

RESEARCH ARTICLE

Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'

Joseph S. Wilson¹*, Aaron D. Pan^{2,3}*, Erica S. Limb¹, Kevin A. Williams⁴

1 Department of Biology, Utah State University, Tooele, Utah, United States of America, **2** Don Harrington Discovery Center, Amarillo, Texas, United States of America, **3** Botanical Research Institute of Texas, Fort Worth, Texas, United States of America, **4** Plant Pest Diagnostics Center, California Department of Food and Agriculture, Sacramento, California, United States of America

* These authors contributed equally to this work.

* joeswilson@gmail.com (JSW); apan@dhdc.org (ADP)



Abstract

Africa has the most tropical and subtropical land of any continent, yet has relatively low species richness in several taxa. This depauperate nature of the African tropical fauna and flora has led some to call Africa the “odd man out.” One exception to this pattern is velvet ants (Hymenoptera: Mutillidae), wingless wasps that are known for Müllerian mimicry. While North American velvet ants form one of the world’s largest mimicry complexes, mimicry in African species has not been investigated. Here we ask do African velvet ant Müllerian mimicry rings exist, and how do they compare to the North American complex. We then explore what factors might contribute to the differences in mimetic diversity between continents. To investigate this we compared the color patterns of 304 African velvet ant taxa using nonmetric multidimensional scaling (NMDS). We then investigated distributions of each distinct mimicry ring. Finally, we compared lizard diversity and ecoregion diversity on the two continents. We found that African female velvet ants form four Müllerian rings, which is half the number of North American rings. This lower mimetic diversity could be related to the relatively lower diversity of insectivorous lizard species or to the lower number of distinct ecoregions in Africa compared to North America.

OPEN ACCESS

Citation: Wilson JS, Pan AD, Limb ES, Williams KA (2018) Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the ‘odd man out’. PLoS ONE 13(1): e0189482. <https://doi.org/10.1371/journal.pone.0189482>

Editor: William J. Etges, University of Arkansas, UNITED STATES

Received: September 19, 2017

Accepted: November 27, 2017

Published: January 3, 2018

Copyright: © 2018 Wilson et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: The authors received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist.

Introduction

Africa is geographically and biologically unique among the continents, being the only land-mass currently extending across both the northern and southern hemispheric subtropical ridges, (~30°N & S) and as such, has the most extensive surface area of any continent lying within the tropical and subtropical zones [1]. While it has been observed that the tropics are generally more species rich and biologically diverse in comparison to higher latitudes (e.g., [2–3]), Africa (excluding Madagascar) has been termed the “Odd Man Out” by Richards [4] due to the depauperate nature of the African rainforest flora in terms of species richness compared to the other tropical regions. This is illustrated by the noticeable absence of or low diversity of

ecologically important and widely distributed plant families (i.e. Arecaceae, Fagaceae, Lauraceae, Myrtaceae, Myristicaceae, and Orchidaceae), and the lower levels of endemic rainforest plant taxa in comparison to the other tropical regions [4]. Africa's "Odd Man Out" status, however, extends beyond its tropical rainforest flora and is also characterized by its relatively low biodiversity and species richness in soil fungi, ants, flies, lepidopterans, aquatic amphibians, and birds in comparison to other tropical regions [4, 5–16]. Some clades, which are often associated with seasonally dry communities, are more species rich and/or diverse in Africa than on the other continental landmasses, including Acacieae and detarioid legumes, viperine snakes, bovids, termites, and velvet ants [17–23].

This last clade, the velvet ants (Mutillidae), represent a diverse group of sexually dimorphic (females are apterous), aposematic aculeate wasps that include around 4,900 named forms worldwide [19, 24–25, pers. obs.]. The African velvet ant fauna includes almost a third of the family's species and subspecies richness (~1600 species and subspecies; [19; pers. obs.]). Recent studies have provided evidence that aposematic colored (diurnal) female velvet ants in North America represent one of the largest known Müllerian mimetic complexes in the world [26–27], yet it has not been investigated if velvet ant Müllerian mimicry complexes occur on other continental landmasses. Like those in North America, the majority of African velvet ant species also exhibit aposematic coloration. It is unclear, however, if similarly colored, unrelated African taxa have concordant geographic ranges, which would indicate mimetic rings. If multiple mimetic rings do occur in Africa, and thus form a mimicry complex, it would be expected that the number of mimetic rings making up this complex would be similar to, or more phenotypically diverse compared to those found in North America, given the greater geographic area and higher velvet ant species richness in Africa. Alternatively, the generally depauperate nature of the African fauna and flora could be reflected in a less diverse African mimetic complex than has been reported in North America [26–27].

We hypothesize that female Müllerian mimicry ring diversity is a reflection of predator diversity/heterogeneity and ecological heterogeneity (which may not be mutually exclusive) rather than simply an echo of species richness. In this regard, we predict that a diverse aposematic clade, like the African velvet ants, while species rich and diverse, will have a less diverse mimicry complex compared to mimicry complexes from areas with a more diverse/heterogeneous predator fauna and/or a higher number of distinct ecological communities.

To test this hypothesis, we assessed the color pattern and distributions of 304 diurnal velvet ant taxa (58 genera from 3 subfamilies), which represents approximately 30% of the described diurnal female species (1010 species and subspecies) known from the African continent (excluding Madagascar). We ask (1) do African female velvet ant Müllerian mimicry rings exist, and if so, are the discrete mimetic rings geographically restricted, thus representing a continental mimicry complex, (2) are the number of African mimetic rings comparable to the number of rings in the North American mimicry complex, (3) is the familial/generic diversity and species richness of insectivorous/omnivorous squamates, particularly iguanians, between both continental faunas related to the mimetic diversity of velvet ants, and (4) is the number of terrestrial ecoregions and landmass sizes of both continents related to the mimetic diversity of velvet ants?

Methods

Specimen sampling

Female African velvet ant specimens (261 taxa: S1 Fig) were photographed from entomological loaned specimens from the following institutional collections: American Museum of Natural History, California Academy of Sciences, Carnegie Museum of Natural History, Florida

Department of Agriculture, Lund University, Muséum National d'Histoire Naturelle, National Museum of Natural History, Naturalis Biodiversity Center, Natural History Museum–London, Royal Belgian Institute of Natural Sciences, Texas A&M University, University of California Davis, University of California Riverside, University of Minnesota Saint Paul, and Utah State University. Specimens were photographed in dorsal and lateral views by one of the authors (K.A. Williams). Forty-three additional taxa were included in the morphological analysis based on published descriptions and associated illustrations. Moreover, an additional 48 diurnal female velvet ant taxa that are known to occur in the Palearctic zone of Africa (from the South Saharan Steppe and Woodlands terrestrial ecoregion northward) were examined; these collection specimens, however, were from localities outside of Africa (Mediterranean Europe and the Middle East). Although not used in the analysis, these 48 specimens were compared with the derived mimicry ring distributions to determine if the study's results were supported by these additional taxa [28].

Morphological analysis

Morphological analyses were performed to determine if the velvet ant species occurred in discrete groupings (indicative of mimicry rings). Methodology and characteristics analyzed follow Wilson et al. [26], including coding of head primary (background) and secondary colors, mesosoma background and secondary colors, petiole color, the presence or absence of a contrasting setal spot on the petiole, metasoma background and secondary colors, the presence of a third color/maculae on the second tergite of the metasoma (T2), contrasting dark and light pattern on T2, light setal fringes on the apical tergites (T3–T5), integument color, leg color, and setal length (S1 Table). Velvet ant species were grouped into putative mimicry rings based on visual similarities. These *a priori* groupings were then examined using nonmetric multidimensional scaling (NMDS) and a permutational analysis of variance (PERMANOVA) calculated using the isoMDS function in the MASS package and the adonis function in the vegan package in R (R Foundation for Statistical Computing). A Gower distance matrix was utilized for the NMDS, due to analysis of categorical data [26–27, 29].

Distributional analysis

Distributions of the velvet ant species were derived from specimen label locality data and published distributions and localities [28, 30–57]. These localities were used to determine the terrestrial ecoregion distributions of each taxon using the World Wildlife Foundation's (WWF) terrestrial ecoregion system. The species distributions were overlaid on each other in Adobe Photoshop CS6 to derive the distribution of each species and their association with possible mimicry rings derived from the NMDS analysis.

Analysis of predator richness

Information on lizard (including amphisbaenians) familial and generic diversity and species richness for Africa (excluding Madagascar, Comoros, Seychelles, and Mascarenes) and North America (including the Greater and Lesser Antilles) was obtained from publications and reptile databases [58–65]. These measures of diversity were then compared between Africa and North America.

Analysis of ecoregion diversity

To compare ecological community diversity and heterogeneity between Africa (excluding Madagascar, Comoros, Seychelles, and Mascarenes) and North America (including Central

America and the Caribbean–Bahamas, Greater Antilles, and Lesser Antilles), we compared the number of WWF terrestrial ecoregions of the two areas, excluding tundra biome communities because no velvet ant or lizard species occur there [66–70]. This system was used because it provides a global classification system for ecological communities on finer scales than previous biogeographic systems and incorporates endemic taxa and ecological processes and phenomena [68].

Results

Mimicry results

Based on our analyses, four distinct mimicry rings can be found in Africa (Fig 1) (each of the four mimicry rings is morphologically distinct: the overall effect of mimicry ring as a categorical variable was $F_{4,271} = 215.55$, $R^2 = 0.761$, $P < 0.001$; and can be distinguished based on integument and setal coloring and patterns (Fig 2). This indicates that a continental mimicry complex does exist for Africa and is made up of four mimicry rings; the Mediterranean-Steppe mimicry ring, the Equatorial mimicry ring, the Arid mimicry ring, and the Pan-African mimicry ring.

The Mediterranean-Steppe mimicry ring is associated with the Mediterranean mountains, highlands, coastal desert, and steppe areas of northernmost Africa, with the core centered in the Atlas and Aurès Mountains. This mimicry ring does not appear to extend southward into the core of the Sahara Desert itself, but occurs along its fringe in the steppe, woodland, and Nilotic areas. The Mediterranean-Steppe ring also appears to be absent from the highlands in the Saharan interior (Hoggar Mountains, Tibesti Mountains, Tassili n'Ajjer, and Air Massif; [71]). Members within the Mediterranean-Steppe mimicry ring have black integumental coloration with bronze, gold, or white setal coloration on the head, mesosoma, and metasoma. The metasoma typically has a bronze, gold, or white colored band on the apical tergites.

The Equatorial mimicry ring is centered in the equatorial region and is found on both the western and eastern sides of the East African Rift. With two main cores, one extending from the Horn of Africa to northeastern South Africa, especially associated with coastal and montane forests, miombo, bushland thickets, and bushveld in the east and southeast, and a western core associated with the moist and wet forest communities of the Guineo-Congolian region. Dolfuss [72] and Nonveiller [51] both noted the association of velvet ant taxa with black mesosomae ('melanic/melanistic forms') in forested communities compared to closely related taxa with red mesosomae in savannas. This mimicry ring is absent from the Cape, Karoo, and most of the Kalahari areas of southwestern Africa. Members of the Equatorial mimicry ring possess black integument with sparse or no setae on the mesosoma, and often with white, yellow, or orange macula(e) on the first and/or second tergite(s) and white or light colored setal bands (sometimes segmented) on the apical tergites.

The Arid mimicry ring is distributed in the semi-arid and arid regions of the continent, particularly areas that have extensive dry seasons. This ring is absent from the more mesic portions of the continent, the Guineo-Congolian region, including the Congo Basin and the West and Central African rain forests. The Arid mimicry ring is particularly abundant in the Sahelian, Sudanian, and Somalian portions of northern and northeastern Africa, occurs in the Sahara Desert and associated steppe communities, East Africa's Great Rift Valley, and the Zambezian, Kalahari, Namib, and Eastern Cape regions of southern Africa. The Arid ring is characterized by red coloration (either due to integument or setae) on the head and mesosoma. The metasoma is black or dark in coloration and often has white, yellow, orange, or gold colored maculae. A number of members of this ring that are distributed in southern Africa from

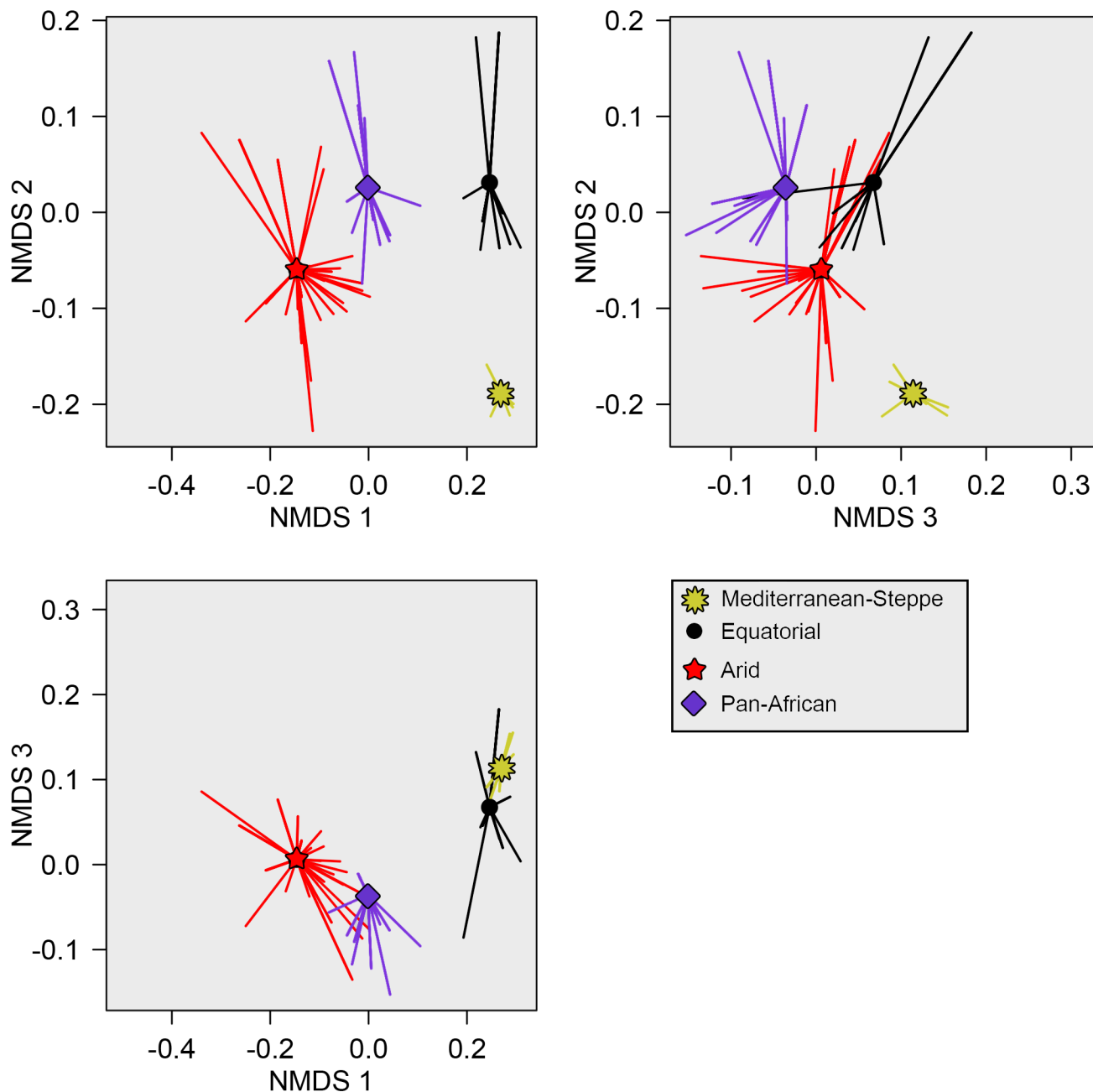


Fig 1. Velvet ant mimicry complex in 3D ordination space. Velvet ant mimicry complexes are differentiated in ordinal space (NMDS). In each comparison of the three NMDS axes, the mean values for each mimicry ring are denoted by symbols, with lines drawn from the means to individual species values.

<https://doi.org/10.1371/journal.pone.0189482.g001>

the miombo communities of south-Central Africa and extending through the Natal, Kalahari, Karoo, Namib, and Cape regions lack maculae on the second metasomal tergite.

The Pan-African mimicry ring is distributed throughout Africa and appears to be associated with multiple ecological communities and climate regimes, being found in arid and mesic environments. This mimicry ring is by far the most speciose and diverse with 187 of the 304 taxa examined included in this ring. The Pan-African mimicry ring consists of individuals

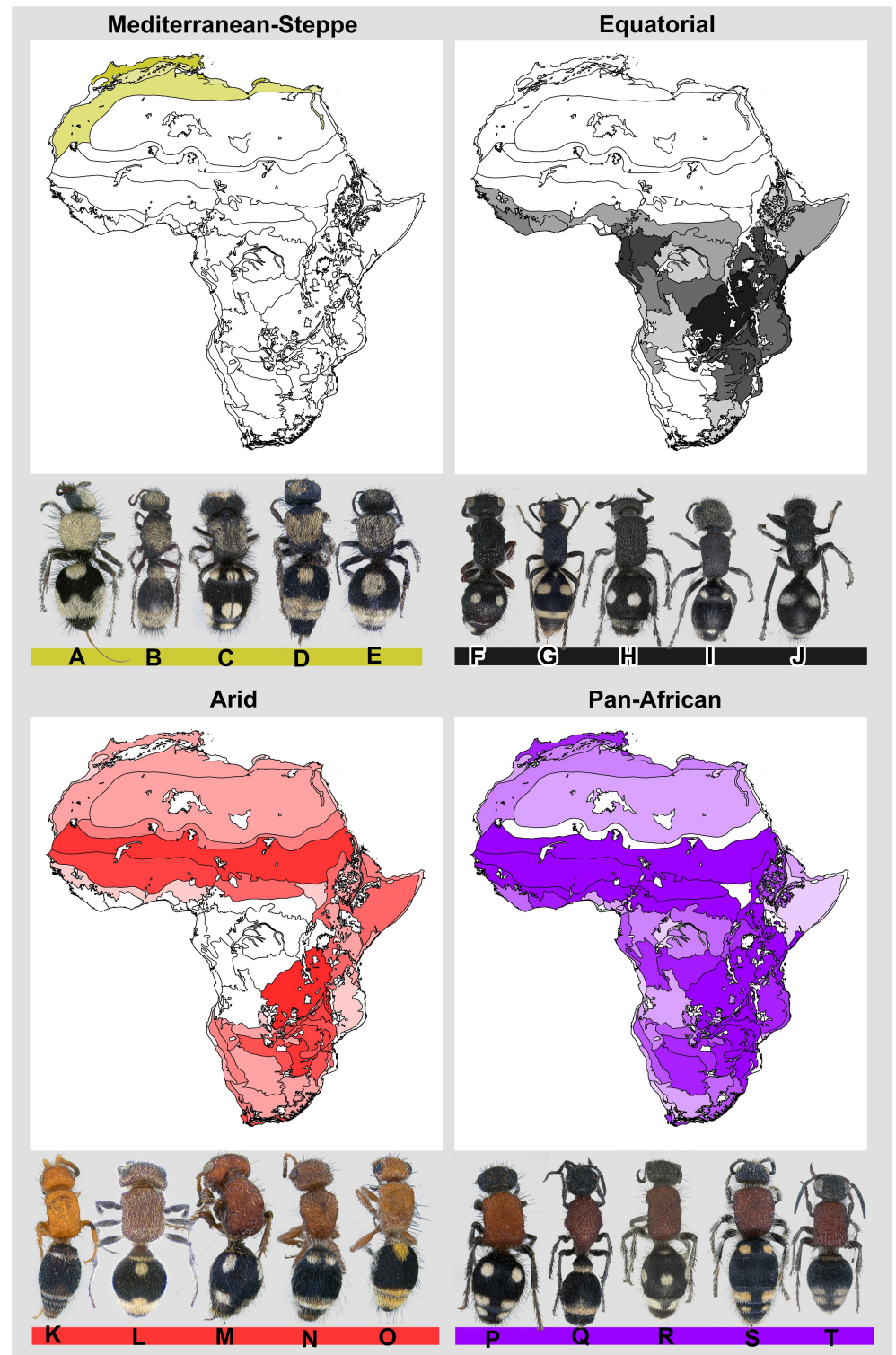


Fig 2. African velvet ant mimicry rings. The morphological and geographic ranges of the four African velvet ant mimicry rings. Each mimicry ring is represented here by five species. These species were selected because they are morphologically closest to the estimated mean for each mimicry ring (see Fig 1). The geographic range of each mimicry ring is presented based on distributional analyses that examined the known range of each species involved in each mimicry ring. The species pictured here are as follows: A *Dasylabris arabica*, B *Stenomutilla argentata*, C *Ronisia maculosa*, D *Nemka viduata tunensis*, E *Smicromyrme*

mareotica, F *Carinotilla* cf *stipnopyga*, G *Trispilotilla africana*, H *Smicromyrme tettensis melanothoracica*, I *Mutilla astarte ignava*, J *Dolichomutilla scutellata*, K *Tropidotilla fimbriata*, L *Sulcotilla sulcata*, M *Glossotilla mogadiscioana*, N *Dasylabroides latona ruficeps*, O *Dasylabris bassutorum*, P *Trogaspidia sulcicada*, Q *Stenomutilla analis*, R *Smicromyrme tettensis tettensis*, S *Odontomutilla calida calida*, T *Cephalotilla ceratophora*.

<https://doi.org/10.1371/journal.pone.0189482.g002>

with black/dark colored head, red mesosoma, and black/dark colored metasoma often with lines and/or maculae of white, yellow, gold, or orange colored setae.

While we were not able to examine every named species from Africa, our sample does contain a representative sample of African velvet ants. For example, for the species rich genus *Trogaspidia*, our study included 22 described species and seven unidentifiable morphospecies. Bischoff's [33] treatment of the genus included 115 described species and subspecies of females that are currently assigned to *Trogaspidia*, [these belong to his *T. divisa* (93 named forms) and *trigonophora* (22 named forms) species-groups]. Based on his identification keys, these species can be tentatively assigned to the following mimicry rings: 15 Equatorial forms (13%), 12 Arid forms (10%), and 88 Pan-African forms (77%). Of the 29 *Trogaspidia* photographed and analyzed in our study, three were Equatorial forms (10%), four were Arid forms (14%), and 23 were Pan-African forms (76%). Although in the present study we were only able to directly examine fewer than 30% of the recognized *Trogaspidia* female forms, we ended up with similar ratios for each mimicry ring. In addition, the genus is not known to include species that do not conform to one of the mimicry rings described herein.

Predator richness results

African non-ophidian squamate (lizard and amphisbaenian) familial diversity is only about 65% compared to that of North American (including Central America and Caribbean) fauna (15 versus 23 families; [58–63, 65]. Generic lizard diversity, however, is more substantial in Africa than North America with 118 and 66 genera, respectively [58–63, 65]. In terms of species richness, both continents are comparable with North America having a higher, but relatively comparable, lizard species richness in comparison to Africa, approximately 980 and 940 species, respectively [58–63, 65]. Insectivorous iguanian lizard familial and generic diversity and species richness is higher in North America (7 families, 19 genera, and over 500 species) compared to Africa (2 families, 12 genera, and over 175 species; [58–63, 65]. Lizard species richness in Africa is highest in the Central Zambebian Miombo Woodlands, Drakensberg Montane Grasslands, Woodlands, & Forests, Nama Karoo, Namibian Savanna Woodlands, Northern Zanzibar-Inhambane Coastal Forest Mosaic, Somali Acacia-Commiphora Bushlands & Thickets, Succulent Karoo, and Zambebian and Mopane Woodlands ecoregions [62, 69]. In North America the ecoregions with the highest species richness of lizards include the California Coastal Sage & Chaparral, Central American Dry Forests; Central American Pine-Oak Forests, Chiapas Depression Dry Forests, Chihuahuan Desert, Isthmian-Atlantic Moist Forests, Petén-Veracruz Moist Forests, Sierra Madre Occidental Pine-Oak Forests, Sonoran Desert, and Southern Pacific Dry Forests [58–65, 67].

Ecoregion diversity results

The African continent and associated small islands (São Tomé, Príncipe, Annobon, Bioko Island, Canary Islands, Cape Verde Islands, and Zanzibar) includes 108 terrestrial ecoregions within 9 biomes extending over nearly 29,200,000 km² [69]. Africa lacks four distinct biome types: boreal forest/taiga, temperate broadleaf and mixed forests, temperate grasslands and savanna, and tropical coniferous forests [69]. North America, including Central America and

Caribbean Islands, contains 168 terrestrial ecoregions within 13 biomes and extends over 17,521,000 km² (excluding tundra biome and associated ecoregions; [66–67, 70]. Some biomes, like the Boreal Forest/Taiga, likely house few, if any, velvet ant species and if these are also excluded, North America still consists of 151 terrestrial ecoregions [66–67].

Discussion

Our results clearly show that Africa does indeed harbor a large velvet ant mimicry complex, composed of four distinct mimicry rings. What is particularly intriguing, however, is that this African velvet ant mimicry complex is less phenotypically diverse than the North American mimicry complex (i.e., there are only 4 African rings compared to 8 North American rings) [26–27]. This lack of phenotypic diversity is especially interesting given the fact that the African velvet ant fauna is more species rich than North America and that Africa is over 1.35 times larger than North America [67, 69, 73]. So, even while velvet ants are more species rich in Africa than in North America, the “odd man out” observation of low richness in African taxa holds true if mimetic diversity is taken into account. There are several potential explanations for this lack of phenotypic diversity in the African velvet ant mimicry complex that we will discuss below.

First, the apparent lack of mimicry ring diversity in the African velvet ant mimetic complex could be related to the diversity of predators. It has been suggested that insectivorous/omnivorous squamates, particularly iguanians, might be a major predator of velvet ants and that they likely play a role in the development of aposematic coloration [29]. Furthermore, in North America there is a link between the species richness of lizard predators and the richness of mimicry rings [29]. While the lizard species richness between Africa and North America is comparable (~940 and 980 species respectively), Africa has a much lower lizard heterogeneity per km² due to its much greater landmass size, especially when considering that large portions of North America are covered by tundra and boreal forest and taiga that include essentially no species of lizards or velvet ants [62, 64, 67]. Furthermore, lizard species richness is spread across the African continent, with many ecoregions harboring relatively rich lizard communities [62]. Alternatively, North American lizard communities are much less equally distributed, with the majority of lizard species being found in only a handful of ecoregions (primarily those in the arid southwest and in the Neotropics [74]. This concentration of lizard richness in North America could have increased selective pressure on the evolution of aposematism and driven the development of a more phenotypically diverse velvet ant mimicry complex compared to the more dispersed lizard richness (and lower phenotypically diverse velvet ant mimicry complex) found in Africa. This is supported by the concordance of the patterns of lizard richness and velvet ant mimicry rings on both continents. For example, the Central Zambesian Miombo Woodlands is among the richest ecoregions for velvet ants, both in terms of species richness and mimicry ring richness (three of four mimicry rings). This same ecoregion also houses one of the richest lizard communities in Africa [62]. Similarly, in North America, the Sonoran and Chihuahuan deserts include five of the eight North American velvet ant mimicry rings [75] and are home to some of the richest lizard communities in North America [74].

These patterns of lizard diversity, and the associated patterns of velvet ant diversity, are likely also connected to ecoregion diversity. Africa, while larger in size than North America, contains fewer ecoregions (108 total ecoregions in Africa, 168 in North America). Furthermore, many of Africa’s ecoregions are much larger than those found in North America. For example, Africa has seven ecoregions that are over 1 million km² in size. North America’s largest ecoregions are all smaller than 1 million km² and most of the largest are in Boreal Forest/

Taiga Biomes. This means that much of the North American habitat conducive to velvet ants (and lizards) is condensed and highly variable with many ecoregions found in relatively small areas. Africa, nearly in its entirety, provides suitable velvet ant (and lizard) habitat, with broad swaths of land maintaining similar habitat characteristics. That habitat variability in North America compared to Africa could be associated with the difference in mimetic diversity between the two continents. Habitat variability could lead to diversification in mimicry complexes; as climatic shifts drove different communities into isolated areas (particularly during the Pleistocene), different selective pressures or genetic drift could have resulted in phenotypically distinct mimicry rings. The more heterogeneous a landmass is, the more likely ancestral communities would have shifted into multiple distinct habitats, resulting in more unique mimicry rings.

It is clear that Africa houses a less phenotypically diverse mimicry complex than North America. Despite this lower diversity, some aspects of the African complex should be discussed further. The Mediterranean-Steppe ring, for example, is the most geographically restricted ring on the African continent and is associated with the Palearctic portion of the continent [68–69]. The ring also extends into the Iberian Peninsula and, as a whole, the African and European portion of the ring likely represents the western extension of a Müllerian mimicry ring that also extends into the steppe areas of the Near East, around the Caspian Sea and into the highland areas of Central Asia in the east. The Mediterranean-Steppe mimicry ring is also the smallest of the four African mimicry rings in terms of species richness. It is notable that the whitish or bronze setae coloration of these mainly highland taxa are reminiscent of similar setal coloration found in the Madrean or Desert Mimicry rings of North America, which are also generally associated with upland environments [26–27]. The restricted nature of the Mediterranean-Steppe ring and the few species that contribute to it, suggest that this ring only recently evolved on the African continent. The northwestern portion of Africa has a noticeably high density of lizard taxa, particularly agamids and lacertids (i.e. *Acanthodactylus* and *Mesalina*) that are known to take ants as a high proportion of their diet [62, 76–78]; these are likely predators of the Mediterranean-Steppe ring.

The Equatorial ring is interesting in that it can be found in both mesic and xeric ecological communities, but is particularly predominant in the tropical moist/wet forests of the Guinean-Congolian region, the Eastern Arc, East African Montane, and coastal forests, and miombo communities of southeastern and East Africa. The black head and mesosoma is not necessarily indicative of aposematic coloration. A number of Afrotropical forest ants (ex. *Ankylomyrma*, *Aphomomyrmex*, *Paltothyreus*, *Phasmomyrmex*, & *Psalidomyrmex*) also have entirely black integument, suggesting a cryptic adaptation [79]. The bright colored maculae and/or setal bands on the tergites of Equatorial mimicry ring velvet ants may provide an aposematic warning to possible predators and discriminates these female velvet ants (mutillids) from rainforest ants (formicids). This ring also appears to be the only one that is a definitively endemic mimicry ring in Africa (although it should be noted that similar colored taxa can be found in Madagascar as well as in Australian and South American taxa).

Both the Arid mimicry ring and the Pan-African mimicry ring represent color patterns that are found in velvet ants across the globe. For example, in North America the Black-headed Timulla and Red-headed Timulla rings share these color patterns [27]. Due to the widespread occurrence of this coloration, it is possible that it represents an ancestral pattern for velvet ants. Another interesting similarity between mimicry complexes on the two continents is that those mimicry rings characterized by having predominantly black coloration with starkly contrasting abdominal patterns are both found primarily in equatorial areas. The Tropical mimicry ring (North America) and the Equatorial mimicry ring (Africa) are both restricted to the tropics (areas between 23.5 degrees N and S). Some of the most widespread mimicry rings in

North America (western, Desert, and Eastern rings) do not have comparable African counterparts in terms of coloration. This could be related to the fact that these unique North American rings are found primarily in the Nearctic regions of the continent, while Africa does not have comparable temperate grassland biomes.

Furthermore, it is apparent in many of the African and North American mimicry rings that the abdominal color patterns are highly variable, even within a given ring. For example, some members of the Pan-African ring have nearly completely black abdomens, while others have large patches of white setae, and these setal patterns often differ between species and regions. Similar patterns of variability can be found in the Equatorial, and Arid African rings, as well as in the Tropical, Madrean, and red-headed and black-headed *Timulla* rings in North America. This variability might indicate that with more sampling at finer scales, these large mimicry rings might be subdivided into smaller more specific sub-rings.

It might be asked why velvet ants have been so successful as a Müllerian mimicry complex. We suggest that the diversity and success of velvet ant mimicry complexes likely is related to the following series of observations and hypotheses [29]. First, ants (Formicidae) are one of the most prolific and ecologically dominant organisms in tropical and subtropical environments [79–80]. Because of the wingless nature of female velvet ants, they resemble ants, hence the common name ‘velvet ant.’ Even more than true ants, velvet ants are highly defended with painful stings, extremely hard cuticles, pungent chemical secretions, and stridulation warning sounds [26]. So, because of their similarity to ants, predators that often eat ants could pose a threat to velvet ants. We suggest that the evolution of aposematism, including the long setae that many velvet ants exhibit, likely evolved as a way to differentiate themselves from true ants as a way to protect themselves from ant specialist predators. Most Diurnal velvet ants either have bright contrasting patterns, which are not seen in true ants, or they have long setae, also rarely seen in true ants. Many velvet ant species have both long setae and aposematic color patterns.

Conclusion

Our study of mimicry in African velvet ants clearly shows that African velvet ants do participate in a large Müllerian mimicry complex. Furthermore we find that, while four distinct mimicry rings are found in Africa, this is less than the number of mimicry rings found in North America, further illustrating the “odd man out” concept of African species richness (in this case mimetic richness). We suggest that the lower number of African mimicry rings could be related to the diversity and distributions of lizards, with Africa having more uniform distribution of lizard species compared to North America's lizard diversity that is concentrated in a few ecoregions. Finally we suggest that the lower number of African mimicry rings is likely associated with the lower number of ecoregions in Africa compared to North America.

These findings of species rich mimicry rings in both Africa and North America expand our understanding of mimicry in velvet ants and clearly show that velvet ants form the world's largest known mimicry complex with nearly 600 species involved in 12 mimicry rings (~350 species in eight mimicry rings in N. America and at least 250 species in four rings in Africa).

Supporting information

S1 Fig. African velvet ant mimicry rings. Images of all of the velvet ant species included in the analysis organized into their respective mimicry rings.
(PDF)

S1 Table. African velvet ant morphological characters. Characters and character states for each of the velvet ant species included in the NMDS analysis.
(XLSX)

Acknowledgments

We thank the anonymous reviewers who improved this manuscript. We also thank the following curators and collections managers who made material available to study and photograph: James Pitts, Christine LeBeau, Brian Harris, Lynn Kimsey, Steve Heydon, Vincent Lee, Frederique Bakker, Gavin Broad, Christer Hansson, Yvonick Gerard, John Rawlins, and Karen Wright.

Author Contributions

Conceptualization: Joseph S. Wilson, Aaron D. Pan, Kevin A. Williams.

Data curation: Aaron D. Pan, Erica S. Limb, Kevin A. Williams.

Formal analysis: Joseph S. Wilson.

Investigation: Joseph S. Wilson, Aaron D. Pan, Erica S. Limb, Kevin A. Williams.

Methodology: Joseph S. Wilson, Aaron D. Pan, Erica S. Limb, Kevin A. Williams.

Project administration: Joseph S. Wilson.

Resources: Joseph S. Wilson, Kevin A. Williams.

Software: Joseph S. Wilson.

Supervision: Joseph S. Wilson.

Validation: Joseph S. Wilson, Erica S. Limb.

Visualization: Joseph S. Wilson, Aaron D. Pan.

Writing – original draft: Joseph S. Wilson, Aaron D. Pan.

Writing – review & editing: Joseph S. Wilson, Aaron D. Pan, Kevin A. Williams.

References

1. Lock JM. The seasonally dry vegetation of Africa: parallels and comparisons with the Neotropics. In: Pennington TR, Lewis GP, Ratter JA, editors. Neotropical savannas and seasonally dry forests: plant diversity, biogeography, and conservation. Boca Raton: Taylor & Francis. 2006. pp. 449–467.
2. Pianka ER. Latitudinal gradients in species diversity: a review of concepts. *Am Nat.* 1966; 100(910): 33–46. <https://doi.org/10.1086/282398>
3. Hillebrand H. On the generality of the latitudinal diversity gradient. *The American Naturalist.* 2004; 163(2): 192–211. <https://doi.org/10.1086/381004> PMID: [14970922](https://pubmed.ncbi.nlm.nih.gov/14970922/)
4. Richards PW. Africa, the “Odd Man Out”. In Meggers BJ, Ayensu E, Duckworth WD, editors. Tropical forest ecosystems in Africa and South America: a comparative review. Washington, D.C.: Smithsonian Institution Press. 1973. Pp. 21–26.
5. Moore HE Jr. Palms in the tropical forest ecosystems of Africa and South America. In Meggers BJ, Ayensu E, Duckworth WD, editors. Tropical forest ecosystems in Africa and South America: a comparative review. Washington, D.C.: Smithsonian Institution Press. 1973. pp. 63–88.
6. Briggs JC. Global Biogeography. *Developments in Paleontology and Stratigraphy.* Vol. 14. Amsterdam: Elsevier; 1995.
7. Craw RC, Grehan JR, Heads MJ. Panbiogeography: tracking the history of life. Oxford University Press; 1999.

8. Mutke J, Barthlott W. Patterns of vascular plant diversity at the continental scales. *Biologische Skrifter*. 2005; 55: 521–531.
9. Kristensen NP, Scoble MJ, Karsholt OL. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa*. 2007; 1668(699): e747.
10. de Jong H, Oosterbroek P, Gelhaus J, Reusch H, Young C. Global diversity of craneflies (Insecta, Diptera: Tipulidae or Tipulidae sensu lato) in freshwater. *Hydrobiologia*. 2008; 595(1): 457–467. <https://doi.org/10.1007/s10750-007-9131-0>
11. Rueda LM. Global diversity of mosquitoes (Insecta: Diptera: Culicidae) in freshwater. *Hydrobiologia*. 2008; 595(1): 477–487. https://doi.org/10.1007/978-1-4020-8259-7_48
12. Vences M, Köhler J. Global diversity of amphibians (Amphibia) in freshwater. *Hydrobiologia*. 2008; 595(1): 569–80. <https://doi.org/10.1007/s10750-007-9032-2>
13. Pape T, Bickel DJ, Meier R, editors. *Diptera diversity: status, challenges and tools*. Brill; 2009.
14. Guénard B, Weiser MD, Dunn RR. Global models of ant diversity suggest regions where new discoveries are most likely are under disproportionate deforestation threat. *Proc Natl Acad Sci*. 2012; 109(19): 7368–7373. <https://doi.org/10.1073/pnas.1113867109> PMID: 22529355
15. Jenkins CN, Pimm SL, Joppa LN. Global patterns of terrestrial vertebrate diversity and conservation. *Proc Natl Acad Sci*. 2013; 110(28): E2602–10. <https://doi.org/10.1073/pnas.1302251110> PMID: 23803854
16. Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, et al. Global diversity and geography of soil fungi. *Science*. 2014; 346(6213): 1256688. <https://doi.org/10.1126/science.1256688> PMID: 25430773
17. Eggleton P. Global patterns of termite diversity. In Abe T, Bignell DE, Higashi M, editors. *Termites: evolution, sociality, symbioses, ecology*. Netherlands: Springer. 2000. pp. 25–51.
18. Mallow D, Ludwig D, Nilson G. *True vipers: natural history and toxinology of old world vipers*. Krieger Publishing Company; 2003.
19. Lelej AS. Catalogue of the Mutillidae (Hymenoptera) of the Oriental region. *Dalnauka*; 2005.
20. Schrire BD, Lewis GP, Lavin M. Biogeography of the Leguminosae. In Lewis G, Schrire B, Mackinder B, Lock M, editors. *Legumes of the World*. Kew: The Royal Botanic Gardens. 2005. pp. 21–54.
21. Traill LW, Wanger TC, Kidd D. Large, particular bovids may require localised conservation effort to prevent extinction. *Raffles Bull Zool*. 2012; 60: 111–116.
22. Azani N, Babineau M, Bailey CD, Banks H, Barbosa AR, Pinto RB, et al. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny The Legume Phylogeny Working Group (LPWG). *Taxon*. 2017; 66(1): 44–77. <https://doi.org/10.12705/661.3>
23. Estrella M, Forest F, Wieringa JJ, Fougère-Danezan M, Bruneau A. Insights on the evolutionary origin of Detarioideae, a clade of ecologically dominant tropical African trees. *New Phytol*. 2017 Jun 1; 214(4): 1722–35. <https://doi.org/10.1111/nph.14523> PMID: 28323330
24. Lelej AS, Brothers DJ. The genus-group names of Mutillidae (Hymenoptera) and their type species, with a new genus, new name, new synonymies, new combinations and lectotypifications. *Zootaxa*. 2008; 1889: 1–79.
25. Brothers DJ, Lelej AS, Madl M. Annotated Catalogue of the Mutillidae (Hymenoptera: Vespoidea) of the Malagasy Subregion. *Linzer biologische Beiträge*. 2011; 43: 115–49.
26. Wilson JS, Williams KA, Forister ML, Von Dohlen CD, Pitts JP. Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nat Commun*. 2012; 3: 1272. <https://doi.org/10.1038/ncomms2275> PMID: 23232402
27. Wilson JS, Jahner JP, Forister ML, Sheehan ES, Williams KA, Pitts JP. North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Curr Biol*. 2015; 25(16): R704–706. <https://doi.org/10.1016/j.cub.2015.06.053> PMID: 26294178
28. Lelej AS. Catalogue of the Mutillidae (Hymenoptera) of the Palaearctic Region. Vladivostok: Dalnauka; 2002.
29. Pan AD, Williams KA, Wilson JS. Are diurnal iguanian lizards the evolutionary drivers of New World female velvet ant (Hymenoptera: Mutillidae) Müllerian mimicry rings? *Biol J Linnean Soc*. 2017; 120(2): 436–447. <https://doi.org/10.1111/bij.12894>
30. André E. *Species de Hyménoptères d'Europe & d'Algérie*. Tome Huitième. Les Mutillides. Paris: Vve Dubosclard & A. Hermann, 480 pp.+ 15 pls (1899) 1–64+ pl. 1–8; (1900) 65–144; (1901) 145–304; (1902) 305–384.
31. Dollman HC. *Glossina morsitans*. Westw.: some notes on the parasitisation of its pupae. *Trans Entomol Soc Lond*. 1915; 1915: 394–396.

32. Turner RE. A New Species of *Mutilla* Parasitic on *Glossina morsitans*. Bull Entomol Res. 1915; 5: 383.: <https://doi.org/10.1017/S000748530003039X>
33. Bischoff H. Monographie der Mutilliden Afrikas. Nicolaische; 1920.
34. Bradley JC, Bequaert J. Studies in African Mutillidae. Revue Zoologique Africaine. 1923; 11: 211–258.
35. Bradley JC, Bequaert JC, Lang H, Chapin JP. A synopsis of the Mutillidae of the Belgian Congo. Bulletin of the AMNH. 1928; 58: article 2.
36. Arnold G. New species of African Hymenoptera No. 12. Occas Pap Natl Mus Rhodesia. 1956; 3(21b), 52–77.
37. Invrea F. Spedizione scientifica all'oasi di Cufra (Marzo-Luglio 1931). Mutillidae e Chrysididae (Hymenoptera). Annali del Museo Civico di Storia Naturale di Genova. 1932; 55: 457–465.
38. Nonveiller G. Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae). I. Contribution à la connaissance du genre *Trispilotilla* Bischoff 1920. Annales de la Faculté des Sciences du Cameroun 1973a; 13: 77–134.
39. Nonveiller G. Recherches sur les Mutillides de l'Afrique, Hymenoptera, Mutillidae II. *Carinotilla* (♂,♀) gen. nov. Annales de la Faculté des Sciences du Cameroun, 1973b; 14: 42–102.
40. Nonveiller G. Recherches sur les Mutillides de l'Afrique—VII *Dentotilla* gen. nov. ♂,♀ (Hymenoptera: Mutillidae). Beiträge zur Entomologie, Berlin. 1977; 272: 255–300.
41. Nonveiller G. Recherches sur les Mutillides de l'Afrique Hymenoptera, Mutillidae. VIII. Révision des genres *Ctenotilla*, *Cephalotilla* et *Pseudocephalotilla* sensu Bischoff. Memoires publiés par l'Institut pour la Protection des Plantes, Belgrad. 1979; 13: 1–184.
42. Nonveiller G. Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae). X. Bref aperçu des résultats des recherches sur la faune des Mutillides du Cameroun, effectuées au cours de la période de 1962–1975. Mémoires de l'institut de protection des Plantes, Belgrade. 1980a; 14: 11–68.
43. Nonveiller G. Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae). XI. Revision des males du genre *Trogaspidia* Ashmead, 1899 ♂, ♀ 28 Advances in the studies of the fauna of the Balkan Peninsula apparentes ou semblables à *medon* (Smith, 1855) ♂, avec description du nouveau sous-genre *Tubercocoxotilla* ♂. Memoires de l'institut de protection des Plantes, Belgrade. 1980b; 14: 69–108.
44. Nonveiller G. Recherches sur les Mutillides de l'Afrique (Hymenoptera, Mutillidae). XII. *Dasylabroides remota* nov. ♂, ♀, espèce nouvelle du Cameroun, représentant le plus avancé vers le nord-ouest du continent d'un genre essentiellement sudafricain, avec des remarques sur des espèces connues et avec des descriptions d'espèces nouvelles du genre. Memoires de l'institut de protection des Plantes, Belgrade. 1980c; 14: 109–147.
45. Nonveiller G. Recherches sur les Mutillides de l'Afrique XVII. Note pour servir à la Connaissance du genre *Pristomutilla* ASHMEAD, 1903 (♂,♀) avec description du mâle encore inconnu du genre, d'espèces nouvelles du genre et des nouveaux sous-genres *Diacanthotilla* (♀♀) et *Acanthomutilla* (♀♀) (Hymenoptera: Mutillidae). Entomofauna, Zeitschrift für Entomologie. 1995; 16: 29–120.
46. Nonveiller G. Remarques sur *Dolichomutilla guineensis* (F., 1793), *Dolichomutillasycorax* (Smith, 1855) et sur certains hôtes du genre *Dolichomutilla* Ashmead, 1899 (Hymenoptera: Mutillidae). (Recherches sur les Mutillides de l'Afrique, note XXVII). Revue française d'entomologie (N. S.), Paris. 1996a; 18(1): 31–34.
47. Nonveiller G. Révision du genre Afrotropical *Odontotilla* Bischoff, 1920 mâle et femelle. Hymenoptera: Mutillidae. Annales de la Société Entomologique de France, N.S. 1996b; 323: 299–357.
48. Nonveiller G. Types de répartition dans la région Afrotropicale basés sur l'étude des Mutillides Hymenoptera, Mutillidae. Bulletin de la Société Entomologique de France. 1996c; 1011: 89–112.
49. Nonveiller G. Corrigenda: a preliminary approach to a revision of the Afrotropical representatives of the genus *Trogaspidia* Ashmead, 1899 (sensu Bischoff, 1920) (Hymenoptera: Mutillidae). (Studies on African Mutillidae: Note XXI); (Third contribution to the knowledge of the Afrotropical *Trogaspidia*). Annales de la société entomologique de France (N. S.), Paris. 1996d; 32(3): 357.
50. Nonveiller G. Description du nouveau genre *Arcuatotilla* (mâle, femelle) avec des remarques sur *Arcuatotilla arcuaticeps* (André, 1905) (mâle, femelle) (Hymenoptera, Mutillidae). (Recherches sur les Mutillides de l'Afrique: Note XXXII). Revue française d'entomologie (N. S.), Paris. 1998; 20(1–2): 17–23.
51. Nonveiller G. A revision of the genus *Lobotilla* Bischoff, 1920 (♂,♀) (Insecta: Hymenoptera: Mutillidae). Entomologische Abhandlungen. 1999; 58: 255–282.
52. Nonveiller G. & Četković A. *Seriatospidia* n. gen. with a description of three new species (Hymenoptera Mutillidae). (Studies on African mutillids, Note XX). Tropical Zoology, Firenze. 1996; 9: 305–314.
53. Mouna M, Bensusan K, Perez C, Cortes J. A review of entomological research on sandy beaches in Morocco, with an emphasis on Coleoptera. Sandy Beaches and Coastal Zone management. 2009; 73: 73–80.

54. Pagliano G, Strumia F. *Smicromyrme corriasi* n. sp. from Sardinia and new data on some Italian *Smicromyrme* and *Stenomutilla* (Hymenoptera, Mutillidae). *Il Naturalista Valtellines*. 2014; 24: 55–66.
55. Pagliano G, Matteini Palmerini M. Contributo alla studio dei Mutillidi della Tunisia (Insecta Hymenoptera Mutillidae). *Quaderni di Studi naturalistici della Romagna*. 2014; 39: 175–209.
56. Cascio PL, Grita F. A new species of *Smicromyrme* from Israel (Hymenoptera: Mutillidae). *Fragmenta Entomologica*. 2014; 46(1–2): 125–128. <https://doi.org/10.4081/fe.2014.76>
57. Turrisi GF, Palmerini MM, Brothers DJ. Systematic revision and phylogeny of the genera *Blakeius* Ashmead, 1903 and *Liomutilla* André, 1907, with description of two new genera (Hymenoptera: Mutillidae, Myrmillinae). *Zootaxa*. 2014; 4010:1–78. <https://doi.org/10.11646/zootaxa.4010.1.1> PMID: 26623841
58. Köhler G. *Reptiles of Central America*, 2nd revised edition. Frankfurt: Herpeton Verlag Elke Kohler. 2008.
59. Köhler G. A new species of anole related to *Anolis altae* from Volcán Tenorio, Costa Rica (Reptilia, Squamata, Polychrotidae). Una nueva especie de lagartija relacionada con *Anolis altae* del Volcán Tenorio, Costa Rica (Reptilia, Squamata, Polychrotidae). *Zootaxa*. 2011; 3120: 29–42.
60. Köhler G, Pérez RGT, Peterson CBP, de la Cruz FRM. A new species of pine anole from the Sierra Madre del Sur in Oaxaca, Mexico (Reptilia, Squamata, Dactyloidae: Anolis). *Zootaxa*. 2014; 3753(5): 453–68. <http://dx.doi.org/10.11646/zootaxa.3753.5.4>
61. Lotzkat S, Hertz A, Bienentreu JF, Koehler G. Distribution and variation of the giant alpha anoles (Squamata: Dactyloidae) of the genus *Dactyloa* in the highlands of western Panama, with the description of a new species formerly referred to as *D. microtus*. *Zootaxa*. 2013; 3626(1): 1–54. <http://dx.doi.org/10.11646/zootaxa.3626.1.1>
62. Lewin A, Feldman A, Bauer AM, Belmaker J, Broadley DG, Chirio L, et al. Patterns of species richness, endemism and environmental gradients of African reptiles. *J Biogeog*. 2016; 43(12): 2380–90.
63. Hedges SB. *Caribherp: West Indian amphibians and reptiles*. Temple University, Philadelphia, PA. 2016. www.caribherp.org.
64. Tingley R, Meiri S, Chapple DG. Addressing knowledge gaps in reptile conservation. *Biol Cons*. 2016; 204: 1–5.
65. Uetz P, Freed P, Hošek J. *The Reptile Database*. 2017. <http://www.reptile-database.org>.
66. Dinerstein E, Olson DM, Graham DJ, Webster AL, Primm SA, Bookbinder MP, et al. A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. Washington, DC: World Bank; 1995.
67. Ricketts TH. *Terrestrial ecoregions of North America: a conservation assessment*. Island Press; 1999.
68. Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood EC, et al. *Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity*. *BioScience*. 2001; 51(11): 933–938.
69. Burgess N, Hales JA, Underwood E, Dinerstein E, Olson D, Itoua I, et al. *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment*. Island Press; 2004.
70. Kappelle M, Horn SP. The Páramo ecosystem of Costa Rica's highlands. In: Kappelle M, editor. *Costa Rican ecosystems*. Chicago: University of Chicago Press; 2016. pp. 492–523.
71. Osborn DJ, Krombein KV. Habitats, Flora, Mammals, and Wasps of Gebel Uweinat, Libyan Desert (No. NAMRU-3-TR-13-70). Naval Medical Research Unit No. 3, FPO New York: 09527. 1969.
72. Dolfuss H. Aculeate hymenoptera collected 1985 in the Republic of Central Africa II (Mutillidae, Sphecidae, Apoidea). *Linzer Biologische Beiträge*. 1993. 25:691–694.
73. Burke K, Gunnell Y. The African erosion surface: a continental-scale synthesis of geomorphology, tectonics, and environmental change over the past 180 million years. *Geological Society of America Memoirs*. 2008; 201: 1–66. <https://doi.org/10.1130/2008.1201>
74. Pianka ER. On lizard species diversity: North American flatland deserts. *Ecology*. 1967; 48(3): 333–351. <https://doi.org/10.2307/1932670>
75. Wilson JS, Jahner JP, Williams KA, Forister ML. Ecological and evolutionary processes drive the origin and maintenance of imperfect mimicry. *PloS one*. 2013; 8(4): e61610. <https://doi.org/10.1371/journal.pone.0061610> PMID: 23593490
76. Hölldobler B, Wilson EO. *Journey to the ants: a story of scientific exploration*. Harvard University Press; 1994. <https://doi.org/10.1371/journal.pone.0061610>
77. Vitt LJ, Pianka ER, Cooper WE Jr, Schwenk K. History and the global ecology of squamate reptiles. *Am Nat*. 2003; 162(1): 44–60. <https://doi.org/10.1086/375172> PMID: 12856236
78. Tamar K, Carranza S, Sindaco R, Moravec J, Trape JF, Meiri S. Out of Africa: Phylogeny and biogeography of the widespread genus *Acanthodactylus* (Reptilia: Lacertidae). *Mol Phylogenet Evol*. 2016; 103: 6–18. <https://doi.org/10.1016/j.ympev.2016.07.003> PMID: 27395778

79. Fisher BL, Bolton B. *Ants of Africa and Madagascar: A Guide to the Genera*. Univ of California Press; 2016.
80. Wilson EO, Hölldobler B. Eusociality: origin and consequences. *Proc Nat Acad Sci USA*. 2005; 102 (38):13367–13371. <https://doi.org/10.1073/pnas.0505858102> PMID: [16157878](https://pubmed.ncbi.nlm.nih.gov/16157878/)