PUBLISHED PAPERS TRANSLATED INTO AFRICAN LANGUAGES

Maluleke, T., Jacobs, D. S., & Winker, H. (2017) Environmental correlates of geographic divergence in a phenotypic trait: A case study using bat echolocation. Ecology and evolution, 7(18), 7347-7361.

Abstract in English

Divergence in phenotypic traits may arise from the interaction of different evolutionary forces, including different kinds of selection (e.g., ecological), genetic drift, and phenotypic plasticity. Sensory systems play an important role in survival and reproduction, and divergent selection on such systems may result in lineage diversification. Such diversification could be largely influenced by selection in different environments as a result of isolation by environment (IbE). We investigated this process using geographic variation in the resting echolocation frequency of the horseshoe bat species, *Rhinolophus damarensis*, as a test case. Bats were sampled along a latitudinal gradient ranging from 16°S to 32°S in the arid western half of southern Africa. We measured body size and peak resting frequencies (RF) from handheld individual bats. Three hypotheses for the divergence in RF were tested: (1) James' Rule, (2) IbE, and (3) genetic drift through isolation by distance (IbD) to isolate the effects of body size, local climatic conditions, and geographic distance, respectively, on the resting frequency of *R. damarensis*. Our results did not support genetic drift because there was no correlation between RF variation and geographic distance. Our results also did not support James' Rule because there was no significant relationship between (1) geographic distances and RF, (2) body size and RF, or (3) body size and climatic variables. Instead, we found support for IbE in the form of a correlation between RF and both region and annual mean temperature, suggesting that RF variation may be the result of environmental discontinuities. The environmental discontinuities coincided with previously reported genetic divergence. Climatic gradients in conjunction with environmental discontinuities could lead to local adaptation in sensory signals and directed dispersal such that gene flow is restricted, allowing lineages to diverge. However, our study cannot exclude the role of processes like phenotypic plasticity in phenotypic variation.

Komiso hi Xitsonga

Maluleke, T., Jacobs, D. S., & Winker, H. (2017). Ku hambana ka ku vumbeka ka mirhi ku ya hi tindzhawu swi fambisana na mbango wa kona: Ndzavisiso hi ku tirhisa mpfumawulo wa mangedyana. Ecology and evolution, 7(18), 7347-7361.

Ku hambana ka ku vumbeka ka mirhi ya swiharhi swi nga vangiwa hi ku hambana ka mintlawa ya swiharhi, kunw'e na mimbango kumbe tindzhawu ta laha swiharhi swi kumekaka kona. Matimba yo twa ya na nkoka eka ku hanya na ku tswala eka swiharhi. Ku hambana ka matimba yo twa hikuya hi

mimbango kumbe tindzhawu ta laha swiharhi swi kumekaka kona swi nga vanga ku hambana ka tinyimba ta swiharhi (lineage diversification). Mahambanelo ya muxaka lowu ya hlohloteriwa ngopfu hi ku hambana ka maxelo ya tindzhawu ta laha swiharhi swi hanyaka kona. Laha hi lavisisile maendlelo lawa hi ku tirhisa mimpfumawulo ya mintlawa ya va mangedyana leyi yi vitaniwaka "*Rhinolophus damarensis*," naswona yi kumekaka eka tindzhawu to hambana hambana. Swiharhi leswi swa vamangedyana swi phasiwile kusukela en'walungwini ku fikela edzongeni (16°S to 32°S) wa xifundza xa vupela dyambu bya le dzongeni wa Africa. Xifundzha lexi xi omile hikokwalaho ka ku pfumaleka ka mpfula yo vonaka. Vukulu na xivumbeko kun'we na mimpfumawulo ya "*R. damarensis"* swi kamberiwile swi tlhela swi pimiwa enhoveni laha swiharhi leswi swi nga khomiwa kona. Ndzavisiso lowu wu kambisise ti "hypotheses" tinharhu. (1) James' Rule, (2) Isolation by environment, and (3) genetic drift through isolation by distance (IbD). Leswi swi endleriwe ku hambanisa vuhlohloteri bya makulelo ya mirhi, maxelo na mimpfhuka eka mimpfumawulo ya mintlawa ya swiharhi leswi swa "*R. damarensis*". Mbuyelo wu kombisile ku ri a kuna vumbhoni lebyi kombaka leswaku kuna vuxaka exikarhi ka mimpfumawulo na "James'Rule." Na kambe ndzavisiso a wu kumanga vuxaka exikarhi ka makulelo ya mirhi na mimpfumawulo ya swiharhi leswi swa *R. damarensis*. Mbuyelo wa "genetic drift through isolation by distance (IbD)" na wona wu kombe leswaku a kuna vuxaka exikarhi ka mimpfumawulo ya swiharhi swa "*R. damarensis*" na mimpfhuka leyi nga kona exikarhi ka mitlawa ya swiharhi leswi. Ehandle ka mimbuyelo leyi, mbuyelo wa "Isolation by environment" wona wu kombe leswaku kuna vuxaka exikarhi ka "Isolation by Environment" na mimpfumawulo ya swiharhi leswi swa "*R. damarensis"*. Leswi swi kombisisa swinene leswaku ku hambana ka maxelo ya tindzhawu ta swiharhi leswi swi hlohlotela mimpfumawulo ya swiharhi leswi. Ku hambana ka maxelo eka tindzhawu ta laha swiharhi leswi swi kumekaka kona swikotlanisana na ku hambana ka tinyimba (genetic divergence) ta swiharhi leswi swa "*R. damarensis*". Ku hambana loku ka maxelo eka tindzhawu ta laha swiharhi leswi swi kumekaka kona swi nga endla leswaku swiharhi leswi swi tekelela kumbe ku tolovela ku hanya eka tindzhawu ta maxelo yo kari hi kuya hi matimba yo twa ya mimpfumawulo ya swiharhi leswi swa "*R. damarensis*". Leswi swi nga endla leswaku ku nga vi na "gene flow" yo ringanela eka mintlawa ya swiharhi leswi na kambe leswi swi nga tlhela swi vanga ku hambana ka tinyimba (genetic divergence) eka mintlawa ya swiharhi leswi. Hambi swiritano, ndzavisiso lowu a wu siyi ehandle maendlelo ya "phenotypic plasticity" eka ku hambana ka ku vumbeka ka swiharhi leswi.

THESES TRANSLATED INTO AFRICAN LANGUAGES

Maluleke, T. (2017) Geographic variation in the phenotype of an African horseshoe bat species, *Rhinolophus damarensis*, (Chiroptera: Rhinolophidae). PhD Thesis, University of Cape Town.

General Abstract in English

Studies involving geographic variation in the phenotypes of bats help scientists to explain why these mammals are the most species rich mammalian order second only to rodents, with well more than 1 300 species occurring worldwide. Such species richness or high diversity is the manifestation of the generation of biodiversity through the splitting of lineages within bat species. A lineage of bat species can diversify into several lineages which then differentiate from each other in allopatry. Thus, the spatial separation of a lineage into several lineages could be attributed to geographical, ecological and environmental factors across the distributional range of the species. Similarly, vicariant events may also play a role in separating lineages within species.

The Damara horseshoe bat species, *Rhinolophus damarensis*, is widely distributed but restricted to the western half of southern Africa, where it occurs across several major biomes. Formerly regarded as the subspecies, *R. darlingi damarensis*, it was elevated to full species status on the basis of genetic and phenotypic differences between it and *R. darlingi darlingi*. *Rhinolophus damarensis* is itself made up of two ecologically separated genetic lineages. A total of 106 individuals of *R. damarensis* were sampled from seven localities across its distributional range, with a view to determining and documenting the extent of geographic variation in body size, echolocation parameters, wing parameters, cranial shape and post-cranial morphology of individuals from populations of R. damarensis across the distributional range of the species.

Firstly, an investigation into geographic variation in resting echolocation frequency (RF) of the horseshoe bat species, *R. damarensis* was carried out in the western half of southern Africa (Chapter 2). Three hypotheses were tested. The first one, James'Rule (JR), states that individuals occurring in hot humid environments generally have smaller body sizes than conspecifics that occur in cooler, dryer environments, and the largest are expected to occur in cool, dry areas. On this basis and because of the known relationship between body size and RF, it was predicted that there should be a correlation between body size and climatic factors and between body size and RF. The second hypothesis was Isolation by Environment (IbE) mediated through sensory drive, which proposes that diversification of lineage may be driven by environmentally-mediated differences in sensory systems. Under this hypothesis, it was predicted that call frequency variation should be correlated with climatic variables. The third hypothesis was that Isolation by Distance (IbD) can influence phenotypic trait variation by restricting gene flow between populations. Under the Isolation by Distance (IbD) Hypothesis, it was predicted that call frequency variation should be partitioned in accordance with geographic distance between populations. To investigate the probability of the JR, IbE and IbD, the Akaike's information criterion AICc candidate models were evaluated with different combinations of environmental (annual mean temperature and relative humidity), spatial (latitude and region) and biological (forearm as a proxy for body size) predictor variables to determine their influence on resting frequency (RF) across the distributional range of *R. damarensis*. Linear mixed effects models (LMEs) were employed to analyse the relationship between the response variable (RF) and the environmental, spatial and biological predictor variables. The influence of prey detection range and atmospheric attenuation was also investigated. The results showed no evidence for JR or for random genetic drift. Body size was neither correlated with RF nor environmental variables, suggesting that variation in RF was not the result of concomitant variation in body size as proposed by JR. Similarly, the Mantel test showed no IbD effect and there was therefore no evidence that genetic drift was responsible for the variation in RFs. In contrast, the LMEs showed that there was support for IbE in the form of an association between RF and region (in the form of the variable

"Reg") which was based on the two geographically separated genetic lineages. Furthermore, RF variation was also associated with the climatic variable AMT.
The taxonomic status of *R. damarensis* was investigated using ecological traits and phenotypic characters including skulls, wings and echolocation (Chapter 3) and three dimensional (3D) scanned skulls and mandibles (Chapter 4). The main objective (Chapter 3 and Chapter 4) was to test whether previously reported genetic divergence between the two *R. damarensis* lineages was associated with phenotypic divergence. Morphometric and echolocation measurements were taken from hand held individual bats in the field, and skull measurements were taken from field collected voucher specimens as well as museum specimens. Discriminant Function Analyses (DFA) revealed that there was geographic variation among populations and lineages of *R. damarensis*. Multivariate Linear Regressions (MLV) and Linear models (LM) on the basal parts of bacula revealed significant differences between the southern and northern lineages of *R. damarensis*. The bacula of the two lineages of R. damarensis appear to have different shapes. Diversification through shape analyses (Chapter 4) was investigated using three dimensional (3D) geometric morphometric analyses based on X-ray microcomputed tomography (μCT) scanning of dried skulls and mandibles of *R. damarensis*. Procrustes Anova results of both mandibles and skulls indicated that there were no significant differences between sexes but that the shape of skulls and mandibles varied across different localities (Chapter 4). Canonical Variate Analysis (CVA) suggested that geographic variation in *R. damarensis* mandibles was based on the shape and thickness of the alveolar bone. Geographic variation in the skulls was based on changes in the rostrum, anterior medial swelling and brain case. Some populations had slightly deeper rostra, slightly larger anterior medial swellings and smaller braincases, whilst others had slightly shallower rostra, slightly smaller anterior medial swellings and larger braincases. The northern lineage was found to be separated from the southern lineage based on the changes in skull and mandible shape. Therefore, separation of lineages within *R. damarensis* (Chapter 4) could be associated with the foraging and feeding behaviour of the species under different ecological conditions due to ecological opportunity. Overall, differences in the RF were found to be associated with Isolation by Environment mediated through sensory drive and this has led to the formation of two regional (northern and southern) groupings in RF (Chapter 2). The two lineages were supported by both the phenotypic divergence (Chapter 3) and shape variation within *R. damarensis* skulls and mandibles (Chapter 4). Thus, phenotypic differences corresponded to genetic differences between the two lineages and provide support for IbE.

<u>Komiso hi Xitsonga</u>

Maluleke, T. (2017). Ku hambana ka ku vumbeka ka mangedyani xa laha Afrika kuya hi tindzhawu ta laha xi kumekaka kona, *Rhinolophus damarensis* (Chiroptera: Rhinolophidae). PhD Thesis, University of Cape Town.

Ndzavisiso wa ku hambana ka swiharhi swo fana na vamangedyani hi kuya hi tindzhawu ta laha swi kumekaka eka tona, swi pfuna vanhu va sayense (science) ku hlamusela kuri hikokwalaho kayini swiharhi leswi swa ku mamisa swi tele ngopfu. Hi kuya hi ndzavisiso wa sayense ya ntumbuluko, swiharhi swo fana na makondlo hi swona leswi nga tala ngopfu i vi ku landzela vamangedyana, tinxaka ta swiharhi leswi ti hundza 1 300 laha emisaveni. Matalelo ya swiharhi leswi ya tikombisa hiku hambana ka tinyimba (genetic lineages) hi kuya hi "species." Ku hambana ka tinyimba (genetic lineages) ku vangiwa hi tindzhawu ta laha swiharhi leswi swi kumekaka kona. Tintshava, malwandle, magova, madamu lamakulu, mimpfhuka, kun'we na maxelo na swona swa vanga mahambanelo ya ti tinyimba (genetic lineages) eka swiharhi.

Xivumbiwa lexi xivitaniwaka Damara horseshoe bat species, *Rhinolophus damarensis*, xi kumeka hi xitalo evupela dyambu bya dzonga wa Africa. Khale xiharhi lexi a xi ri “subspecies” leyi a yi ri R. darlingi damarensis, kambe xi vuye xi tlakusiwa xi nyikiwa “full species status” hi kuya ka ku hambana ka tinyimba (genetic lineages) na xivumbeko exikarhi ka xiharhi lexi na xin’wana lexi a xi ri R. darlingi darlingi. *R. damarensis* xi na tinyimba (genetic lineages) timbirhi hi kuya hi laha xi kumekaka kona. Ndazvisiso lowu wu phasile wu tlhela wu khoma swiharhi swa 106 swa R. damarensis eka tindzhawu to ringana nkombo. Xikongomelo a kuri ku lava ku tiva ku ri swiharhi leswi swi hambana njhani hi kuya hi laha swi kumekaka kona. Ndzavisiso wu lavisise ku hambana ka mirhi, mimpfumawulo, swivumbeko swa tipiku na swivumbeko swa marhambu ya tinhloko/swipalapala ta swiharhi lexi xa *R. damarensis*.

Xosungula ndzavisiso wu kongomisiwe eka kuhambana ka mimpfumawulo hi kuya hi tindzhawu ta laha swiharhi swa *R. damarensis* swi kumekaka kona evupela dyambu bya dzonga wa Africa. Ndzavisiso lowu wu kambisise ti “hypotheses” tinharhu. Yo sungula, “James’Rule (JR), states that individuals occurring in hot humid environments generally have smaller body sizes than conspecifics that occur in cooler, dryer environments.” Hi kuya hi hypothesis leyi na vuxaka lebyi byi tivekaka exikarhi ka vukulu bya mirhi na mimfumawulo ya *R. damarensis*. Ndzavisiso wu bvumbe ku ri ku ta va na ku kotlana na vuxaka exikarhi ka vukulu bya mirhi na mimpfumawulo ya *R. damarensis*. “Hypothesis” ya vumbirhi, “Isolation by Environment (IbE) mediated through sensory drive, and it was hypothesised that there should be an association between phenotypic differences (i.e resting frequency) and environmental differences.” Hi kuya hi hypothesis leyi, ndzavusiso wu bvumbe ku ri kuhambana ka mimpfumawulo swi ta kotlanisana na ku hambana ka maxelo ya tindzhawu ta swiharhi leswi. “Hypothesis” ya vunharhu, “the third hypothesis was that Isolation by Distance (IbD) can influence phenotypic trait variation by restricting gene flow between populations.” Hi kuya hi hypothesis leyi, ndzavisiso wu bvumbe ku ri ku hambana ka mimpfumawulo swi fanele ku kotlanisana na mipfhuka ya mitlawa ya swiharhi swa *R. damarensis*. Ku lavisisa vu hlohloteri bya “Jame’s Rule, Isolation by Environment kun’we na Isolation by Distance hypotheses”eka swiharhi leswi swa *R. damarensis*. Ndzavisiso wu lavisise ku ringana ka ti “candidate models” ta “Akaike’s information criteria” kun’we ni mintlawa ya ta maxelo, ndzhawu na mirhi wa swiharhi ku kambisisa kucetelo wa mimpfumawulo ya swiharhi leswi. “Linear Mixed Effects models” ti tirhisiwile eka ndzavisiso lowu ku xopaxopa vuxaka exikarhi ka mimpfumawulo na ndzhawu laha swiharhi swa R. damarensis swi kumekaka kona. Vu hlohloteri bya “prey detection range” na “atmospheric attenuation” na byona by lavisisiwile eka ndzavisiso lowu. Mbuyelo wu kombisile ku ri a kuna vumbhoni lebyi kombaka leswaku kuna vuxaka exikarhi ka mimpfumawulo na “James’Rule.” Na kambe ndzavisiso a wu kumanga vuxaka exikarhi ka makulelo ya mirhi na mimpfumawulo ya swiharhi leswi swa *R. damarensis*. Mbuyelo wa “mantel test” na wona wu kombe leswaku a kuna vuxaka exikarhi ka mimpfumawulo ya swiharhi swa *R. damarensis* na mimpfhuka leyi nga kona exikarhi ka mitlawa ya swiharhi leswi. Ehandle ka mimbuyelo leyi, mbuyelo wa “Linear Mixed Effects Models” wona wu kombe leswaku kuna vuxaka exikarhi ka “Isolation by Environment” na mimpfumawulo ya swiharhi leswi swa *R. damarensis*. Leswi swi kombisisa swinene leswaku ku hambana ka maxelo ya tindzhawu ta swiharhi leswi swi hlohlotela mimpfumawulo ya swiharhi leswi. Ndzavisiso wa “taxonomic status” ya *R. damarensis* wu lavisisiwile hi ku tirhisa ndzavisiso wa ndzhawu leyi swiharhi leswi swi kumekaka kona, swi vumbeko leswi swi katsaka marhambu ya tinhloko/swipalapala, tipiku ta swiharhi leswi na mimpfumawulo ya swona kun’we na marhambu ya tinhloko/swipalapala leswi nga sikeniwa (scanned) na marhambu ya tihlaya leti nga sikeniwa (scanned) ta swiharhi swa *R. damarensis*. Xikongomelo xikulu xa a ku ri ku kambela kuri ku hambanaka ka ti tinyimba (genetic lineages) ta *R. damarensis* swi seketeriwa hi swivumbeko swa mirhi ya swiharhi leswi swa *R. damarensis*. Vukulu na vuvumbeko kun’we na mimpfumawulo ya R. damarensis swi kamberiwile swi tlhela swi pimiwa enhoveni laha swiharhi leswi swi khomiweke kona. Marhambu ya tinhloko ta *R. damarensis* ma tekiwe eka ti “voucher specimens” (i.e voucher specimens ensure that the identity of organisms studied in the field or in the laboratory experiments can be verified). Man’wana marhambu ya tinhloko ta *R. damarensis* ma lombiwile eka ti “museum”.

Vuxopaxopi bya “Discriminant Function Analyses” byi kombise leswaku swiharhi swa *R. damarensis* swa hambana hi kuya ka tindzhawu ta laha swi kumekaka kona. “Multivariate Linear Regressions” na “Linear Models” swi kombe leswaku ti “bacala” (penile bones) ta swiharhi leswi ta hambana swinene exikarhi ka swiharhi leswi swi kumekaka en’walungwini ni le dzongeni wa xifundza xa vupela dyambu bya le dzongeni wa Africa. Leswi swi tikombe hi ku hambana ka swi vumbeko swa ti “bacula” ta *R. damarensis*. Ku hambana ka mintlawa ya *R. damarensis* swi lavisisiwile na kambe hi ku tirhisa “three dimensional (3D) geometric analyses” laha ndzi nga tirhisa muchini wa “X-ray micromputed tomography” ku kambela marhambu ya tinhloko/swipalapa na ya tihlaya ta mintlawa ya R. damarensis. Mbuyelo wa “Procrutes Anova” wu kombe leswaku a kuna ku hambana ka vumbewu exikarhi ka marhambu ya tinhloko kun’we na ya tihlaya ta mintlawa ya *R.damarensis*. Vumbewu byi ti kombe ku hambana hi kuya ka vuvumbeko na tindzhawu ta laha mintlawa ya *R. damarensis* yi kumekaka kona. Mbuyelo wa “Canonical Variate Analyses” wu kombe leswaku ku hambana hi kuya ka swivumbeko swa tihlaya ta mintlawa ya *R. damarensis* swi tikombisile swinene hi ku anama ka marhambu ya alivhiyola (alveolar bone). Ku hambana exikarhi ka mintlawa ya tinhloko/swipalapala swi tikombise hi macincelo yaku anama ka marhambu ya tinhompfu na ya byongo. Ku hambana exikarhi ka mintlawa ya le dzongeni na ya le n’walungwini swi kombisa leswi swiharhi swa *R. damarensis* swi hlotaka ha kona ni leswi swi dyisaka xi swona enhoveni etindzhawini leti hambaneke. Hi ku angarheta, ku hambana ka mimpfumawulo ya swiharhi leswi swi kongomisana na ku hambana ka tindzhawu ta mimbangu ya laha swiharhi leswi swi kumekaka kona. Leswi swi endle leswaku ku va na mintlawa yi mbirihi hi kuya hi mimpfumawulo ya swharhi leswi kun’we ni tindzhawu ta mimbangu ya laha swi kumekaka kona. Mintlawa leyi yi mbirhi ya le n’walungwini na le dzongeni wa ndzhawu ya laha swiharhi leswi swi kumekaka kona yiseketeriwa hi ku hambana ka mipfumawulo, vukulu bya tipiku, vukulu bya marhambu ya tinhloko/swipalapala na hi ti “bacula” kun’we na swivumbeko swa marhambu ya tinhloko/swipalapala na marhambu ya tihlaya ta swiharhi leswi. Mahambanelo ya swivumbeko swa mintlawa bya swiharhi leswi swi kotlanisana ni mahambanelo ya tinyimba (genetic lineages) exikarhi ka mintlawa ya swiharhi swa *R. damarensis*. Mbuyelo lowu wu seketeriwa hi ku hamabana ka mimbago ya tindzhawu leti swiharhi leswi swi kumekaka eka tona.