in habitat use as a predisposing factor in sub-regional species dental relief differences observed among age groups and sexes of the species from three geographic climatic areas and also represents quality of the eco-habitats.

Keywords*: Procyon cancrivorus, premolar, dental wears, mesowear*

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INTRODUCTION

The knowledge of range distribution, diet and spatial interaction of tropical raccoons, *Procyon cancrivorus* in Nigeria with respect to geographic and climatic variations has not been documented beyond primary records in the South-Western regions compared to the *Procyon oideslotor* or the common raccoons (Happolds and Happolds, 1987; Mackwell, Simon-Miller *et al*, 2013). A fauna qualitative and quantitative accessibility difference exists within the three ecological zones and impact on diet composition (Drygala and Zoller, 2013). Dietary components in raccoons consists of 40% invertebrates, 33% plant materials and 27% vertebrates (Zeveloff, 2002), this proportion alters with season and availability (Kitchen *et al*, 1999; Feldhamer *et al*, 2003) and are dependent on ocean tides, temperature deviations, precipitations and intercontinental discontinuity shifts especially in competitive or tolerant interactions and colonization of spatial territories (Pergams and Lawler, 2009) occasioned by climate dynamics (National Meteorological Agency, 2010). Lower coastal temperatures, longer period of rain and thick under vegetation in coastal and mangrove areas; characterizes the South-Western rain forest and favorable for richer fauna while the Semi-Savanna and arid Savanna zones are synonymous with a higher and sustained temperature deviations coupled with thin sparse vegetation supporting fewer prey species (NIMET, 2010; Rivals, Solounias and Mihlbachler, 2007). The three ecological zones evaluated for the diet partitioning in Nigeria are separately characterized by varied precipitation and consequent fauna and flora types (Happolds and Happolds, 1987). Rainfall in the rainforest zone averages 2500mm but 250-750mm in the Sahel zone (NMET, 2010). Vegetation varies with soil structure, available water and photoperiodicity (Happolds and Happolds, 1987; Calandra *et al*, 2016). Dental-based method as suggested by Fortelius and Solounias (2000), Kaiser (2002) and Franz-Odendaal and Kaiser (2003) allows for dietary reconstructions through the use of mesowear method on dental structures alone and has been employed in comparison-inference based differences in food availability and habitat structure (Schulz *et al*, 2007). This study captions age class identity diet type by mesowear equilibrium and age segregations in relation to fauna quality (ecologic zones). Age segregations is also assessed relative to locality climate, and further evaluate sexual segregations in food type selection, availability and spatial interaction using mesowear equilibrium; a method which assess dental occlusal relief relative parameters in inference of diet types. The resolution of accuracy of this method increases with

sample size and has been speculated to find utility in demographic studies and determination of fauna index (Popowics, 2003). This species' peculiar behavior in different ecologic environment variations might be a substrate in conservation efforts on the coastal extant species (International Union of Conservation of Nature, IUCN, 2012). We therefore hypothesize that:

- The mesowear equilibrium should reflect either differential food availability to different age classes or ontogenetic gradients in tooth wear and morphology
- Age segregation should be related to environmental conditions and dietary signals should therefore reflect abiotic habitat parameters such as the local climate and geomorphology.
- The mesowear equilibrium should resolve proposed sexual segregation in forage selection and availability

A combination of the machinery of principal components, cluster analysis and correlations was utilized in the discrimination of dietary traits evidenced from the dental profiles exhibited by this species from three ecological zones in Nigeria (Happolds and Happolds, 1987).

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MATERIALS AND METHODS

Sampling (ethics, sites, technique and time): Ethical approval for the study was given by the University of Ibadan Animal Care, Use and Research Committee (UI-ACUREC/App/2015/055). For the purpose of this investigation, 376 maxillary dentitions were obtained from wild-captured *Procyon cancrivorus* species from three locations in Nigeria: South West rain forest (Oyo state), the middle belt semi-savanna (Benue state) and Savanna (Adamawa state) eco-environmental zones respectively (Happolds and Happolds, 1987; Winkler *et al*, 2016). The specimens represented an aggregate of museum skulls and currently captured forty animals. Samples from the climes had an average of a year difference in date of collection while climatic data remains valid.

Samples distribution and animal aging: One hundred and eighty-eight dentulous maxilla comprising of 27 females (54 P^4) and 33 males (66 P^4), 30 females (60 P^4) and males (60 P^4) apiece, and 35 females (70 P^4) and 33 males (66 P^4) were used for the study. This comprised of 120 P^4 from the rain forest, semi-savanna (120 P^4) and savanna zones (136 P^4) respectively. They all contributed 376 upper 4^{th} premolars (Females =184, Males=192). Age determination was according to Grau *et al*, 1970; Samaranch and Gonzalez, 2000; Androukaki *et al*, 2002. The age classes 1-9 were recognized but animals under 2years (age class 1-6) were ignored for attrition-abrasion equilibrium stability while age class 7-9 were utilized for the study.

Images: Images of the 4^{th} upper premolar were taken with a digital camera CANON EOS 1200D with EFS 18-55mm and stabilizer equipped with HAMA tripod (Figure 1A-C). Digital images were taken with a DIN 6cm, focal length of 5.6cm, ISO speed 200, sensitivity of 1/500 and a ruler scale. Linear evaluations of occlusal surface, cusp depths and height changes were analyzed with Motic ® Images 2.01.

Mesowear method and modifications: Mesowear method measures attrition/abrasion equilibrium in tooth wear and has been used extensively in quantifying herbivores and ungulates dental wears. It provides an average wear signal over a considerable period of time (Calandra *et al*, 2016; Kaiser, 2002). Lingual/mesial surface images of maxillary 4^{th} premolar (P^4) were taken for lingual mesial aberrations (Ellis *et al*, 2008; Ulbricht *et al*, 2015), occlusal surface relief (OSR) and cusps shape (Fortelius and Solounias, 2000). Polysiloxane putty was employed in molding tooth surface layer after cleaning with hydrogen peroxide 6.6% w/v. The sharper lingual surface cusps of P^4 were scored relative to the deepest valley between adjacent cusps. The surface relief was classified as either low (l) or high (h) (limit set arbitrarily at 0.15mm based on the average of total sample range) by the relief profiles observed in samples from the three locations in a co-relative and subjective manner and represented in our analyses as percentages of sample population (per high= percentage high, %h) and (per low= percentage low, %l).

The degree of cusp facet development and distinctness forms the basis of a second mesowear variable as characterized by sharpness (s, terminates in a sharp point with no beveling on both mesial and distal phase facets), roundness (r, with distinctly rounded apex and facets are observable on the lower slopes) or bluntness (b, no observable facets altogether). These variables are also represented as percentages of morbid populations (Pers (%s) = percentage sharp, Perr (%r) = percentage round and Perb (%b) = percentage blunt) (Table 2).

Principal component analysis (%h, %s, %r and %b factors), hierarchical clustering based on Euclidean distance using paired group matrix analysis (UPGMA) algorithm was used in ordering the cluster trees as a reflection of dietary classifications according to ecological areas. Surface analysis was also done using PAST (Paleontological statistical package) 3.01 versions (Hammer *et al*, 2001).

RESULTS

The age class distribution considered for the purpose of this survey was 7-9years (Androukaki et. al., 2002). Mean individual age in CpRF (*P. cancrivorus* from the rain forest zone), CpSS (*P. cancrivorus* from Sudan Savanna zone) and CpS (*P. cancrivorus* from Sahel Savanna zone) were 12.2, 13.3 and 16.3 years respectively. Two sample tests showed males (9 years) were significantly ($p<0.01$) older than females (8 years) in CpRF whereas there were no significances ($p<0.5$) in the other groups (Table 1).

Table 1:
Sample distribution and structure in *P. cancrivorus* taken from three geographical areas. SID: sample identification, (CpRF: *P. cancrivorus* from the rain forest zone, CpSS: *P. cancrivorus* from Sudan Savanna zone and CpS: *P. cancrivorus* from Sahel Savanna zone), ♂=female, ♀= male, SD= standard deviation

SID	Sex symbol	Number of specimen	Age distribution	±SD
CpRF	♂	127	8.02	1.06
CpRF	♀	133	8.78	0.99
CpSS	♂	130	8.81	1.94
CpSS	♀	130	9.00	1.00
CpS	♂	135	7.54	0.89
CpS	♀	133	8.80	1.77

Table 2:
Mesowear datasets of *P. cancrivorus* from the rainfall ecological zone (CpRF) Sudan (CpSS) and Sahel (CpS) Savanna zones. Numbers 7-9 denote age classes considered. (SID: sample identification)

SID	%h	%s	%r	%b	Number	p value
CpRF(mean)	36.20	10.10	68.60	23.00	160	<0.001
CpSS(mean)	42.80	16.80	33.20	50.00	160	<0.001
CpS (mean)	54.20	46.60	22.50	30.90	168	<0.001
CpRF♂	34.20	8.90	65.10	21.00	127	<0.001
CpRF♀	40.20	11.90	71.80	25.00	133	<0.001
CpSS ♂	46.04	29.76	31.24	39.00	130	<0.003
CpSS ♀	40.89	10.07	62.70	26.60	130	<0.006
CpS ♂	67.60	58.20	19.78	22.02	135	<0.003
CpS ♀	44.30	30.10	18.67	51.23	133	<0.006
CpRF7	14.20	7.20	47.00	45.80	75	<0.030
CpRF8	48.80	13.00	86.00	1.00	62	<0.070
CpRF9	2.70	0	80.00	20.00	23	<0.020
CpSS7	23.40	13.70	71.40	14.90	32	n.s
CpSS8	22.10	22.30	45.20	32.50	64	<0.4
CpSS8	11.00	19.10	20.00	61.90	64	n.s
CpS7	38.30	31.10	61.90	7.10	48	<0.973
CpS8	45.00	35.20	32.00	32.80	39	<0.232
CpS9	11.00	0	72.60	27.40	81	<0.239

The first two principal components factors from age and sex based segregation analysis (Figure 1D and 2A) represents a minimum of 52% of the total variance. Resolution of discrimination in dietary habits is made obvious by Principal Component Analysis (PCA) and clustering analysis (Figure 2C and D). The pattern demonstrated by the cluster tree (Figure 2D) is used in circumscriptions of lines in the PCA plot (Figure 2C) within the spectrum of dental signatures expressed by all considered groups in making inferences on predominant dietary type expositions in all groups. Figure 2C showed that the average mesowear signal of both raccoon populations (RF and SS mean) was dominated with abrasion compared to the CpS (attrition dominated).

Table 3 demonstrates the sexual dimorphism in the different geographical locations assessed in this study. There were significant dimorphic scores between the females and males of CpSS as well as CpS. Figure 3A differentiates the species along ecologic and sex biases; whereas the species from the rain forest zones (both males and females) (the leader and first joiners) were more significantly affected and followed by the Sudan savanna males. Sahel savanna females remained the least joiners. Loading plot of occurrences among the parameters evaluated demonstrated percentage sharp (%s) recorded as the highest incident while the percentage round (%r) had the least scores.

Table 3:
Scores in both sexes across geographical locations (sexually significant dimorphic scores are bold)

Specimen	PC 1	PC 2	PC 3	PC 4
CpRF♂	-29.20	2.29	-5.36	0.71
CpRF♀	-30.05	5.43	4.38	1.49
CpSS♂	**14.51**	**-8.18**	-0.32	0.42
CpSS♀	**-23.79**	**0.74**	1.02	-2.60
CpS♂	**42.93**	**21.58**	-0.20	-0.11
CpS♀	**25.60**	**-21.86**	0.48	0.09

(Principal component (PC) CpRF: P. cancrivorus from the rain forest zone; CpSS: P. cancrivorus from Sudan Savanna zone; CpS: P. cancrivorus from Sahel Savanna zone; ♂=female; ♀= male)

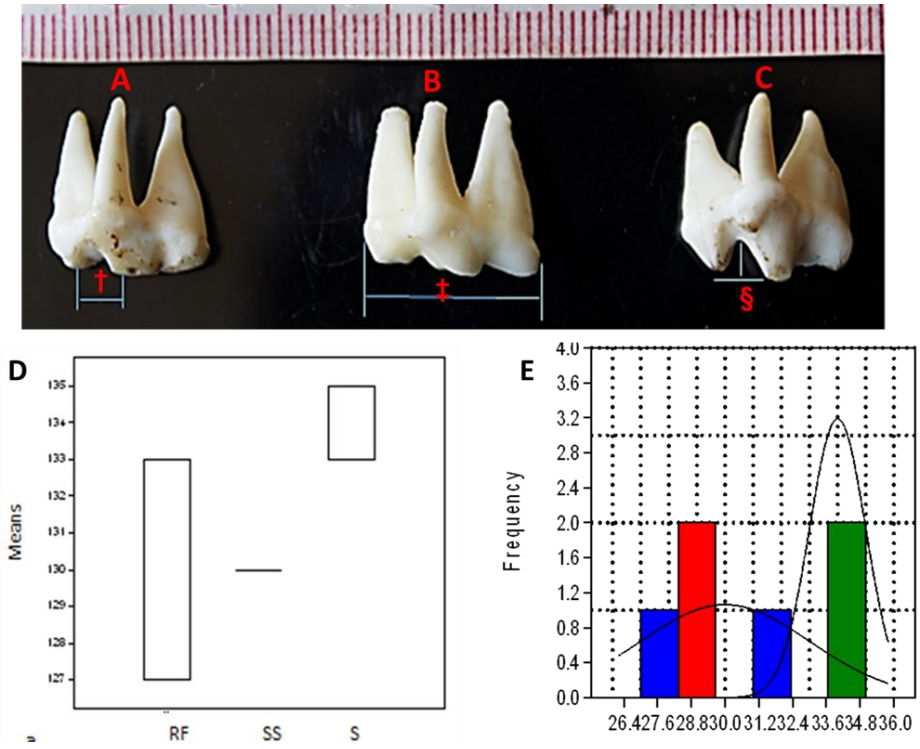
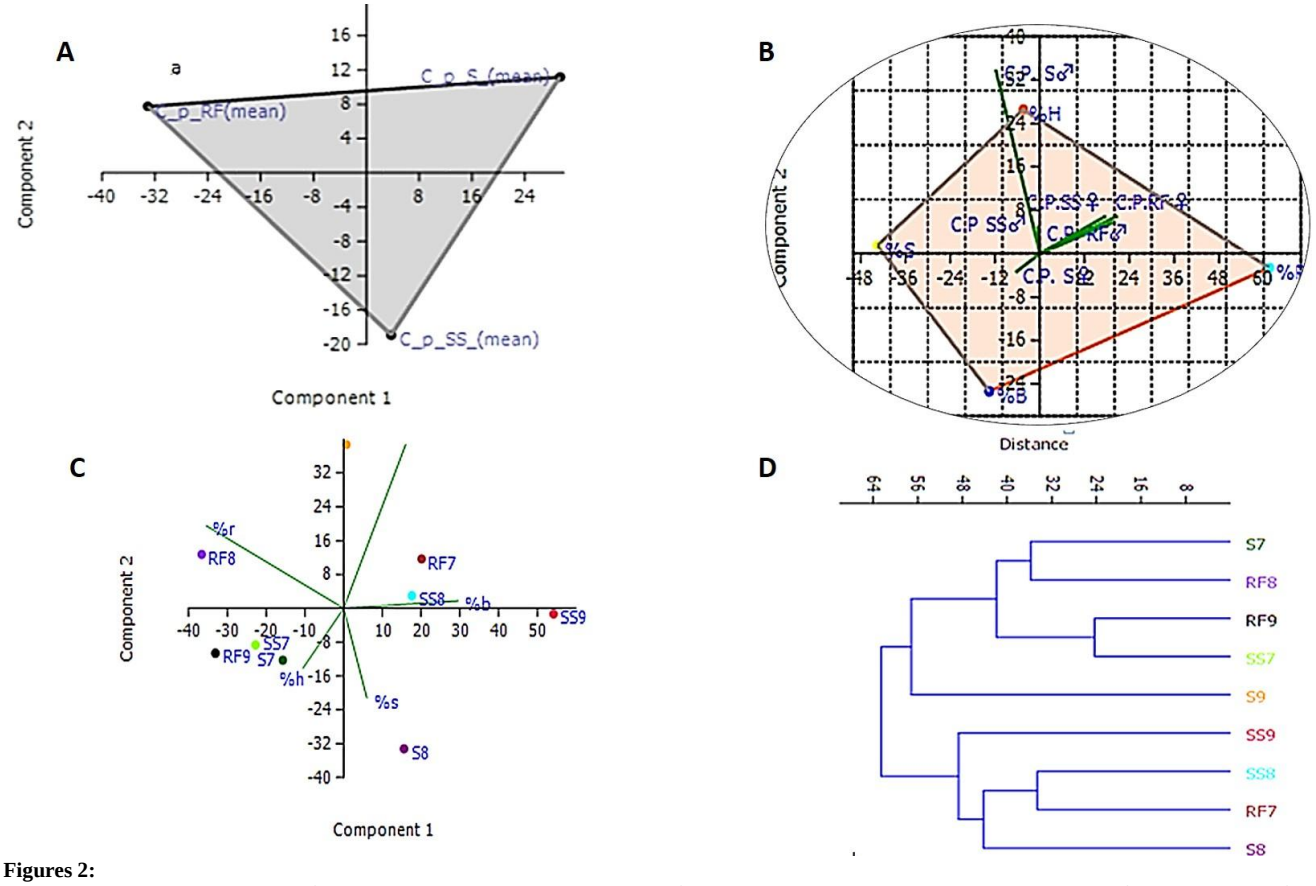


Figure 1:
Sample pictures of upper 4th premolar (P^4) teeth showing lingual surface projection in the three ecological zones (A) rain forest zone (B) Sudan Savanna zone (C) Sahel Savanna zone (†: distance between adjacent cusps; ‡ : width of the premolar tooth mesiodistally; §: depth between cusps); (D) Bar chart of means and confidence interval or quartiles box plot for the three locations and (E) histogram plot with normal fit of sex frequency distribution representing specific age class. RF (rainfall zone samples); SS (Sudan Savanna samples); S (Sahel savanna samples).



Figures 2:
(A). Principal component analysis of ecologic zone sample population means of percentage occlusal wear, (B) Sexual segregation of samples analysis from the three zones; PC = 81.81%, PC 2 = 16.93% of the total variance respectively; females of CpS had a highest %s and %h whereas CpRF and CpSS males are intermediate for %r while CpSS females and CpS males are lowest for %b PCA with Biplot of the samples from the three regions evaluated (CpRF: *P. cancrivorus* from the rain forest zone, CpSS: *P. cancrivorus* from Sudan Savanna zone, CpS: *P. cancrivorus* from Sahel Savanna zone, ♂=female, ♀= male; %s, %h, %r, %b: percentage sharp, high, round and blunt respectively); (C) Principal component analysis PC1 = 2.60%, PC2 = 27.03% of the total variance respectively (scatter plot of sample population from ecologic zones and parameters occurrence distribution with convex hulls; biplot), (D) hierarchical cluster tree based on mesowear variables %h, %s, %r and %b depending on age group segregation, rounded rectangles age group diet with higher animal tissue percentage content revealed lowest %h while rectangles showed the age group with lowest %s and highest %r (RF: Rain Forest zone; SS: Sudan Savanna zone; S: Sahel Savanna zone; 7,8,9: age classes considered; ♂=female; ♀= male; %s, %h, %r, %b: percentage sharp, high, round and blunt respectively).

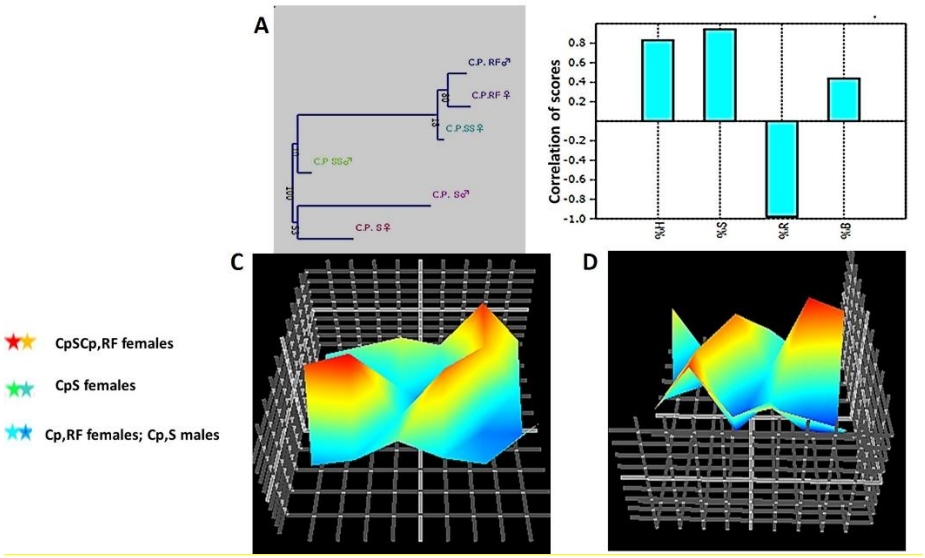


Figure 3:
(A) closest neighbor joining (NJ) bootstrapped (n=1000) based on ecologic relationship depending on sex group segregation. The first leader and joiner are CpRF and CpSS males, but Cp SS females possess the shortest branch length (B) Loading plot of correlation scores of evaluated variables %s, %h, %r, and %b. (CpRF: *P. cancrivorus* from the rain forest zone, CpSS: *P. cancrivorus* from Sudan Savanna zone and CpS: *P. cancrivorus* from Sahel Savanna zone), ♂=female, ♀= male; %s, %h, %r, %b: percentage sharp, high, round and blunt respectively); (C&D): Gender-based 4th premolar surface plot showing CpRF (Females), CpRF (Males), CpSS (Females), CpSS (Males), CpS (Females) and CpS (Males) samples versus %h, %s, %r and %b values at 0º Azimuth, 40º elevations and 180º Azimuth and 40º elevations respectively based on mesowear variables from the geographic location. Star colors show samples with highest and lowest values for the parameters in the order. (CpRF: *P. cancrivorus* from the rain forest zone, CpSS: *P. cancrivorus* from Sudan Savanna zone, CpS: *P. cancrivorus* from Sahel Savanna zone, ♂=female, ♀= male; %s, %h, %r, %b: percentage sharp, high, round and blunt respectively)

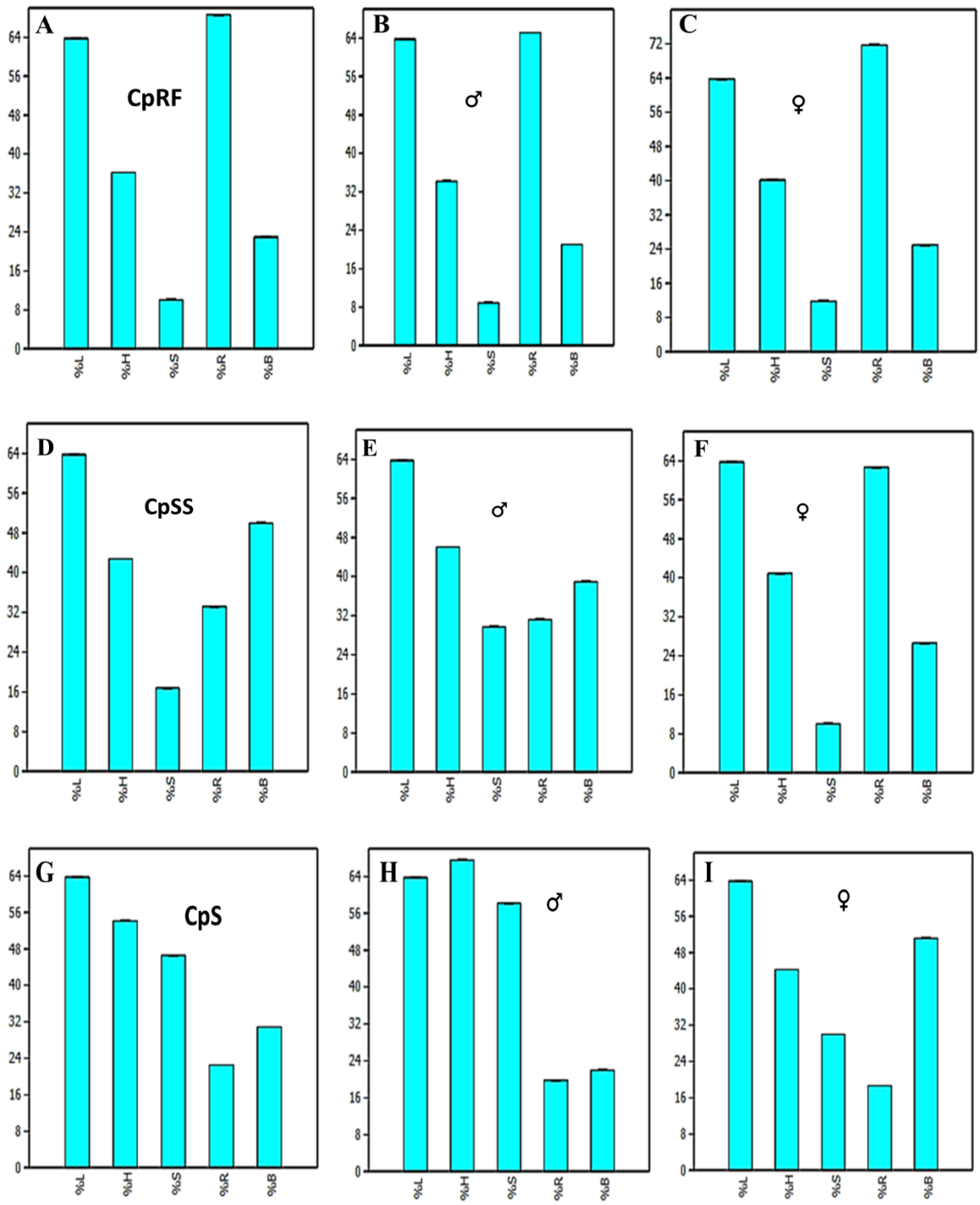


Figure 4
(A-I): Bar charts showing frequencies of cusp shape and occlusal relief parameters (%L, %H, %S, %R, %B: percentage low, high, sharp, round and blunt respectively; ♂=female, ♀= male)

Sexual segregation in both sexes from the geographical habitats of the species was significant as the three groups plots far from the population means (Figure 2A) with males (♀) differing generally more widely from the population means than females (♂) (Figure 2B). Female specimen samples from the rain forest zones demonstrated lower % R (percentage round) cusps (65.1%) compared to the males (71.8%) and a %B of 21 and 25% respectively in similar order (Table 2). Gender-based 4thpremolar surface plot showing CpRF (Females), CpRF (Males), CpSS (Females), CpSS (Males), CpS (Females) and CpS (Males) samples versus %h, %s, %r and %b values at 0º Azimuth, 40º elevations and 180º Azimuth and 40º elevations respectively based on mesowear variables from the geographic location (Figure 3C and D).

The trend (lower occlusal relief in females) is similar to occlusal surface relief results (Figure 4B and C) for %h observed to be 40% in males and 34% in females. Figure 4E

and F demonstrates a reversal of the trend in CpSS males shown to have lower occlusal surface relief of 48% and 40% for ♂ perh. Females and males had 31.24%, 62.7% perr, and then 39% and 26.6% perb respectively. In CpS, a slight significance ($p<0.003$) 19.78% and 18.67% perr exists in ♂ and ♀, then 22.02% and 51.23% perb in a similar order. The ♂ had a lower relief 67% compared to (44%) perh in ♀ (Figure 4H and I). The mesowear signatures observed in both CpSS8 and S8 were constant with advancing age (Figure 1D) while CpRF9, SS7 and S7 were observed to be closely linked with similar pattern in an overlap of age group and eco-geographic habitat axis. The results also revealed that older age brackets compared to the younger ones exposed more abrasions in all the groups except in the CpS9 group.

DISCUSSION

We have been able to ascertain that there are no shifts in the dental signatures irrespective of age. The three ecological zones evaluated for the diet partitioning in *P. cancrivorus* in Nigeria are separately characterized by varied precipitation, fauna and flora qualities (Happolds and Happolds, 1987). Rainfall in the rainforest zone averages 2500mm but 250-750mm in the Sahel zone [8]. Vegetation varies with soil structure, available water and photoperiodicity (Happolds and Happolds, 1987; Rivals *et al*, 2007). On the contrary, population differences in age classes may not be satisfactorily elucidated by the mesowear method, we observe a drift in mesowear equilibrium in dental signatures towards abrasion dominance with increasing age in the studied dental specimens from the rain forest, Sudan and Sahel savanna zones but in varying degrees which is consistent with the observations of Fortelius and Solounias, (2000) and Calandra *et al* (2016). A closer phenetic tree branch relationship was observed between RF9 and SS7 age groups, whereas S9 showed the farthest tree branch to the former. The means of the zonal group has been initially corroborated (Rivals *et al*, 2007) where sample population means showed varied patterns of occlusal relief with highest frequencies of percentage height and lowest percentage sharp occurring in *P. cancrivorus* from the rain forest zone. However, the opposite occurred in species from the Sahel with lowest percentage height and highest percentage sharp means which is in consonant with studies on the vertebrate feeding long-nose mongoose (*Xeno galenaso*) and the flat headed Cusimanse (*Crossachus platycephalus*) (Gilchrist *et al*, 2009). The above observation therefore satisfied our first hypothesis that the mesowear equilibrium should reflect either differential food availability to different age classes or ontogenetic gradients in tooth wear and morphology.

Age segregation in relation to environmental conditions was confirmed by the results of the investigation in terms of climatic, geomorphology with mean individual age in CpRF, CpSS and CpS which is an obvious evidence of relative longevity (*ceteris paribus*) in the latter of about three years older at death compared to others from rain forest and Sudan savannah zones.

We hypothesized that available diet type to the Sahel population of the species is more heterogeneous in composition (Rivals *et al*, 2007; Calandra *et al*, 2016) with less abrasive diet when compared to those from rain forest and Sudan Savanna areas, this therefore demonstrate the divergent fauna structure in the three habitats. The species from Sudan savanna area demonstrated intermediate dietary behavior between the other two, which impacted on the mesowear principal component analysis (PCA) revealing a negative percentage high in SS7 (positive percentage blunt) with major displacement on principal component 1 axis. Environmental factors which are likely to favor or disfavor availability of preferred food type in this habitat area is shown by percentage round in RF8 and percentage sharp in S8 which are more related to principal component 2 axis in distribution. These include flood and precipitation around the plateau where vegetation and climate types favor better food availability of varieties (Happolds and Happolds, 1987; NIMET, 2010; Winkler *et al*, 2016) or drought with concomitant increased forest fire incidences (jeopardizing food availability) scattered around areas in this location; thus establishing our second hypothesis. Our findings also revealed that a closer relationship exists between RF9 and SS7 male age groups while RF and S females were distinctly dissimilar. Limited resources in this location due to reduced/absent coastal and mangrove biomes, soil type as well as waning rainfall levels with increasing altitude above sea level northwards may have accounted for these results (Ita, 1994; Mackwell *et al*, 2013). A more anthropogenous habitat with relatively more abundant lower animal food resource characterization (Drygala and Zoller, 2013; Calandra *et al*, 2016) compared to a mosaic structure with multilayered dense forests allows the interpretation of abrasive-dominated mesowear dental signatures of the southern rainforest zone in our dataset to reflect a differential in food type availability (Schulz *et al*, 2007; Hirasawa and Kanda, 2006; Ulbricht *et al*, 2015) in the three habitats considered. This is also consistent with a similar investigation in other invasive species (Winkler *et al*, 2016). Patterns in forest fragmentation (not included in this study) due to structure differentiates the species in habitat utility (Ward and Wurster-Hill, 1989; Winkler *et al*, 2016) and its attendant migrations is evident in the level of occlusal surface wear in the teeth structure.

Both sexes revealed more intra-specific territory influenced diet character differences than geographic placement which suggests females are more exposed to wears due to competitive feeding (Winkler *et al*, 2016) due to nursing needs and urbanization of their ranges, leading to contraction and overlaps of spatial territories. They exhibit more reluctance to increase home range areas and are spatially restricted to fewer food resource choices (IUCN, 2012). Since niche partitioning is a mechanism for achieving co-existence of multiple species in a similar habitat (Okabe & Agetsuma, 2007) with spatial dietary resource overlaps, as demonstrated in Caiman alligator, *Melanosuchus niger* (Foth, Bona and Desojo, 2015) in relation to diet-partitioning. The raccoon dog (*Nyctereutes procyonoides*) and the red fox (*Vulpes vulpes*) (Drygala and Zoller, 2013) are comparably similar-body-sized mammals found in the same eco-environment. The percentage sharp frequencies were least and similar in CpRF and CpSS males respectively. The principal component scores between males and females in rain forest specimen are not significantly different when viewed against scores of specimens from other climes. Highest sex specific significant scores observed in CpS females inferred to

belong to a diet of least fracture content thus validating our third hypothesis. Interactions between species and environment represented by fauna (quality and quantity), forest types and water source proximity is a regular trigon whose relative proximity impacts on food type consumption as well as dental occlusal surface topography,

On the basis of the factors considered above, we therefore postulate that the possibility of an early compromised dental prey handling ability exist more in the rain forest zone group compared to other zones resulting in dietary imbalance and a reduced competitive ability especially in a competitive-tolerant spatial eco-environment

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