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Seasonal variation in wing size and shape between geographic populations of the malaria vector, *Anopheles coluzzii* in Burkina Faso (West Africa)

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ABSTRACT

The mosquito, *Anopheles coluzzii* is a major vector of human malaria in Africa with widespread distribution throughout the continent. The species hence populates a wide range of environments in contrasted ecological settings often exposed to strong seasonal fluctuations. In the dry savannahs of West Africa, this mosquito population dynamics closely follows the pace of surface water availability: the species pullulates during the rainy season and is able to reproduce throughout the dry season in areas where permanent water bodies are available for breeding. The impact of such environmental fluctuation on mosquito development and the phenotypic quality of emerging adults has however not been addressed in details. Here, we examined and compared phenotypic changes in the duration of pre-imaginal development, body dry mass at emergence and wing size, shape and surface area in young adult females *An. coluzzii* originated from five distinct geographic locations when they are reared in two contrasting conditions mimicking those experienced by mosquitoes during the rainy season (RS) and at the onset of the dry season (ODS) in Burkina Faso (West Africa). Our results demonstrated strong phenotypic plasticity in all traits, with differences in the magnitude and direction of changes between RS and ODS depending upon the geographic origin, hence the genetic background of the mosquito populations. Highest heterogeneity within population was observed in Bama, where large irrigation schemes allow year-round mosquito breeding. Further studies are needed to explore the adaptive value of such phenotypic plasticity and its relevance for local adaptation in *An. coluzzii*.

1. Introduction

Species living in dry savannahs of West Africa, including the malarial mosquito *Anopheles coluzzii* (Diptera, Culicidae), have to face high seasonality in their environment, with the occurrence of an adverse dry season during which mean temperatures rise, relative humidity decreases, and water collections dry up. In such environment, the population dynamics of anopheline species follow the pace of water collections availability (Adamou et al., 2011; Lehmann et al., 2014, 2010; Yaro et al., 2012). However, larval instars of *An. coluzzii* can be found in both temporary (*i.e.* rain-filled) and permanent (*i.e.* generally man-made) water collections (Costantini et al., 2009; Gimonneau et al., 2012). Hence, in areas where large anthropogenic (*e.g.* dams, ricefields, etc.) or natural (*e.g.* ponds, river edges, etc.) surface water collections are available all year round, mosquitoes persist and reproduce all year long, whereas in areas where only temporary waters are available, local mosquito populations virtually disappear during the

Abbreviations: RH, relative humidity; RS, rainy season; ODS, onset of the dry season; LM, landmarks; CS, centroid size; GPA, generalised procrustes analysis; PCA, principal component analysis; PC1, first axis of the principal component analysis; PC2, second axis of the principal component analysis; ΔD, vector length; MD, metric disparity.

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dry season. In such area, *An. coluzzii* females might enter a state of quiescence/diapause and persist throughout the dry season by aestivation (Dao et al., 2014; Lehmann et al., 2010). In this context, mosquitoes may have developed local behavioural, physiological and/or morphological adaptations to survive and persist during the adverse conditions of the dry season. There is indeed evidence in the recent literature for seasonal physiological adjustments in some anopheline species, including *An. coluzzii* (Adamou et al., 2011; Hidalgo et al., 2014; Huestis et al., 2012, 2011; Huestis and Lehmann, 2014; Lehmann et al., 2010; Mamai et al., 2014; Yaro et al., 2012). Whether these physiological changes sustain variation in other fitness traits of the mosquito remains unknown and their evolutionary and adaptive value has yet to be assessed.

Environmental conditions (*i.e.* biotic and abiotic factors) perceived by larvae during development are known to pilot insect's developmental rate (Couret et al., 2014; Damos and Savopoulou-Soultani, 2012; Lyons et al., 2013; Mouline et al., 2012) with consequences on adults' overall phenotypic quality, including their morphometric properties (*i.e.* shape, size, asymmetry) (Aboagye-Antwi and Tripet, 2010; Atkinson, 1994; Czarnoleski et al., 2013; Kingsolver et al., 2009; Pétavy et al., 2004). Morphological approaches have recently received increasing attention mainly with the advent of new applications and current developments in geometric morphometrics (Ayala et al., 2011; Sadeghi et al., 2009 Zimmermann et al., 2012). Although morphometric methods were traditionally used at the upper taxonomic level (*i.e.* at the genus/species level), geometric morphometrics now offers powerful analytical and graphical tools for quantitative assessment and visualisation of morphological variations within and among species. Currently, geometric morphometric approaches are increasingly applied to a wide range of research fields including systematics, phylogeny and population genetics, ontogeny and developmental stability (Debat et al., 2011; Klingenberg and Marugán-Lobón, 2013; Klingenberg and McIntyre, 1998; Morales Vargas et al., 2013; Savriama et al., 2012). One of the main added values of geometric morphometrics is its ability to consider the variation of both size and shape of individuals and/or organs separately. As such, wings have been the subject of many geometric morphometric analyses in insects (Baylac and Daufresne, 1996; Rohlf and Slice, 1990), and many of these studies characterised populations within species among geographic and climatic variations (Haas and Tolley, 1998; Hoffman and Shirrifs, 2002; Morales Vargas et al., 2013 Roggero and d'Entrèves, 2005). Indeed, it was shown that wing shape variation can inform on current or recent population events and contains a great deal of information on genetic variation among populations (Dujardin, 2011, 2008). On the other hand, insect wing size, often used as a proxy of whole-insect size, has been shown to vary chiefly according to larval growth conditions (Koella and Lyimo, 1996; Lyimo et al., 1992; Mouline et al., 2012). Recently, Andersen et al. (2005) showed that both size and shape of the wing of *Drosophila mercatorum* (Diptera, Drosophilidae) changed as a response to the maternal and developmental temperature. Similarly, Ayala et al. (2011) further argued that changes observed in wing morphometric properties of *Anopheles funestus* mosquitoes are the result of natural selection and may contribute to local adaptation in wild populations of this mosquito. Accordingly, developmental plasticity expressed under various environmental conditions may result in morphological changes in adults that contribute to local adaptation.

To test this hypothesis, we monitored larval development and assessed adult phenotypic variation in five ecologically and geographically distinct populations of *An. coluzzii* exposed to contrasted environmental cues mimicking the rainy and dry season conditions in Northern Burkina Faso. Desiccation has been proposed as a major threat when larvae develop in temporary waters. It is therefore expected that mosquito populations adapted to breed in rain-dependent collections will speed-up their development in response to increased desiccation threat in dry season conditions (Diabaté et al., 2008). On the other hand, because drying-out of the breeding site is not a threat when larvae develop in permanent waters, we predicted that the duration of larval development will increase in the dry season conditions, reflecting suboptimal growth conditions (*e.g.* exposure to extreme temperatures and fluctuations thereof, see Colinet et al., 2015). The impact of changing developmental duration on the overall adult fitness should vary according to the level of local adaptation of the population under scrutiny. Here, we used wing geometric morphometrics and we monitored dry weight at emergence to explore phenotypic plasticity in emerging adult females when larvae were reared under contrasted environmental conditions.

2. Materials and methods

2.1. Sample populations

In Burkina Faso (West Africa), annual rainfalls and duration of the rainy and dry seasons vary along a latitudinal gradient. Although, rainfalls do not exceed 300 mm during the 2–3 months of the rainy season in the northernmost regions (*i.e.* 9–10 months of dry season), it can be as high as 1200 mm during the 5–6 months of the rainy season in the southernmost regions (*i.e.* 6–7 months of dry season; see Fig. 1). The experiments were conducted using four mosquito populations derived from the progeny of wild-caught *An. coluzzii* females from North and South Western Burkina Faso. Gravid female mosquitoes were sampled from within human dwellings in localities where *An. coluzzii* mosquitoes are present all year long (*i.e.* presence of year-round mosquito breeding opportunities in Oursi [14°40′N, 0°27′W] and Bama [12°01′N, 04°23′W]) and in localities where no permanent breeding is possible and the mosquito populations are highly seasonal (*i.e.* Déou [14°35′N, 0°43′W] and Soumousso [11°01′N, 04°02′W]; Fig. 1). Before experiments, all populations were reared for six generations in order to eliminate any potential trans-generational effect driven by the native environment and/or stress from transportation, while limiting acclimation to laboratory conditions and trait homogenization. All colonies were reared at the Institut de Recherche en Sciences de la Santé (IRSS) in Bobo-Dioulasso under controlled conditions (27 ± 1 °C, 80 ± 10% relative humidity with LD cycles of 12 h:12 h). Females were routinely blood fed on restrained rabbits,

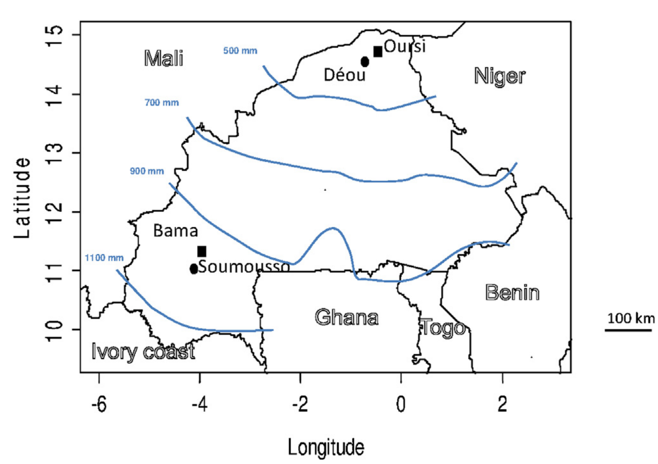

Fig. 1. Geographical localisation of the four localities where wild *An. coluzzii* mosquitoes were collected in northern and south-western regions of Burkina Faso (West Africa). Squares represent permanent mosquito populations and circles represent temporary populations (see text). Blue lines represent mean annual rainfall in mm (derived from Clavel et al., 2009).

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