

## LETTER TO THE EDITOR

Local adaptation for body color in *Drosophila americana*: commentary on Wittkopp *et al.*

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Wittkopp *et al.* (2011) report clinal variation of cuticle coloration among populations of *Drosophila americana* despite the high levels of gene flow across collection sites, providing evidence for local (darwinian) adaptation of body coloration in this species. Several mechanisms have been proposed to explain the evolutionary patterns of pigment variation in ectothermic organisms such as *D. americana*. For example, the occurrence of dark-pigmented populations of several *Drosophila* spp. has been associated with dry environments (for example, Parkash *et al.*, 2010). This relationship represents the main hypothesis tested by Wittkopp *et al.* (2011), and the authors conclude that pigmentation and desiccation resistance are not unequivocally linked among the populations investigated. However, other climatic explanations that are not addressed in the study may explain these color patterns. For example, the thermal melanism hypothesis (TMH) suggests that if all else is equal, darker individuals may heat up faster and reach higher equilibrium temperatures than lighter individuals, providing a benefit in cooler conditions (Clusella-Trullas *et al.*, 2007). Recently, the TMH has received support at several spatial scales in reptiles (Clusella-Trullas *et al.*, 2008, 2009) and has also been demonstrated in many insect species (for example, Brakefield and Willmer, 1985; reviewed in Clusella-Trullas *et al.*, 2007). Wittkopp *et al.* (2011) showed that longitude was a better explanatory variable than environmental relative humidity. However, latitude and longitude are typically used as proxies of climate (for example, temperature and humidity) and site (topography) variation. The use of longitude as a predictor of pigment variation does not indicate which climate variables (or interactions thereof) might best explain the patterns observed, and therefore provides little insight into the potential evolutionary mechanisms at work.

Using the data from Wittkopp *et al.* (2011), we re-analyzed their largest dataset (Table 1, dataset A, p 6), seeking the most likely climatic explanation for the observed geographic variation in pigment intensity (with light-colored populations having higher values of pigment intensity than darker populations). We used an information-theoretic model selection approach (Burnham and Anderson, 2002) to address both the TMH and the desiccation resistance hypothesis as potential explanations. The best model, judged from its Akaike information criterion (AIC) value, includes solar radiation and mean diurnal temperature range as explanatory variables (Table 1). The results of our analyses indicate that this explanatory model has a 43.1% probability of being the best model out of all those compared (as indicated by the model Akaike weights,  $w_i$ ) (Table 1). By contrast, longitude as a single predictor also has some support

( $\Delta AIC = 2$ ), but a much lower probability of being the best model (Burnham and Anderson, 2002). Nonetheless, the best model indicates that the relationship between *D. americana* pigmentation intensity and solar radiation is positive and in line with the TMH. Darker populations tend to be in areas with lower solar radiation and mean diurnal temperature range compared with lighter populations. Therefore, these relationships suggest that, in cooler environments, being dark could be an advantage as individuals may heat up faster and reach preferred body temperatures sooner, thereby increasing the activity time. Additional population data on pigmentation of *D. americana* across a broader range of microclimates and incorporating cuticle reflectance across the full spectrum of solar radiation (ultraviolet, visible and near-infrared) may help distinguish among competing hypotheses for color variation in ectotherms. It is clear from our analyses of Wittkopp *et al.*'s (2011) data that the TMH may provide the major explanation for color variation in *D. americana* and requires closer scrutiny. Nevertheless, and in agreement with Wittkopp *et al.* (2011), it seems that the desiccation resistance hypothesis is an unlikely explanation in this species. Studies should consider both hypotheses simultaneously when attempting to explain pigment variation of ectotherms in relation to climate. A strong inference approach with multiple working hypotheses (see, for example, Huey *et al.*, 1999) may provide a suitable way forward in future.

**Table 1** The ten best environmental climate models of 28 models tested explaining variation in pigmentation intensity among *Drosophila americana* populations from dataset A in Wittkopp *et al.* (2011)

Rank	Model	AIC	$w_i$
1	SOLRAD+MDTR	92.040	0.431
2	MDTR	93.993	0.162
3	LONG	94.090	0.155
4	SOLRAD+TMIN+SOLRAD*TMIN	95.787	0.066
5	LAT+LONG	96.033	0.058
6	LAT+LONG+LAT*LONG	97.950	0.022
7	RH+SOLRAD+SOLRAD*RH	98.220	0.020
8	SOLRAD+APP+MAT	98.513	0.017
9	SOLRAD+TMIN	98.725	0.015
10	SOLRAD+APP+TMIN	99.688	0.009

Abbreviations: AIC, Akaike information criterion; APP, mean annual precipitation (mm); LAT, latitude (°); LONG, longitude (°); MAT, mean annual temperature (°C); MDTR, mean diurnal temperature range (°C); RH, relative humidity (%); TMIN, minimum temperature of the coldest month (°C);  $w_i$ , Akaike weight. Climate variables were extracted from <http://www.worldclim.org> (at 2.5 arc min resolution) for data gathered over 1950–2000 and mean annual solar radiation (SOLRAD,  $W m^{-2}$ ) was obtained from the IPCC Data Distribution Centre (0.5° resolution). Only non-collinear variables were included in each model.

## Conflict of interest

The authors declare no conflict of interest.

S Clusella-Trullas<sup>1</sup> and JS Terblanche<sup>2</sup>

<sup>1</sup>Centre for Invasion Biology, Faculty of Science,  
Stellenbosch University, Stellenbosch, South Africa and

<sup>2</sup>Conservation Ecology & Entomology Department,  
Faculty of AgriSciences, Stellenbosch University,  
Stellenbosch, South Africa  
E-mail: jst@sun.ac.za

## References

- Brakefield PM, Willmer PG (1985). The basis of thermal melanism in the ladybird *Adalia bipunctata*: differences in reflectance and thermal properties between the morphs. *Heredity* **54**: 9–14.
- Burnham KP, Anderson DR (2002). *Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer: New York.
- Clusella-Trullas S, Terblanche JS, Blackburn TM, Chown SL (2008). Testing the thermal melanism hypothesis: a macrophysiological approach. *Funct Ecol* **22**: 232–238.
- Clusella-Trullas S, van Wyk JH, Spotila JR (2007). Thermal melanism in ectotherms. *J Thermal Biol* **32**: 235–245.
- Clusella-Trullas S, van Wyk JH, Spotila JR (2009). Thermal benefits of melanism in cordylid lizards: a theoretical and field test. *Ecology* **90**: 2297–2312.
- Huey RB, Berrigan D, Gilchrist GW, Herron JC (1999). Testing the adaptive significance of acclimation: a strong inference approach. *Am Zool* **39**: 323–336.
- Parkash R, Kalra B, Sharma V (2010). Impact of body melanisation on contrasting levels of desiccation resistance in a circumtropical and a generalist *Drosophila* species. *Evol Ecol* **24**: 207–225.
- Wittkopp PJ, Smith-Winberry G, Arnold LL, Thompson EM, Cooley AM, Yuan DC *et al.* (2011). Local adaptation for body color in *Drosophila americana*. *Heredity* **106**: 592–602.