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ORIGINAL ARTICLE

Smaller, lighter coloured and less hairy *Procladius* (Diptera, Chironomidae) in warmer climate

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Abstract

The relationship between body size, colour and hairiness of *Procladius* of the Diptera family Chironomidae and climate measured as annual mean air temperature was analysed. The study was based on 453 males representing 31 species from 253 localities in 27 countries in Europe and six elsewhere. Wing length as well as three other characters reflecting body size showed significant decrease with warmer climate conditions. The results are in line with several other studies of insects concluding that adult insects are smaller in warmer climate, also considering the implications of global warming. Likewise, all five characters representing colour lightness showed significantly lighter coloured *Procladius* specimens with warmer climate. The relationship between hairiness and annual mean air temperature was weaker than that of size or colour and temperature, but all five characters studied showed a statistically significant decrease in hairiness with warmer climate. The biological relevance of smaller size, lighter colour and less hairiness in warmer climate can be related to several factors regulating flight and swarming, including less need of protection against cold weather, overheating avoidance, mating success agility and predator escape.

Keywords *Procladius* midges · Morphological features · Mean annual temperature · Biological relevance

Introduction

Morphological adaptations of insects to temperature conditions have been discussed in many scientific papers. The ongoing change towards a warmer climate due to human influence has motivated intensified research.

Studies of dragonflies (Odonata), hymenopterans (Hymenoptera) and butterflies (Lepidoptera) have shown that several species spread northwards when climate becomes warmer (Hickling et al. 2005; Netherer and Schopf 2010; Delava et al. 2014). Species may alternatively remain where they are and experience physiological, behavioural and morphological changes as a result of changing climate (Musolin and Saulich 2012; Larson et al. 2019). Morphological adaptations include traits such as size, colour and pilosity, and frequently related to thermoregulation (Scaven and Rafferty 2013; Scheffers et al. 2016).

While working on a taxonomical revision of the European species of the Chironomidae genus *Procladius,* we noted that specimens collected in southern regions seemed to be smaller than those in colder northern regions. The comparatively large material of more than 450 specimens from more than a hundred sites all over Europe together with pertinent information on annual mean air temperatures provided an opportunity to analyse how size and other morphometric traits of *Procladius* such as colour and hairiness are influenced by temperature conditions. Morphological consequences of climate change could possibly also be predicted.

Larvae of *Procladius* are omnivorous (Armitage 1968; Izvekova 1975), occurring worldwide and very common in lakes and smaller water bodies in the northern hemisphere. Flying adults can be found during the whole year in southern Europe (Prat 1979) with annual mean air temperature 15–20 °C, while mainly during summer in northern regions of Europe, Asia and North America. The coldest conditions for a species of *Procladius* is reported from a lake in a district with annual mean air temperature about - 15 °C

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in Arctic Canada, also representing among the coldest conditions for insect life (Oliver 1963).

Materials and methods

The material for the study consisted of 453 adult males of *Procladius* including 31 species of which 27 are present in Europe according to the preliminary results of the taxonomical revision. The material was collected at 253 localities in 27 European countries, and also Canada, Greenland, Lebanon, Russia (Asian part), Tunisia and USA.

Most of the material is on slides as this preparation method is common practice within taxonomy of Chironomidae and makes it easier to study characters needing high magnification such as small body hairs.

Size was measured using four characters (Table 1) of which body length and wing length are commonly used in taxonomic studies of Chironomidae. Measure of body length of a specimen can be complicated as the abdomen is somewhat extensible. Therefore, the length of the non-extensible thorax was included as a character of size. The fourth size character was the width of the gonocoxite basally which also reflects the width of the ninth tergite. It is unknown if this character is valuable for size estimates, but it is easy to measure accurately.

Colour lightness was estimated according to a 9-point grading scale ranging from white to black (Table 2). The method was applied for five characters: two of the thorax and one each of the head, legs and abdomen of the specimen. Specimens which have been bleached due to maceration or storage in alcohol for more than ten years were excluded.

Five characters of different body parts were selected to assess hairiness: two of the thorax and one each of the head, legs and wings (Table 3). The front leg BR-ratio and number of hairs (setae) of the scutellum are frequently used in studies of Chironomidae taxonomy. The number or hairs of the chosen characters can be counted more accurately than hairs of other hairier body parts such as the abdominal tergites and the legs. Several body hairs fall off when the specimens are placed in alcohol after sampling. This is not a problem for counting hairs as the small hole where the hairs rose from can usually be seen well under the microscope.

Table 2 Colour categories of male *Procladius* used for statistical analyses of size versus annual mean air temperature of the locality where the specimen was collected

Colour categories	Colours
0	White to whitish
0.5	Whitish to light yellowish
1	Light yellowish to yellowish
1.5	Yellowish to light brownish
2	Brownish (medium brown)
2.5	Brownish to almost dark brownish
3	Dark brownish
3.5	Dark brownish at least partly blackish
4	Blackish to black

Categories arranged from the lightest colour (0) to the darkest (4)

Among the fourteen selected characters, wing length, hind colour of tergite II-IV and the front leg BR-ratio are particularly important for species identification of *Procladius*.

A simple linear regression model with an intercept was used to statistically test each of the fourteen characters. Mean annual air temperature was the dependent variable and one at the time the fourteen characters were used as the independent variable. The regression estimates a coefficient and its p value for each of the fourteen characters. This p value was used to test if the coefficient is significant or not.

Estimation of mean annual air temperature expressed as °C to one decimal place was carried out for localities where specimens of *Procladius* were sampled. ArcGIS WGS84 data of the localities were adjusted to two decimal places.

WorldClim bioclimatic variables dataset BIO1 provide range maps of mean annual temperature based on measurement records of the 1950–2000 period (Hijmans et al. 2005; https://www.arcgis.com/home/item.html?id=d721580786614e54ac8d0672dad7a23a). Extrapolation of mean annual temperature of a sampling locality was achieved using high resolution altitude data in FreeMapTools (Elevation Finder https://www.freemaptools.com/elevation-finder.htm) and temperature measurement data in

Table 1 Characters of male *Procladius* used for statistical analyses of size versus annual mean air temperature of the locality where the specimen was collected

Body part	Character description
Body	Length from tip of clypeus to end of gonostylus process, mm
Thorax	Length laterally from tip of antepronotum to end of postnotum, mm
Wing	Length from base of squama to tip of wing, mm
Genitalia	Width of base of gonocoxite, µm

Table 3 Characters of male *Procladius* used for statistical analyses of hairiness versus annual mean air temperature of the locality where the specimen was collected

Body part	Character description
Head	Clypeus, number of setae
Thorax	Antepronotum, number of setae
Thorax	Scutellum, number setae
Wings	Vein R1, number of setae
Legs	Front leg BR (bristle ratio or beard ratio), length of longest seta (hair or bristle) of a tarsal segment divided by the width of tarsal segment where the seta originates

Timeanddate (World Temperatures — Weather Around The World https://www.timeanddate.com/weather/@8133074/climate). Finally, adjustment of locality temperature for year of sampling was done by consulting NASA Earth Observatory global temperature anomaly 1930–2021 relative to 1951–1980 (https://www.weforum.org/agenda/2022/07/global-heat-maps-temperature-anomaly-climate-change/).

Results

All fourteen characters of body size, body colour and body hairiness of *Procladius* showed a significant (***, $p < 0.001$) relationship with climate expressed as annual mean air temperature (Table 4).

A decrease in body size with warmer climate was indicated for all four characters measuring body size (R^2 0.13–0.24). The strongest correlation was for the width of the gonocoxite (Fig. 1a). The relationship between shorter wing length and warmer climate was almost as high (R^2 0.22) (Fig. 1b).

All five characters of body colour showed lighter colours with warmer climate conditions. The correlation was strongest for colour lightness of the thorax scutellum (Fig. 2a), front tibia and abdomen tergite II-IV hind colour (Fig. 2b) (R^2 0.20–0.26), while the correlation between lighter frons colour of the head and higher annual mean air temperature was relatively weak (R^2 0.07).

Body hairiness characters showed a comparatively weak relationship with climate (R^2 0.05–0.13), but all five characters indicated less hairiness with warmer climate conditions. The strongest correlation was for fewer setae on the clypeus with warmer annual mean air temperature (Fig. 3a) followed by the front leg tarsal BR (Fig. 3b).

Table 4 Simple linear regression analysis between characters representing size, colour lightness and hairiness of *Procladius* and annual mean air temperatures at the localities where the specimens were collected

Characters	Variation	Specimens	Model adjusted R^2	Intercept (significance)	Coefficient (significance)	Model F-value
Size						
Thorax length, mm	0.79–2.23	326	0.13	14.07 (***)	−6.52 (***)	48.87 (***)
Wing length, mm	1.7–4.6	373	0.22	16.91 (***)	−4.06 (***)	104.30 (***)
Body length, mm	3.0–8.1	298	0.13	13.53 (***)	−1.73 (***)	47.17 (***)
Gonocoxite width, µm	162–531	415	0.24	14.53(***)	−0.03 (***)	131.53 (***)
Colour lightness						
Frons colour	0–3	304	0.07	8.33 (***)	−2.24 (***)	22.38 (***)
Humeral colour	0.5–3.5	326	0.11	9.08 (***)	−2.35 (***)	39.78 (***)
Scutellum colour	1–4	340	0.20	11.51 (***)	−2.57 (***)	83.13 (***)
Front tibia mid colour	0.5–3.5	337	0.26	9.87 (***)	−3.07 (***)	117.81 (***)
Tergite II-IV hind colour	0–4	341	0.25	9.41 (***)	−3.05 (***)	111.37 (***)
Hairiness						
Clypeus setae	12–60	314	0.13	9.89 (***)	−0.20 (***)	47.29 (***)
Antepronotum setae	3–38	253	0.10	9.01 (***)	−0.26 (***)	27.57 (***)
Scutellum setae	14–117	262	0.10	9.11 (***)	−0.08 (***)	30.80 (***)
Wing vein R1 setae	2–95	321	0.05	7.25 (***)	−0.05 (***)	18.89 (***)
Front leg tarsal BR	1.5–12.5	276	0.11	8.64 (***)	−1.26 (***)	35.47 (***)

The characters are explained and categorised in Tables 1, 2 and 3. ***means $p < 0.001$

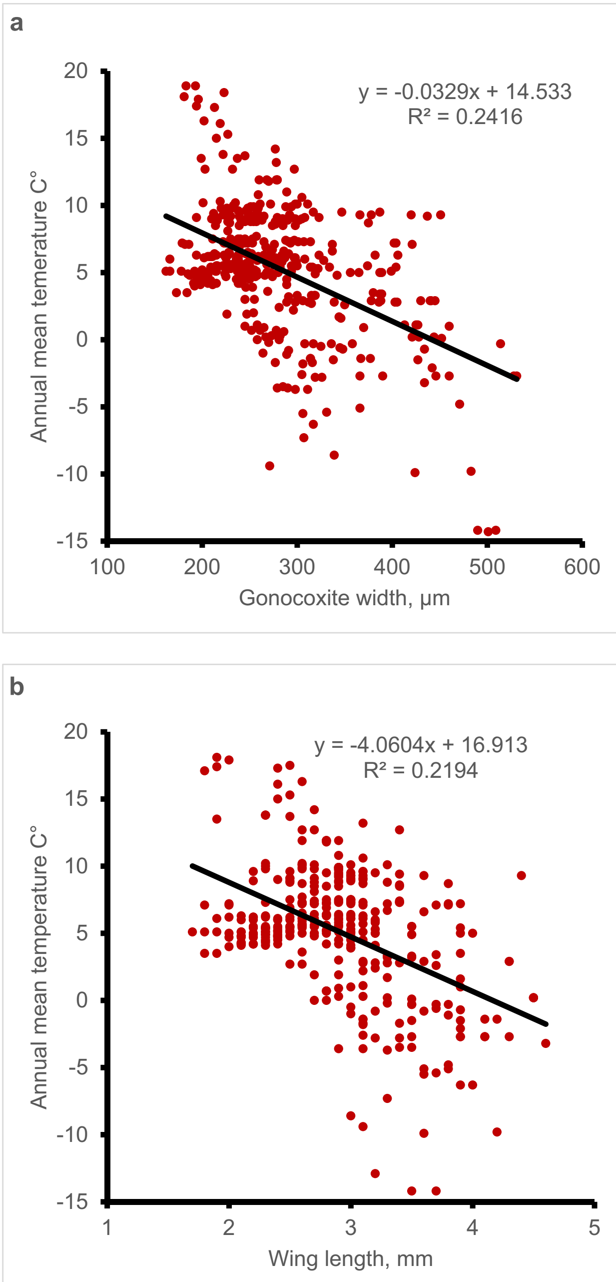

Fig. 1 Simple linear regression of the **a** gonocoxite width and **b** wing length of *Procladius* specimens versus annual mean air temperature at the localities where they were collected

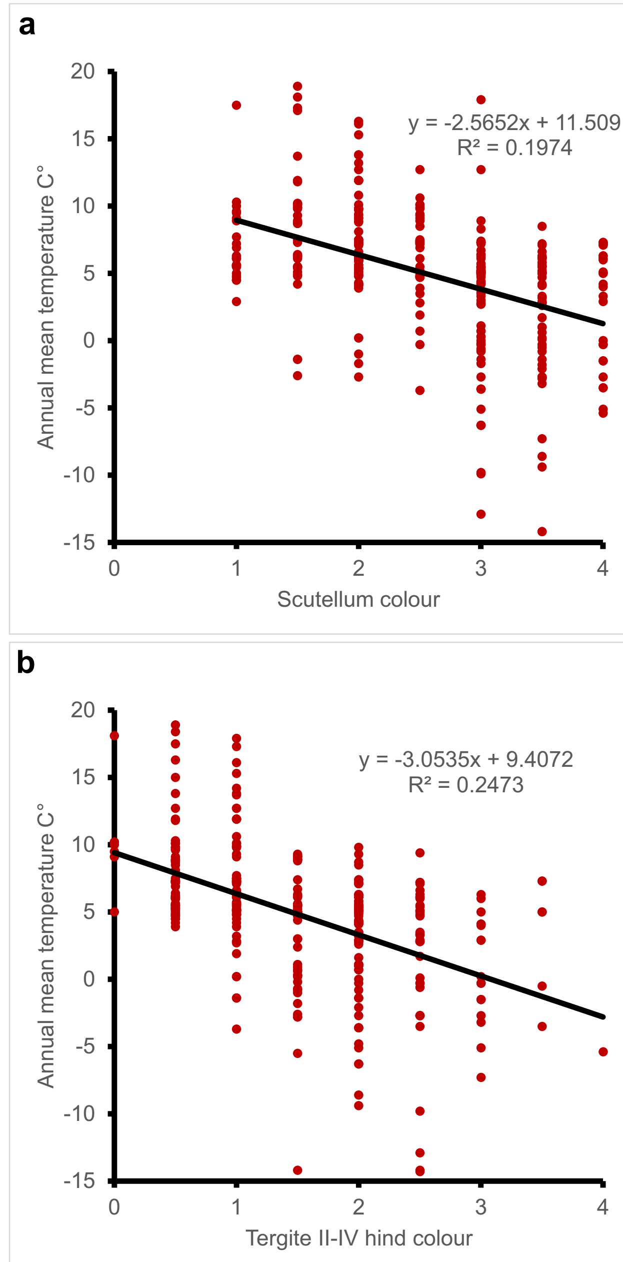

Fig. 2 Simple linear regression of the **a** scutellum colour and **b** tergite II-IV hind colour of *Procladius* specimens versus annual mean air temperature at the localities where they were collected

Discussion

Our study revealed a statistically significant, with comparatively low R^2 values, decrease in size, colour darkness and hairiness of adult *Procladius* with increased mean annual air temperature. The low R^2 values can be attributed to the extensive intraspecific variation in external morphology related to size, colour and hairiness found in many studies of Chironomidae and other Diptera (Hirvenoja 1973; Ståhls et al. 2008; Carew et al. 2011). As an example, a study of Chironomidae species including one of *Procladius* showed that the wings of larger specimens can be about twice as long as those of smaller specimens of the same species emerging from the same small ponds and year (Wonglersak et al. 2021).

The low R^2 values indicate that the observed morphological trends within *Procladius* adults can only to a limited degree be explained by the chosen indicator

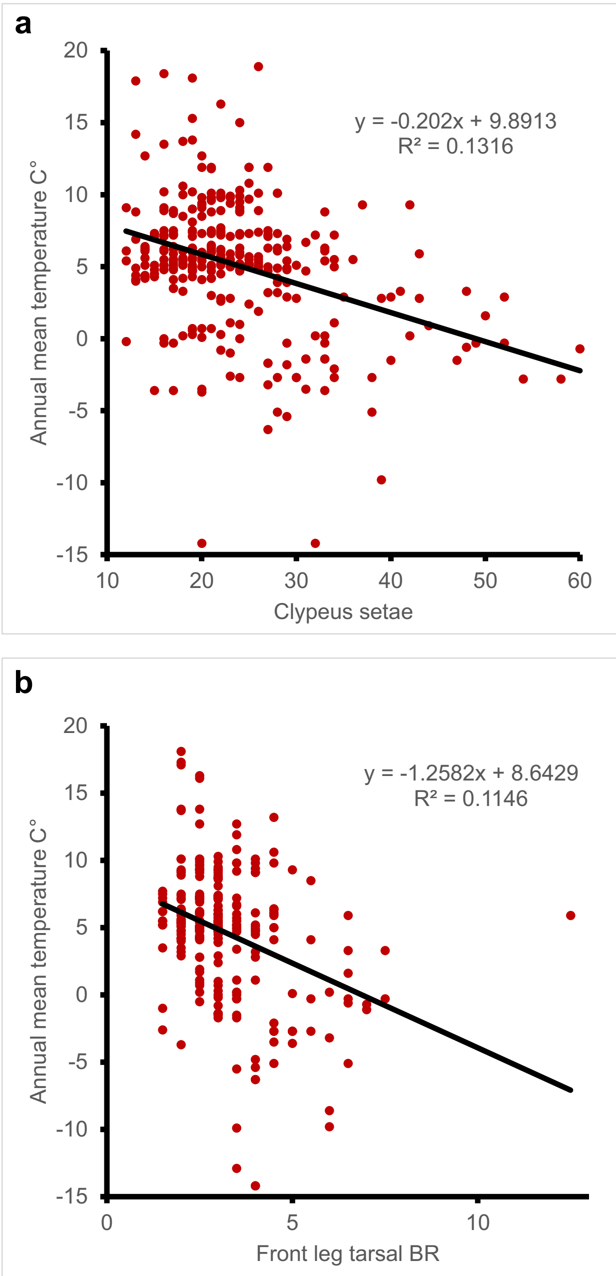

Fig. 3 Simple linear regression of the **a** clypeus setae number and **b** front leg tarsal BR of *Procladius* specimens versus annual mean air temperature at the localities where they were collected

mean annual air temperature. Several factors related to the living conditions of the *Procladius* larvae may contribute to the decreases in size, colour darkness and hairiness of the adults. In a study of global trends in size of Chironomidae genera versus latitude and mean annual air temperature, Baranov et al. (2021) suggested food availability, predation, oxygen conditions, generations per year to be important in determining adult size.

The relationship between insect size and climate is by far more studied than the relationship between insect colour or hairiness and climate. The size studies often refer to Bergmann's rule (Bergmann 1847) stating that individuals of a species or groups of related species will be smaller at lower latitudes and altitudes than those of higher ones. Near-surface air temperature is a governing factor. The lower the latitude and elevation, the warmer the climate, and vice versa.

Bergmann's rule has often been shown to be applicable for warm-blooded organisms such as mammals and birds, while the results for insects are variable. A review by Shelomi (2012) based on 779 scientific papers on several insect orders worldwide showed that about 28% of the studied insect species or groups seem to apply with Bergman's rule, while about 30% showed the opposite and about 41% of the studies showed no significant relationship. Other more recent reviews including several insect orders have also shown variable results whether species are on average smaller in warmer climate conditions (Horne et al. 2017).

Diptera, based on 134 studies, was the insect order that by far was best in line with Bergmann's rule in the paper by Shelomi (2012). About 62% of the Diptera species or species groups studied turned out to be smaller at lower latitudes and altitudes, and only 10% had an opposite trend. Thus, as well as for *Procladius* of the present study, it might be common among Diptera that species or species groups such as well-defined genera are on average smaller at higher annual mean air temperatures than those at lower temperatures. This has been shown by Baranov et al. (2021) in a global study of Chironomidae genera. The study did not include *Procladius*, but other studies on *Procladius* species have reached the same conclusion. A study of Wonglersak et al. (2021) on males and females of *Procladius ferrugineus* (Kieffer, 1918) (as *Procladius crassinervis* (Zetterstedt, 1838)) reported smaller specimens when reared in warmer conditions in temperature controlled ponds. Hodkinson et al. (1996) noted that Arctic species of Chironomidae, including at least one species of *Procladius,* became smaller as summer progressed and daily mean air temperatures increased.

Studies of pigmentation of insects in relation to climate have also produced variable results, although many suggest that warmer climate results in lighter coloured species or groups of species.

A study by Zeuss et al. (2014) based on 107 species of dragonflies concluded that species have become on average lighter coloured in Europe during the last century as a possible consequence of global warming. In concordance with our study of *Procladius,* Zeuss et al. (2014) showed that also European butterflies (367 species studied) are on average lighter coloured the warmer the climate measured as annual mean air temperature.

In a global scale, Rapoport (1969) showed that springtails (Collembola) are lighter coloured in warmer climates than in cooler ones, and that this difference is most expressed when comparing warm tropics with very cold conditions.

Colours of adult Diptera in relation to climate conditions seems to be relatively little studied in comparison with other major insect orders. Some experimental studies on Diptera have found that higher rearing temperatures result in lighter coloured individuals, e.g. of Drosophilidae (vinegar flies) in a paper by Gibert et al. (1998). No scientific paper on Chironomidae thoroughly addressing this issue was found in our literature search. Indications of species being lighter coloured in warmer regions are found in a taxonomic revision by Hirvenoja (1973) covering 58 *Cricotopus* species in Europe. Roback (1971) noted that the common and widely distributed species *Procladius bellus* (Loew, 1866) in the USA and Canada tends to be on average darker and larger in northern colder regions.

Relatively few studies have addressed the impact of climate on the hairiness of insects. The shorter leg hairs (lower BR-ratio) of *Procladius* species in warmer climate indicated in the present study is congruent with the findings that bumble bees in subtropical and tropic zones have shorter thoracic hairs than those living in colder climates (Peat et al. 2005). Also for bees and butterflies a connection between less hairy individuals and higher temperatures have been noted (Southwick and Heldmaier 1987; Sømme 1989; Danks 2004). The comprehensive study of *Cricotopus* (Hirvenoja 1973) mentioned earlier provides morphological data indicating that the most hirsute species in terms of number of hairs of the abdomen are more northerly distributed in Europe than less hirsute ones. *Procladius* and *Cricotopus* thus seem to be examples of Chironomidae genera that are on average less hairy in warmer climate conditions.

Being bigger, darker and hairier could be an advantage for insects in colder environments in order to reach and maintain a body temperature high enough for flying (Crusella Trullas et al. 2007; Kingsolver et al. 2011; Roquer-Beni et al. 2020).

Ability to fly in the often cold spring or summer weather of the Subarctic and Arctic regions might be crucial for males of *Procladius* which as other males of Chironomidae only live a few days as adults (Armitage 1995) and form aerial swarms for mating purposes (Kon 1987). In these regions, it is possible that bigger, darker and even more hairy males of *Procladius* have a better chance to mate with females and pass on their genes to the next generation.

In warmer climate, circumstances may change in favour of smaller, lighter coloured and less hairy specimens as there is less need to invest in morphological structures to keep the body warm. Scientific papers have revealed that the development of insect larvae in warmer conditions results in smaller adults (Atkinson 1994; Kingsolver and Huey 2008). Studies of Chironomidae swarms have shown that smaller males have higher mating success possibly because of being more agile (Neems et al. 1998). Being a smaller and more agile *Procladius* might also be advantageous to reduce predation pressure from other insects, or birds and bats. Zeuss et al. (2014) and several other studies have suggested that lighter coloured insects have a better capacity to avoid overheating, a trait that can be important for insects active in hot weather such as in southern Europe during summer. The functional significance of smaller size, lighter colour and less body hairs in warmer conditions is however far from well understood and several examples of no or inverse relationship are available. A better knowledge of the relationship between insect morphology and climate is needed taking into consideration the ongoing global warming because of human activity. Our results give a hint that increased annual mean air temperature can result in smaller, lighter coloured and less hairy species of *Procladius* and groups of other insects.

Conclusions

Analysed morphological characters indicated that specimens of the midge genus *Procladius* collected in warmer climate are on average smaller, lighter coloured and less hairy than specimens in colder climate. All fourteen characters showed a statistically significant relationship with climate, but with comparatively low R^2 values partly attributed to extensive intraspecific morphological variation.

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Authors' contributions Yngve Brodin gathered and analyzed the data and led the writing of the paper. Jörgen Hellberg did the statistical analyses and contributed to the writing of the paper.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Research involving animals, their data or biological material No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with unregulated invertebrate species.

Conflict of interest The authors declare that there is no conflict of interest.

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