International Journal of Zoology and Applied Biosciences
Volume 2, Issue 3, pp: 145-154, 2017
https://doi.org/10.5281/zenodo.1311753
ISSN: 2455-9571
http://www.ijzab.com

Research Article

MORPHOLOGICAL VARIATION OF WILD DOGS ACROSS AFRICA

Tafadzwa Shumba[1, 2*], Robert A. Montgomery[1, 3], Claudio Sillero-Zubiri[1, 4] and Gregory S. A. Rasmussen[1, 2, 4]

[1]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford,
Recanati-Kaplan Centre, Tubney House, Tubney OX13 5QL, UK

[2] Painted Dog Research Trust, P O Box 285, Victoria Falls, Zimbabwe

[3] Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA

[4] IUCN SSC Canid Specialist Group, Oxford, UK.

Article History: Received 16th April 2017; Accepted 1st June 2016; Published 26th June 2017

ABSTRACT

Body form and function of animal species have been shaped over time in response to prevailing local conditions that affect survival and reproduction. Morphological variation in size and shape thus occurs within-species across eco-geographic regions. Different theories have been proposed to explain this variation. For example, Bergmann's rule posits that intra-species body size increases positively with latitude and negatively with temperature. Alternatively, the resource rule suggests that the quantity and quality of available resources is the primary determinant of body shape and size. Here, we used photogrammetry to quantify morphological variation among wild dogs (*Lycaon pictus*) across eight African countries within three regions (western, eastern and southern), using the skeletal ratio of shoulder height to body length. We found that morphological variation was explained mostly by country and region, with latitude also being an influential predictor. Wild dogs in eastern Africa (Kenya and Tanzania) had the lowest measured skeletal ratio while the western population especially in Senegal had the highest. The effect of latitude, although not strongly linear, suggests some support for Bergmann's rule. However, variations in latitude are associated with changes in other environmental conditions that directly influence resource availability. This makes the resource rule a better theory to explain morphological variation among wild dogs. Nevertheless, these findings indicate phenotypic plasticity among wild dog populations which can be taken as basis for rigorous genetic comparisons. Also, these remaining populations should all be conserved regardless of current size and movement between them should occur naturally without translocation especially for populations which are phenotypically distinct.

Keywords: Bergmann's rule, Photogrammetry, *Lycaon pictus* resource rule, Shoulder height.

INTRODUCTION

Animal bodies have been evolutionarily shaped over time in relation to the impact of abiotic and biotic characteristics on animal survival and reproduction (Kruuk and Parish, 1985). While the general form of a species might appear relatively consistent across its range, variation in body shape and size does exist (Cavallini, 1995). Various theories have been presented to explain such variation. For instance, Bergmann's rule states that among homeothermic species, body size tends to be positively associated with latitude and negatively with temperature (Mayr, 1956). Animals from comparatively colder and higher latitudes thus tend to have bigger bodies than their counterparts in warmer and lower latitudes (Rensch, 1938). An alternative theory, broadly referred to as the resource rule (McNab, 2010) suggests that differences in body size can be attributed to spatial variation in resource availability. According to the rule, there is a correlation between resource availability and body size, with a reduction in

---

*Corresponding Author: Mr. Tafadzwa Shumba, Junior Researcher, Painted Dog Research Trust, P O Box 285, Victoria Falls, Zimbabwe, Email: tafadzwashumba@rocketmail.com, Mobile: +263 775 880 162/ +263 717 324 734.

available resources being linked to a corresponding reduction in body size (McNab, 2010; McNutt and Gusset, 2012). The resource rule was however synthesized from a collection of rules which have a direct link to resource availability. These include Bergmann's rule, island rule, Dehnel's phenomenon, and Cope's rule (McNab, 2010). The island rule states that large mammals on small islands reduce both in mass and mass-independent expenditures due to a reduction in available resources (McNab, 1994). Dehnel's phenomenon states that species reduce in size towards winter (Dehnel, 1949), while Cope's rule proposes a general increase in mammal body mass and size over time due to increased thermal efficiency, competence in hunting for example in carnivores and increased longevity (Stanley, 1973; Kingsolver and Pfenning, 2004). These theories have however not been widely tested on large and highly mobile carnivore species occurring over a broad geographical scale (Mayr, 1956; Girman *et al*., 2001) .

Wild dogs (*Lycaon pictus*) are the only surviving species of the *Lycaon* genus following the Pleistocenextinction of *Lycaon sekowei* (Girman *et al*., 1993; Hartstone-Rose *et al*., 2010). Their phylogenetic distinctiveness and ecological niche as hyper-carnivorous cursorial hunters makes them a species of conservation concern (Girman *et al*., 1997; Hartstone-Rose *et al*., 2010). Although their long distance dispersal ensures genetic stability by decreasing the probability of inbreeding, their cursorial nature and commensurate high energetic requirement (Rasmussen *et al*., 2008), makes them highly sensitive to variation in environmental factors. They are therefore a good model species to understand morphological variations across populations and or conformity to eco-geographic rules.

In this study, we used photographs and photogrammetry to quantify morphological variation among wild dogs residing in eight African countries. Photogrammetry is particularly useful for non-invasive morphological studies on species highly sensitive to human handling (Bell *et al.*, 1997; Trimble *et al.*, 2011). Consequently, it is a valuable research tool for threatened species such as wild dogs. Further, these techniques have been productively applied to a number of species involving different questions such as body weight estimation in Southern elephant seals *Mirounga leonina* (Bell *et al*., 1997), sub-species classification in grey wolves (*Canis lupus;* (Cavallini, 1995), fluctuating asymmetry in wild dogs (Edwards *et al*., 2013) and age determination in lions *Panthera leo* (Ferreira and Funston, 2010). Using the skeletal ratio equivalent of shoulder height to body length ratio as our response variable we compared different populations of wild dogs for morphological differences. We hypothesised that most variation would be explained by country and/or region, due to differences in geographical conditions, which directly influence resource availability. Examining such variation in morphological characteristics provides insights into the adaptations and ecological importance of individual natural populations (Haush *et al.*, 2013). The understanding of the available morphological differences in morphology also provides a foundation for rigorous genetic comparison and the classification of wild dogs into unique ecotypes (varieties of the same species adapted to a specific environment) which is essential for effective conservation strategies.

MATERIALS AND METHODS

Data collection

We collected photographs of wild dogs from tourists, safari guides and researchers across eight African countries between 2005 and 2014. Among the large batch of photographs that we collated, we used only those which showed the entire body of an individual from either the left or right-side. Measurements, with precision at pixel level, were completed using Adobe Photoshop CS3 (Andrews, 2007), using the protocol shown in Figure 1. We made a total of 13 morphometric measurements (Figure 1) from each picture. Body length (*BL*) was measured from the caudal ischiatic process on the pelvis that forms a taxonomically discrete point to the protruding anterior side of the greater tubercle on the humerus. Three metrics of shoulder height (*FL1* + *FL2* + *FL3*) were taken from the bottom of the foot to the top of the shoulder blade via the hock and elbow. We also measured the back leg length taking the summation of metatarsus, tibia and femur (*HL1* + *HL2* + *HL3*). To account for cases when the dog was not standing perpendicular to the camera, we recorded the angles of a FL3 and BCL and used trigonometric equations to adjust the shoulder height using the formula shoulder height = *FL1* + *FL2* + (Tan (*FL3 BCL* angle) * FL3). In other studies, camera-specific calibration formulae that translated pixel counts from the photograph into centimetres were used (Trimble *et al.,* 2011). While some used distance between the camera, animal and camera focal length to calculate the actual height of the animal (Shrader *et al.*, 2005; Ferreira and Funston, 2010). For our study such data were not available hence our measurements were done at pixel level. Because photographs were captured at different distances with different cameras, we converted our measurements from pixels to ratios relative to *BL* to enable comparisons between populations, age classes and sexes (Clarke, 1995).

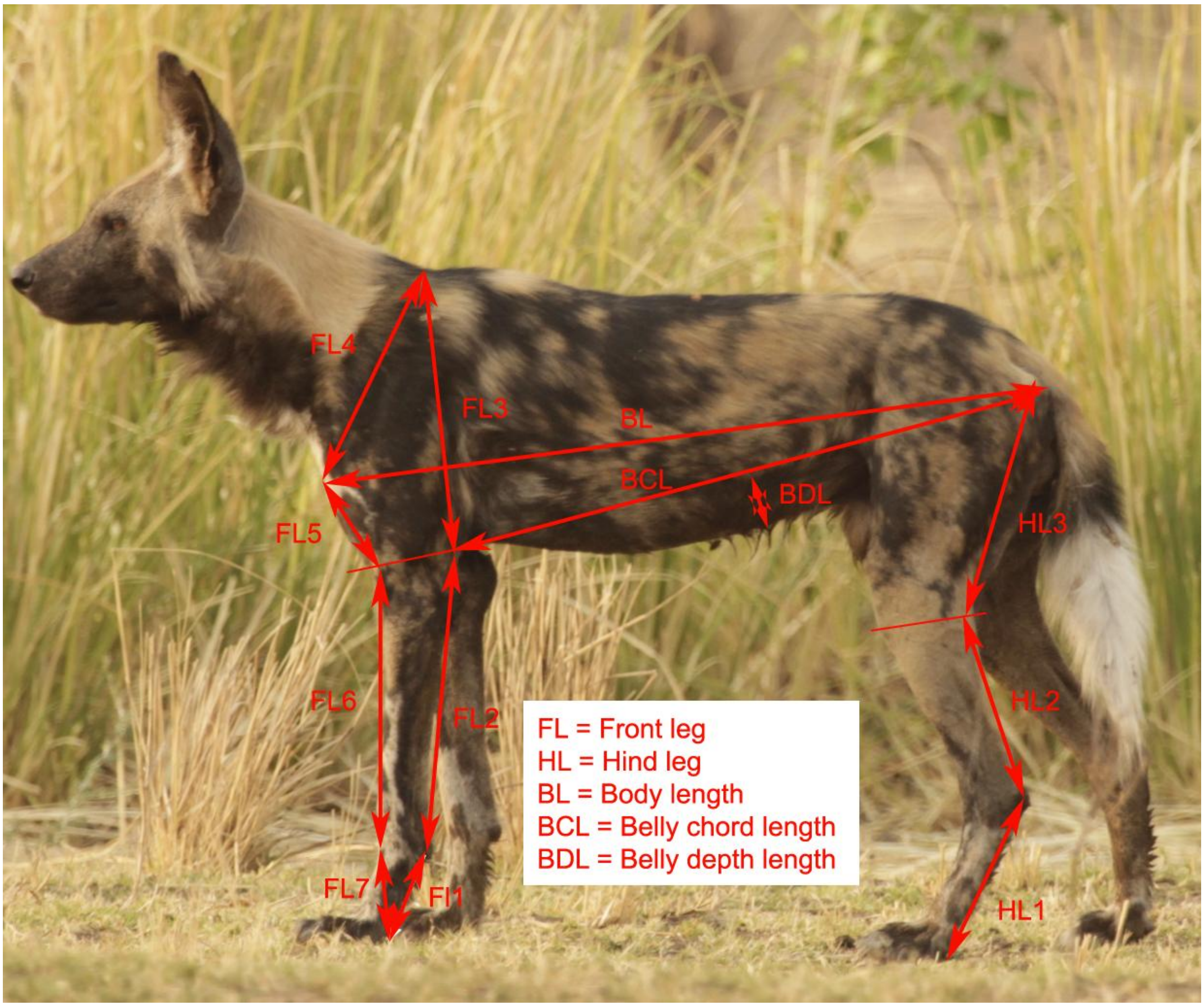

Figure 1. Protocol for photogrammetric measurements in pixels using Adobe Photoshop CS3. A total of thirteen measurements were made from each photograph.

Explanatory variables

We developed a database of six variables to explain morphological variation among wild dogs. This included *country, region, latitude, sex, age class* and *pack size*. Our wild dog data were collected across eight African nations (Figure 2), which we then grouped into three regions; western (Senegal and Central African Republic), eastern (Kenya, Tanzania and Mozambique) and southern (Zambia, Zimbabwe and Botswana) as in (Girman *et al.*, 1993; Woodroffe *et al.*, 1997). When known, the age class (pups <1 year, yearling 1-2 years, and adults > 2 years), sex and pack size were recorded.

Data analysis

With shoulder height to body length ratio as our response variable ($FL1 + FL2 + FL3 / BL$), we fitted generalized linear models (GLMs) from the Gaussian family with an identity link to quantify morphological variation in wild dogs. We developed models using all possible combinations of explanatory variables. We then ranked model performance using Akaike's Information Criterion corrected (AICc) for small sample sizes, with the model with the lowest AICc being the most supported (Burnham and Anderson, 2002). We then performed further tests to determine the magnitude of effect of each explanatory variable in the top performing models as well as to determine the specific differences between countries, regions, age classes, sexes as well as the effect of latitude and pack size. In all post-hoc tests we tested the null hypotheses of no significant differences between countries, regions, age classes, sexes and no effect of latitude and pack size using regression analysis. All statistical analyses were done using R software (R Core Development Team, 2014) and significance was taken $p < 0.05$.

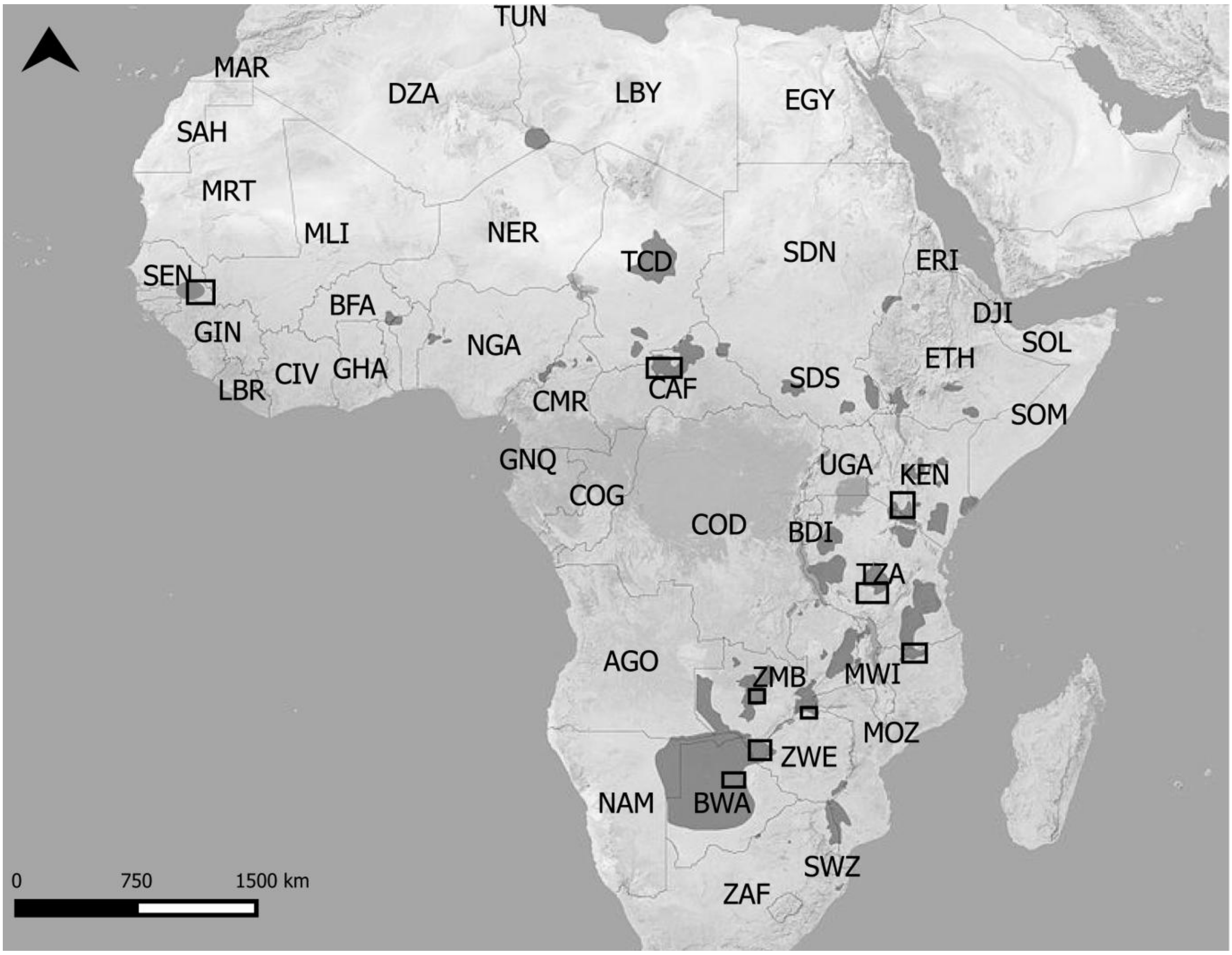

Figure 2. Map showing distribution of African wild dogs, with sampling locations indicated by small rectangles. Country codes Senegal, SEN; Kenya, KEN; Tanzania, TZA; Mozambique, MOZ; Zambia, ZMB; Zimbabwe, ZWE; and Botswana, BWA.

RESULTS

We collected a total of 279 photographs of wild dogs across eight African countries between 2005 and 2014. These included 152 individuals from Zimbabwe, 23 from Botswana, 8 from Zambia, 24 from Tanzania, 36 from Kenya, 30 from Mozambique, 4 from Senegal, and 2 from the Central African Republic. From the total samples, 210 were adults (102 males, 106 females and 2 unknown sex), 28 were yearlings (17 males and 11 females) and 41 were pups (19 males, 16 females and 6 unknown sex).

The least parameterized model with *country* only was the best-performing model amongst the considered (Table 1). This model had the lowest AICc and received almost half of the total weight of evidence ($w_i = 0.45$). The second-ranked model included *country*, *region* and *latitude* as explanatory variables. This model had a ΔAICc of 1.51 and a $w_i = 0.21$ which shows that it’s also a plausible model.

There were also significant differences in morphology between countries ($F_{7,\ 278} = 5.34$, $p < 0.001$). A multiple country by country pairwise post-hoc analysis of the top model with country only as the explanatory variable, showed that significant differences were between Kenya and Botswana, Tanzania and Botswana, Zimbabwe and Botswana, Tanzania and Mozambique, Tanzania and Senegal, and Zimbabwe and Tanzania (Table 2; Figure 3).

Table 1. Top performing models with ΔAICc < 6 for explaining morphological variation among African wild dogs in Africa, K is the number of parameters, ΔAICc is the difference in AICc between each model and the best model, wi is the model AICc weight and cum wi is the cumulative AICc weight.

Model	K	AICc	ΔAICc	w_i	cum w_i
country	9	-739.05	0.00	0.45	0.45
country + region + latitude	10	-737.54	1.51	0.21	0.67
country + age	11	-736.90	2.16	0.15	0.82
country + sex	11	-736.24	2.82	0.11	0.93
country + sex + age	13	-734.34	4.71	0.04	0.98
country + sex + age+ latitude	14	-733.08	5.97	0.02	1.00

Table 2. Multiple pairwise country by country comparison of morphological differences in African wild dogs across eight range states.

Comparison	Difference	Lower	Upper	*P*	Significance
Central Africa-Botswana	-0.05	-0.19	0.09	0.96	ns
Kenya-Botswana	-0.06	-0.11	-0.004	0.02	*
Mozambique-Botswana	-0.04	-0.09	0.02	0.36	ns
Senegal-Botswana	0.04	-0.07	0.14	0.95	ns
Tanzania-Botswana	-0.1	-0.15	-0.042	<0.0001	***
Zambia-Botswana	-0.03	-0.11	0.05	0.95	ns
Zimbabwe-Botswana	-0.05	-0.1	-0.003	0.03	*
Kenya-Central Africa	-0.006	-0.15	0.13	1	ns
Mozambique-Central Africa	0.01	-0.13	0.15	0.99	ns
Senegal-Central Africa	0.09	-0.08	0.25	0.75	ns
Tanzania-Central Africa	-0.05	-0.19	0.09	0.96	ns
Zambia-Central Africa	0.02	-0.13	0.17	0.99	ns
Zimbabwe-Central Africa	0.004	-0.13	0.14	1	ns
Mozambique-Kenya	0.017	-0.03	0.07	0.95	ns
Senegal-Kenya	0.09	-0.01	0.19	0.09	ns

Tanzania-Kenya	-0.04	-0.09	0.01	0.18	ns
Zambia-Kenya	0.03	-0.05	0.1	0.95	ns
Zimbabwe-Kenya	0.01	-0.03	0.05	0.98	ns
Senegal-Mozambique	0.08	-0.03	0.18	0.3	ns
Tanzania-Mozambique	-0.06	-0.11	-0.007	0.015	*
Zambia-Mozambique	0.01	-0.07	0.09	0.99	ns
Zimbabwe-Mozambique	-0.01	-0.05	0.03	0.99	ns
Tanzania-Senegal	-0.14	-0.24	-0.03	0.002	**
Zambia-Senegal	-0.07	-0.19	0.05	0.7	ns
Zimbabwe-Senegal	-0.08	-0.18	0.013	0.15	ns
Zambia-Tanzania	0.07	-0.01	0.15	0.13	ns
Zimbabwe-Tanzania	0.05	0.01	0.095	0.005	**
Zimbabwe-Zambia	-0.02	-0.09	0.05	0.99	ns

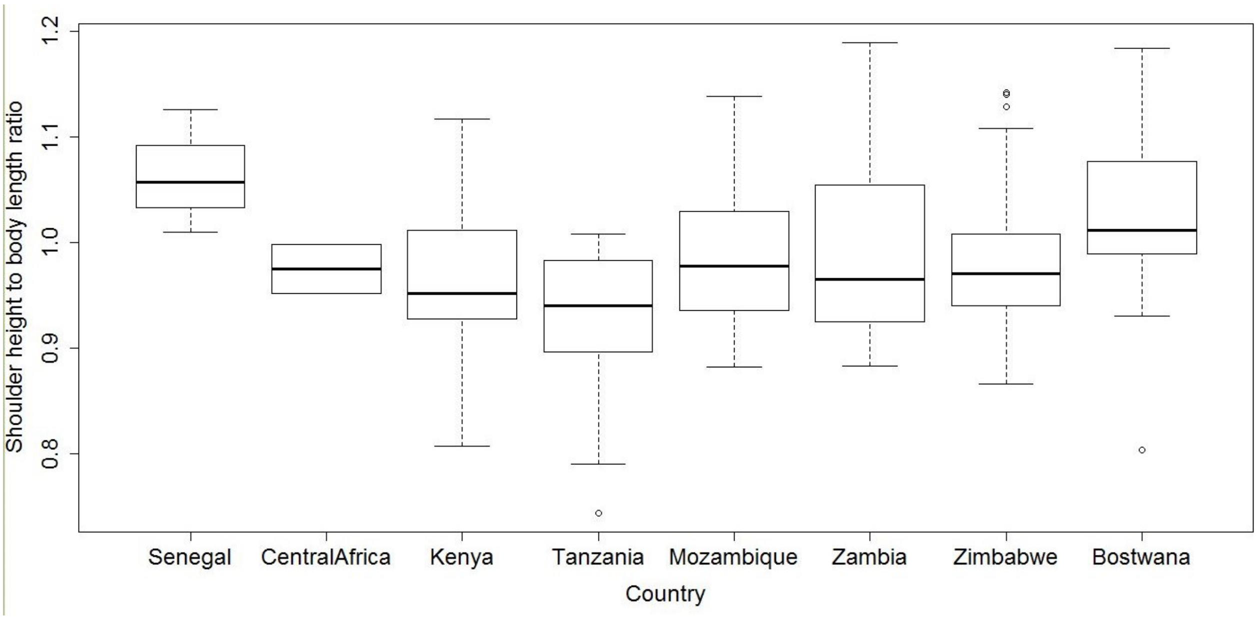

Figure 3. Box and whisker plot showing differences in shoulder height to body length ratio (FL1 + FL2 + FL3 / BL) for African wild dogs across eight African range states using digital photogrammetry.

Wild dogs in Senegal had the highest shoulder height to body length ratio, while Tanzania had the lowest (Figure 3). There were also significant differences between the three regions $F_{2,\ 278} = 5.09$, $p = 0.007$), with significant differences being between the eastern and southern region ($p = 0.015$) and between the eastern and western region ($p = 0.01$). The eastern region (Kenya and Tanzania) had the lowest shoulder height to body length ratio, while the western had the highest (Figure 4).

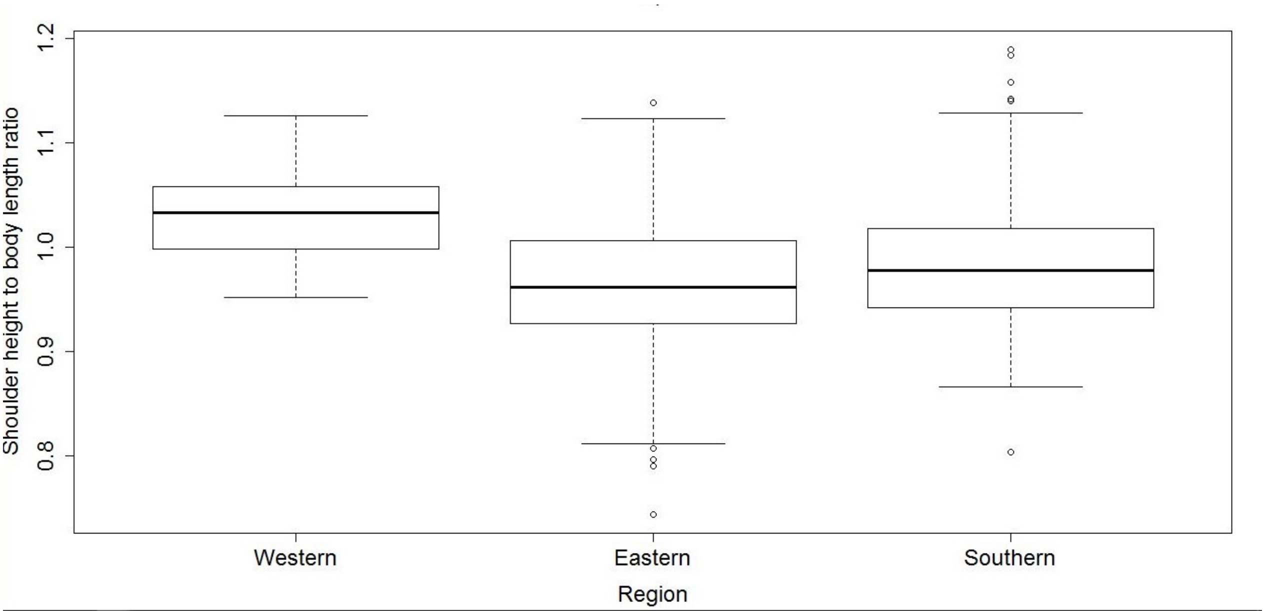

Figure 4. Box and whisker plot showing differences in shoulder height to body length ratio (*FL1 + FL2 + FL3 /* BL) for African wild dogs in their three current regional populations; western (Senegal and Central African Republic), eastern (Kenya, Tanzania and Mozambique) and southern (Zambia, Zimbabwe and Botswana) using digital photogrammetry.

Shoulder height to body length ratio was also significantly influenced by latitude (*p* = 0.005), however, the relationship was not strongly linear (*r* = 0.17). In general, wild dogs shoulder height to body length ratio decreased as we got closer to the equator with Tanzania and Kenya having the least ratios. There were no significant differences in morphology between the different *age classes* (*p* = 0.35) and across different *sexes* (*p* = 0.58) in our data There was also no significant influence of *pack size* on the observed morphological variations (*p* = 0.87, *r* = 0.03), and all models, which included *pack size* as an explanatory variable, performed poorly.

DISCUSSION

We found that differences in wild dog morphology across Africa could be explained mostly at country and regional levels. Although eco geographic rules have mainly used body size to describe factors which influence morphological variation (Bergmann's rule, resource rule, Island rule, Cope's rule among others), we believe that shoulder height to body length ratio can also be used to understand morphological variation among wild dog populations, and the factors involved as applied to the different eco-geographic rules proposed. According to Bergmann's rule, body size is positively associated with latitude and negatively with temperature (Mayr, 1963; Meiri *et al.*, 2007). In our study latitude significantly influenced the variation in shoulder height to body length ratio, but its effect was not strongly linear as predicted by Bergman's rule rule. Others have however suggested that these relationships may not be linear as predicted by Bergman's rule (Blackburn and Hawkins, 2004; Rodriguez *et al.*, 2010), which agrees with the lack of a strong linear relationship in our results. These associations between body size and shape, temperature and latitude have been shown to be stronger in colder regions of northern Europe and weaker in warmer regions (Rodriguez *et al.*, 2010). However, because wild dogs are only found in Africa there is no data over a broader latitudinal scale, with which stronger relationships could be expected.

Changes in latitude are associated with changes in other environmental variables, which indeed vary between the countries and the regions considered (McNab, 2010). Often it is the change in those environmental variables that affect food availability to animals that dictate morphological differences (Yom-Tov and Geffen, 2006). However, because such variables are related to latitude the results are often misinterpreted as conforming to Bergmann's rule (Yom-Tov and Geffen, 2006). Our observed morphological differences between populations are thus likely to be greatly influenced by differences in primary productivity, temperature, species diversity, vegetation, terrain, competition and prey density across the countries and regions. Such variables have a direct influence on prey availability to wild dogs and all form basis for the resource rule. According to the rule, reduction in resource availability leads to reduction in body size and or mass-independent energy expenditure (McNab, 2010), hence can explain our observed differences in shoulder height body length ratio. In Botswana, wild dogs were shown to have decreased by 17% over the past 20 years attributed to a 30% decrease in the density of impalas

(*Aepyceros melampus*) in the ecosystem (McNutt and Gusset, 2012), which supports the resource rule. Among cheetah (*Acinonyx jubatus*) resource availability was also the main factor influencing morphological variations observed between Botswana and Namibia (Boast *et al.*, 2013). Because the two have little variation in latitude makes the resource rule more appropriate to explain the observed variation. Future studies should however, seek to quantify the effect of several environmental predictors before concluding which one best explains morphological variation (Yom-Tov and Geffen, 2011).

We did not get many samples from the western population, which is justifiable given that the species is endangered and there are fears that the western population might now be functionally extirpated (Sillero-Zubiri, 1995; Breuer, 2003; Angwafo, 2006; Croes *et al.*, 2012). Our data shows that the population is different from other populations. Populations near the equator (Kenya and Tanzania) had the smallest shoulder height to body length ratio (shorter legs in relation to body length) while the western population particularly Senegal had the biggest indicating longer legs in relation to body length. These variations indicate phenotypic plasticity among wild dogs, probably due to long term adaptation to prevailing conditions for maximising food acquirement. The species is well known to hunt small to medium prey in its geographical extent (Reich, 1981; Hayward *et al.*, 2006), hence morphological differences i.e. of shoulder height to body length are likely to favour survival within the different regions. Nevertheless, these wild dog populations should all be conserved regardless of current size. Small populations such as the those in the western region are mostly likely to be ignored in favour of bigger populations, with which conservation actions are likely to yield better results within a short period of time (Dickman *et al.*, 2015; Lindsey *et al.*, 2015). However, their status and distribution have potential to recover if management strategies and regulations are put in place (Croes *et al.*, 2012). Also, because of the distinctiveness of regional populations we recommend that movement between populations should only be allowed to occur naturally and not involve translocation especially if the population are very phenotypically or genetically distinct.

We found no significant differences between male and female wild dogs in our study, supporting the lack of sexual dimorphism in this species as previously observed (Girman *et al.*, 1993), and common among the Canidae (Bekoff *et al.*, 1981). Our results however, contradict those from Botswana in which significant sexual differences in all morphometric measurements were observed (McNutt and Gusset, 2012), with fluctuations in food supply being thought to constrain growth patterns between sexes (Isaac, 2005; McNutt and Gusset, 2012; Boast *et al.*, 2013). Age also did not significantly explain morphological variation in wild dogs as observed in Botswana (McNutt and Gusset, 2012), and there were no significant differences between the different age classes. The morphometric skeletal ratio of shoulder height to body length can therefore not be used to distinguish age classes among wild dogs. With lions, age assignment using shoulder height was also more precise for lions below two years, after which shoulder height becomes constant across all ages (Ferreira and Funston, 2010).

CONCLUSION

Morphological variation among wild dogs was explained mainly by country, region and latitude, whilst age, sex and pack size were all insignificant. Shoulder height to body length ratio can therefore be used to effectively distinguish populations, but not age or sex. Nevertheless, our study sheds light on the phenotypic plasticity and possible adaptations to the different geographical conditions within which the species exist. Such results can be taken as a basis for rigorous genetic comparisons of the populations, in order to classify them as ecotypes or as different sub-species, which for now should all be conserved regardless of current population size. Our study also highlights the importance of non-invasive techniques such as photogrammetry in understanding morphological variation among rare and wide ranging wildlife populations.

ACKNOWLEDGEMENTS

The Director General of the Zimbabwe Parks and Wildlife Management Authority is thanked for allowing research in its estates in Zimbabwe. We would also want to thank researchers, tourist, and safari guides for their generous submission of photographs and their locations, which made this work feasible. We would also want to thank the financial support by Wildlife Conservation Research Unit (WildCRU) at University of Oxford during the analysis and writing up of this project.

REFERENCES

Andrews, P., 2007. Adobe Photoshop CS3 A-Z: Tools and features illustrated ready reference. Focal Press, Armsterdam.

Angwafo, T., 2006. Status of Wildlife and its Utilisation in Faro and Benoué National Parks North Cameroon: Case study of the Derby Eland (Taurotragus derbianus gigas Gray, 1947) and the African Wild Dog (Lycaon pictus Temminck, 1840). Brandenburg Technical University, Cottbus, Germany.

Bekoff, M., Diamond, J. and Mitton, J., 1981. Life-history patterns and sociality in canids: body size, reproduction and behaviour. *Oecologia,* 50, 386-390.

Bell, C.M., Hindell, M.A. and Burton, H.R., 1997. Estimation of body mass in the southern elephant seal, Mirounga leonia, by photogrametry and morphometrics. *Mar. Mamm. Sci.,* 13, 669-682.

Blackburn, T.M., and Hawkins, B.A., 2004. Bergmann's rule and the mammal fauna of northern North America. Ecography, 27, 715-724.

Boast, L.K., Houser, A.N., Good, K. and Gusset, M., 2013. Regional variation in body size of the cheetah (*Acinonyx jubatus*). *J. Mammal.,* 94, 1293-1297.

Breuer, T., 2003. Distribution and conservation of African wild dogs in Cameroon. Canid News.

Burnham, K.P. and Anderson, D.R., 2002. Model selection and multimodel inference. 2and edition. Springer, New York.

Cavallini, P., 1995. Variation in the body size of the red fox. *Ann. Zool. Fenn.*, 32, 421 427.

Clarke, G., 1995. Relationships between developmental stability and fitness. *Conserv. Biol.,* 9, 18-24.

Croes, B., Rasmussen, G.S.A., Buij, R. and de Longh, H., 2012. Status of the African wild dog in the Bénoué Complex, North Cameroon.

Dehnel, A., 1949. Studies on the genus *Sorex* L. *Ann Univ Marie Curie Sklodowska Section C. Biology,* 4, 1674-1684.

Dickman, A.J., Hinks, A.E., Macdonald, E.A., Burnham, D. and Macdonald, D.W., 2015. Priorities for global felid conservation. *Conserv. Biol.*, 29, 854-864.

Edwards, C., Rasmussen, G.S.A., Riordan, P., Courchamp, F. and Macdonald, D.W., 2013. Non-adaptive phenotypic evolution of the endangered carnivore Lycaon pictus. *PLoS ONE*, 8, 1-7.

Ferreira, S., and Funston, P.J., 2010. Age assignment to individual African lions. S. *Afr. J. Wildl. Res.*, 40,1-9.

Girman, D.J., Kat, P.W., Mills, M.G.L., Ginsberg, J.R., Borner, M., Wilson, V., Fanshawe, J.H., Fitzgibbon, C., Lau, L.M., and Wayne, R.K. 1993. Molecular genetic and morphological analyses of the African wild dog (*Lycaon pictus*). *J. Hered.*, 84, 450-459.

Girman, D.J., Mills, M.G.L., Geffen, E., and Wayne, R.K. 1997. A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus*). *Behav. Ecol. Sociobiol.,* 40, 187-198.

Girman, D. J., Vila, C., Geffen, E., Creel, S., Mills, M. G. L., McNutt, J. W., Ginsberg, J. R., Kat, P. W., Mamiya, K. H., and Wayne, R. K. 2001. Patterns of population subdivision, gene flow and genetic variability in the African wild dog (*Lycaon pictus*). *Mol. Ecol.,* 10:1703-1723.

Hartstone-Rose, A., Werdelin, L., De Ruiter, D.J., Berger, L.R., and Churchill, S.E., 2010. The plio-pleistocene ancestor of wild dogs ancestor of wild dogs, *Lycaon sekowei* n.sp. *J. Paleontol.,* 84, 299-308.

Haush, S., Shurin, J. B. and Matthews, B. 2013. Variation in body shape across species and populations in radiation of diaptomid copedods. PLoS ONE 8, 68272.

Hayward, M. W., Hofmeyr, M., O'Brien, J. and Kerley, G. I.H., 2006. Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *J. Zool.*, 270, 615-627.

Isaac, J.L., 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mamm. Rev.*, 35, 101-115.

Kingsolver, J.G. and Pfenning, D.W., 2004. Evolution, 58, 1608-1612. 2004. Individual level selection as a cause of Cope's rule of phyletic increase. *Evolution,* 58, 1608-1612.

Kruuk, H., and Parish, T., 1985. Food, food availability and weight of badgers (*Meles meles*) in relation to agricultural changes. *J. Appl. Ecol.*, 22, 705-715.

Lindsey, P.A., Alexander, R., Du Toit, J.T. and Mills, M. G.L., 2015. The cost efficiency of wild dog conservation in South Africa. *Conserv. Biol.*, 19, 1205-1214.

Mayr, E., 1956. Geographical character gradients and climatic adaptation. *Evolution,* 10,105-108.

Mayr, E., 1963. Populations, Species and Evolution. Belknap Press, Cambridge, Mass.

McNab, B.K., 1994. Resource use and the occurrence of land and freshwater vertebrates on oceanic islands. *Am. Nat.,* 144, 643-669.

McNab, B.K., 2010. Geographic and temporal corrections of mammalian size reconsidered: a resource rule. Oecologia 164:13-23.

McNutt, J. W. and Gusset, M. 2012. Declining body size in an endangered large mammal. Biol. J. Linn. Soc. 105:8-12.

Meiri, S., Yom-Tov, Y., and Geffen, E. 2007. What determines conformity to Bergmann's rule? *Global Ecol. Biogeog.,* 16, 788-794.

R Core Development Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasmussen, G.S.A., Gusset, M., Courchamp, F. and Macdonald, D.W., 2008. Achilles' Heel of Sociality Revealed by Energetic Poverty Trap in Cursorial Hunters. *Am. Nat.*, 172, 508-518.

Reich, A., 1981. The behavior and ecology of the African wild dog *(Lycaon pictus*) in the Kruger National Park. Dissertation Abstracts International B Sciences and Engineering.

Rensch, B., 1938. Some problems of geographical variation and species formation. *Proc. Linn. Soc. London,* 150, 275-285.

Rodriguez, M.A., Olalla-Tarraga, M.A. and Hawkins, B.A., 2010. Bergmann's and the geography of mammal body size in the Western Hemisphere. *Global Ecol. Biogeogr.,* 17, 274-283.

Shrader, A.M., Ferreira, S.M., and van Aarde, R.J., 2005. Digital photogrametry and laser rangefinder techniques to measure African elephants. *S. Afr. J. Wildl. Res*., 36, 1-7.

Sillero-Zubiri, C. 1995. A survey of African wild dogs in southeastern Senegal. *Canid News*, 3, 33-35.

Stanley, S.M., 1973. An explanation for Cope's rule. *Evolution*, 27, 1-26.

Trimble, M.J., Van Aarde, R.J., Ferreira, S.M., Norgaard, C.F., Johan Fourie, J., Lee, P.C. and Moss, C.J., 2011. Age determination by back length for African savanna elephants: extending age assessment techniques for aerial-based surveys. *PLoS ONE* 6:e26614.

Woodroffe, R., Ginsberg, J.R. and Macdonald, D.W. 1997. The African Wild Dog: Status Survey and Conservation Action Plan. IUCN/SSC Canid Specialist Group, Gland, Switzerland.

Yom-Tov, Y. and Geffen, E., 2006. Geographic variation in body size: The effects of ambient temperature and precipitation. *Oecologia*, 148, 213-218.

Yom-Tov, Y. and Geffen, E., 2011. Recent spatial and temporal changes in body size of terrestial vertebrates: probable causes and pitfalls. *Biol. Rev*., 86, 531-541.