



# Genetic variation in light vision and light-dependent movement behaviour in the eyeless Collembola *Folsomia candida*



Marta Gallardo Ruiz<sup>a,\*</sup>, Jean-François Le Galliard<sup>a,b</sup>, Thomas Tully<sup>a,c</sup>

<sup>a</sup> Sorbonne Universités, UPMC Univ Paris 06, CNRS, IRD, INRA, Institut d'écologie et des sciences de l'environnement (IEES), Paris, France

<sup>b</sup> Ecole Normale Supérieure, PSL Research University, CNRS, Centre de recherche en écologie expérimentale et prédictive (CEREEP-Ecotron IleDeFrance), UMS 3194, 78 rue du château, 77140 Saint-Pierre-les-Nemours, France

<sup>c</sup> Sorbonne Universités, Paris-Sorbonne Univ Paris 04, ESPE de l'académie de Paris, Paris, France

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## ABSTRACT

Animals can cope with spatiotemporal variation in their environment through mobility and selective habitat choice. Intra-specific variation in habitat choice has been documented especially for host plant preferences and cryptic habitat selection in insects. Here, we investigated the genetic variation in light sensitivity and light-dependent habitat choice in the eyeless Collembola *Folsomia candida* with a choice test under four different lighting conditions (control dark condition, two simulations of undergrowth natural light conditions and red light). We tested twelve clonal strains from diverse geographical origins that are clustered in two evolutionary clades with contrasting fast or slow life-history strategies. The clones differed in their mean movement probabilities in the dark treatment. These differences were related to the two different phylogenetic clades, where fast-life history clones are on average more mobile than slow-life history counterparts as predicted by the 'colonizer syndrome' hypothesis. We found behavioural avoidance of light in the three light conditions. Moreover, photophobia was stronger when the simulated light spectrum was brighter and included non-red light. Photophobia was similar among all clonal lineages and between the two clades, which suggests that this behaviour is a shared behavioural trait in this species. We discuss the use of light as an environmental cue for orientation, displacement and habitat choice under natural conditions.

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## 1. Introduction

Animals use various environmental cues for habitat choices, and different individuals from a single species may show contrasting habitat preferences depending on their sex, stage, size and genetic background for instance (Stamps, 2001; Matthysen, 2012). This intra-specific variation of behavioural responses may influence a wide range of eco-evolutionary processes (Sih et al., 2012; Ronce and Clobert, 2012; Edelaar and Bolnick, 2012). Inter-individual differences in habitat choice behaviours may be genotype-dependent and related to differential performance in specific habitats or niches (Sih et al., 2012; Edelaar and Bolnick, 2012; Hawthorne and Via, 2001; Cousyn et al., 2001; De Meester, 1996; Jaenike and Holt, 1991). Genetic variation in habitat choice behaviour is common in animals and has been well documented

for host plant preferences and cryptic habitat selection in insects (reviewed in Jaenike and Holt, 1991).

One of the cues animals use to select their habitat is light which animals may be positively or negatively attracted to. For example, negative phototaxis acts as a predator-avoidance mechanism in some aquatic organisms (De Meester, 1996; Cousyn et al., 2001; Michels and De Meester, 2004; Borowsky, 2011) and may help some soil organisms that are very sensitive to relative humidity to prevent desiccation by looking for deeper and more humid soil layers (Salmon et al., 2014; Salmon and Ponge, 2012). Nevertheless, different individuals or populations within the same species may present different phototactic preferences. For example, clonal populations of *Daphnia magna* (a zooplankton species) exposed to high levels of predatory pressure are more photophobic than clonal populations less exposed to predation (Cousyn et al., 2001; De Meester, 1996). In general, differences in phototaxis may have a heritable, genetic basis (e.g., Markow and Smith, 1977; De Meester, 1996; Cousyn et al., 2001) or could be the result of non-genetic, phenotypic plasticity and personality (is this too anthropomorphic for *Daphnia* or springtails?) differences among individuals (e.g.,

\* Corresponding author.

E-mail address: [marta.gallardo\\_ruiz@etu.upmc.fr](mailto:marta.gallardo_ruiz@etu.upmc.fr) (M. Gallardo Ruiz).

Kain et al., 2012). Quantifying sources of variation in phototaxis is therefore important to understand the evolution of this widespread behavioural trait. Here, we investigate the genetic variation in light sensitivity and light-dependent movement behaviour in the eye-less springtail *Folsomia candida* Willem 1902 (Collembola, Isotomidae), an hemi-edaphic and cosmopolitan soil organism inhabiting various habitats such as caves, forest litter and man-made habitats (Fountain and Hopkin, 2005).

The degeneration or even loss of the visual system is a convergent and frequent evolutionary phenomenon in soil-dwelling and cave animals (Christiansen, 2005). Nevertheless, even eyeless and eye-reduced species often retain some sensitivity to the ambient light level through extra-ocular photoreceptors (EOP, Taddei-Ferretti and Musio, 2000; Ullrich-Lüter et al., 2011), which are useful for the maintenance of circadian rhythms (Friedrich, 2013) or for orientation and habitat choice (Timmermann and Plath, 2008; Borowsky, 2011). Indeed, previous works strongly suggest that *F. candida* is sensitive to light despite being eyeless. In choice-test experiments, *F. candida* avoids UV light moving to warmer locations exposed to white light, prefers darkness over cool white light (Fox et al., 2007), and displays a dose-response avoidance of UV-B light relative to darkness (Beresford et al., 2013). Yet, to our knowledge, no study has examined the wavelengths of maximum sensitivity of the ocular or extra-ocular photoreceptors (EOPs) of these animals (Barra, 1971; Jordana et al., 2000; Fox et al., 2007). In true insects (Pterygota), few species are able to detect wavelengths longer than 600 nm (red light), which suggests a red-blind common ancestor (Briscoe and Chittka, 2001). In addition, the behavioural tests mentioned above could not always prevent confounding effects of differences in temperature or humidity associated with the lighting treatment. This is of great importance, as *F. candida* needs a relative humidity close to saturation (Holmstrup, 2002; Waagner et al., 2011) and is very sensitive to temperature (Boiteau and Mackinley, 2012; Boiteau and MacKinley, 2013).

Although sexual reproduction exists in some populations of *F. candida* (Frati et al., 2004), this species is generally recognized as asexual, and most studies using *F. candida* as a model species have used parthenogenetic lineages (Fountain and Hopkin, 2005). Earlier studies on several parthenogenetic lineages have uncovered substantial intra-specific genetic and morphological polymorphism (Chenon et al., 2000; Tully et al., 2006; Tully and Potapov, 2015). Intra-specific diversity is organised in two major evolutionary clades (Tully et al., 2006; Tully and Potapov, 2015), and life history studies have shown that two contrasted biodemographic strategies evolved along the divergence of these two clades (Tully and Ferriere, 2008; Tully, 2004; Tully and Lambert, 2011; Mallard et al., 2015). One clade has a high reproductive potential: when sufficient food is available, these springtails produce on average larger clutches than the ones from the other clade (Tully and Ferriere, 2008), but they have shorter mean lifespans than the less fecund clade and also reach a smaller adult body size (Tully and Ferriere, 2008; Tully and Lambert, 2011; Mallard et al., 2015). These two groups of clonal lineages fit well to the typical slow (A) and fast (B) life history syndromes (or r-K life histories, see Reznick et al., 2002). But, until now, the ecological conditions in which they have evolved and the time elapsed since the divergence of the two clades remain to be determined. Intra-specific variation in habitat choice behaviour and mobility has so far neither been examined in this species nor in other Collembola. Instead, the few works that relate the habitat preference or distribution and colonization ability of Collembola with their morphological and life history traits are focused on the study of collembolan community composition (Salmon et al., 2014; Ponge and Salmon, 2013; Huebner et al., 2012; Salmon and Ponge, 2012; Ponge et al., 2006). Intraspecific variation in phototactic behaviour and life history

traits has been well investigated in *Daphnia magna*. In this species, positive phototactic clones present a fast life history strategy whereas negative and intermediate phototactic clones present a slow life history strategy (e.g., De Meester, 1994).

We tested if springtail clonal variation in light-dependent habitat choice exists using an experimental setup to control the lighting conditions while maintaining constant temperature and moisture. We tracked springtail movements under this setup to quantify their spatial preference for shaded versus illuminated areas as a measure of the habitat choice behaviour. We first tested whether *F. candida* can use light as an environmental cue for habitat choice under different lighting conditions, including natural shaded and sunny understory spectra and an artificial red-light spectrum. We measured springtail sensitivity to long wavelengths because these wavelengths are dominant under the forest canopy (Smith, 1994) while red and far red are the principal wavelengths that penetrate the soil (Bliss and Smith, 1985). We hypothesised that *F. candida* should not detect or react to red and far-red light *per se* if the incapability to detect these wavelengths was a shared condition of most true insects and Collembola, even though most springtails are sensitive to heat generated by red light (Briscoe and Chittka, 2001). We further studied the sensitivity to light of twelve clonal lineages of *F. candida* including eleven lineages belonging to the two evolutionary clades described earlier (Tully et al., 2006; Tully and Ferriere, 2008; Tully and Lambert, 2011; Tully and Potapov, 2015). We addressed the following questions: Do light sensitivity and habitat choice behaviour vary between clonal lineages, as has been found in other taxa (Jaenike and Holt, 1991; De Meester, 1996; Cousyn et al., 2001)? If such clonal variation exists, how is it organised relative to the phylogenetic clades and what are the links between the behavioural responses and the main life history strategies of each clade? We predicted that lineages from the slow life history group would be more photophobic (De Meester, 1994, 1995), given that photophobia is likely to be associated with life in more stable habitats, which usually selects for a slow life history (Pianka, 1970; Reznick et al., 2002).

## 2. Materials and methods

### 2.1. Maintenance and origin of the studied springtails

We used twelve clonal lineages of the Collembola *Folsomia candida* labelled AP, BR, BV, DK, GB, GM, HA, ME, PB, TO, US and WI (Tully et al., 2006). Information about the phylogenetic relationships and habitat and geographical origin of all strains except ME can be found in previous studies (Tully et al., 2006; Tully and Potapov, 2015). Clones AP, BV, BR, GB and HA belong to the “slow clade” A while the “fast clade” B comprises the clones DK, GM, PB, TO, US and WI (Tully and Ferriere, 2008). The new clone ME was collected in November 2013 from some decaying wood beams into an abandoned man-made tunnel in the Mercantour French National Park (South-East of France, 44° 7.026'N, 7° 16.727'E, 1530 m). The life history strategy of this clone and its phylogenetic relationships with the other clones are currently unknown.

All clonal populations were reared in similar conditions in polyethylene vials (inner diameter 52 mm, height 65 mm) filled with a 30 mm layer of plaster of Paris mixed with Indian ink to increase visual detectability of individuals (Tully and Ferriere, 2008). Populations were kept in incubators at 20 °C (±0.5 °C) in the dark and fed with pellets of a mixture of agar and dried yeast (Tully and Ferriere, 2008). We established synchronised populations of each clone in the same way and at the same time by transferring 10–12 randomly chosen adult females from stock cultures to new culture vials. Females were transferred to new vials every week and old vials were kept at 20 °C for laid eggs to hatch since this

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