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## Extended winters entail long-term costs for insect offspring reared in an overwinter burrow

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### ABSTRACT

Winter imposes an ecological challenge to animals living in colder climates, especially if these adverse conditions coincide with reproduction and offspring rearing. To overcome this challenge, some insects burrow in the soil to protect adults, larvae, or eggs from negative effects of winter. However, whether this protection is effective against any long-term consequences of changes in winter duration is unclear. Here, we investigated the long-term effects of winter length variation on eggs of the European earwig *Forficula auricularia*. In this insect, females construct and maintain a burrow between late autumn and spring, in which they provide extensive forms of care to their eggs and then juveniles. We experimentally maintained earwig females under two winter durations of either four or six weeks and examined the resulting effects in terms of 1) hatching date, 2) developmental time of juveniles until adulthood, 3) adult mass at emergence, and 4) investment of adult offspring females in three key immune parameters: hemocyte concentration, phenoloxidase, and prophenoloxidase activities. Because earwigs' resistance against pathogens relies on their social environment, effects of winter length on immunity were tested on females exposed to different social environments: with familiar conspecifics, unfamiliar conspecifics, or in isolation. Our results reveal that after the winter treatments, eggs reared in short winters hatched earlier and the emerging juveniles reached adulthood faster than juveniles from eggs exposed to long winters. We also showed that prophenoloxidase was 30% higher in females from the long compared to short winter treatment, regardless of social environment. Finally, we found that hemocyte counts were twice as high in short compared to long winter females, but only with unfamiliar conspecifics. Overall, our study reveals that maintaining and caring for eggs in a burrow does not prevent the costs associated with increased winter duration.

### 1. Introduction

Winter can be a major challenge to all animals living in temperate and cold climates. Both the severity and duration of winter alter many life history traits, such as size and time of first reproduction (Altizer et al., 2006; Fretwell, 1972), as well as affect the mobility and metabolism of individuals from many species and taxa (Adamczewski et al., 1993; Bale, 1987; Danks, 2000; Lee Jr, 1991). Moreover, winter often reduces the availability of resources for overwintering individuals, generally resulting in food deprivation, desiccation, and increased mortality (Danks, 2000; Lee and Dellinger, 1991; Sperry and Weatherhead, 2012; Williams et al., 2015).

Ectotherms are often considered particularly sensitive to changes in temperature during winter because they cannot regulate their body temperature physiologically (Huey, 1976). While this lack of regulation often explains the severely limited geographic range of many vertebrate ectotherms (Buckley et al., 2012), invertebrate ectotherms – and insects

in particular – can be found in surprisingly many cold climates (Downes, 1965; Turnock and Fields, 2005), indicating that they have evolved adaptations to endure and thrive in the cold (Lee and Dellinger, 1991). These adaptations are generally divided into physiological mechanisms that allow them to either avoid or tolerate freezing (Bale, 1987; Lee and Dellinger, 1991; Sinclair, 2015; Zachariassen, 1985), and into behavioral strategies involving seeking out protective microhabitats such as shelter below tree bark, rocks, or in constructed burrows (Baer and Schmid-Hempel, 2005; Baust, 1976; Danks, 2002; Gehrken, 1984; Sinclair, 2001).

Burrowing into the soil and remaining inactive to avoid sub-zero temperatures has been well-studied in a number of insect species (Danks, 2002), such as carabid and crysometid beetles (Costanzo et al., 1997; Montero and Lietti, 1998) and noctuid moth larvae (O'Brien and Kurczewski, 1982; Young and Price, 1977). While these strategies are often accompanied by pre-programmed or environmentally queued states of energy conservation involving metabolic changes such as

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dormancy, quiescence or diapause (Hahn and Denlinger, 2011; Košťál, 2006), some species remain surprisingly active in their burrow, such as the European earwig which continually provides maternal care (Lamb, 1976). In these species, such an activity is expected to be costly to the fitness of an individual (e.g. due to cannibalistic consumption of eggs or increased mortality) and thus lead to important trade-offs between the benefits of protection from cold and energy conservation on one hand, and the ability to perform complex behaviors such as parental care toward overwintering eggs on the other hand (Clarke et al., 2013; Danks, 2002; Koch and Meunier, 2014; Ruf et al., 2012).

The success of ectotherm overwintering, however, is not only tied to the degree of winter cold, but also to its duration (Colinet et al., 2015; Lee and Dellinger, 1991). In species that cease feeding during overwintering, and thus determine their investment into cryoprotective and/or energy reserves at the beginning of winter, longer winters can lead to energy depletion and lower winter survival rates (Han and Bauce, 1998; Morris and Fulton, 1970). Furthermore, prolonged cold can lead to an accumulation of chilling injuries, which can further decrease survival either on their own or in interaction with energy depletion (Košťál, 2006; Sinclair, 2015). Finally, since individual metabolism and performance depend on the thermal conditions experienced during development, the duration of cold periods is expected to shape adult performance of offspring reared during winter (Le Lann et al., 2011).

The duration of winter length is often a flexible parameter, which varies not only between geographic locales, but also from year to year (Bonan, 2015). Interestingly, the accelerating global climate change reported over the last decades is a novel major cause of changes in mean temperature and season duration across the planet, which may profoundly shape the phenology and abundance of many plant and animal species (Butler and Tran, 2017; Estrella and Menzel, 2013; Parmesan, 2006; Princé and Zuckerman, 2015; Ramseyer et al., 2009; Stålhandske et al., 2015; Vitasse et al., 2017; Williams et al., 2017).

In this study, we investigate whether winter duration has long-term effects on offspring of the European earwig, *Forficula auricularia*, a hemimetabolous cosmopolitan insect exhibiting pre- and post-hatching maternal care (Kölliker, 2007; Meunier et al., 2012). In this species, females provide pre-hatching care by constructing a burrow in late autumn or early winter to lay their eggs and overwinter with the clutch until hatching occurs in early spring (Koch and Meunier, 2014; Lamb, 1976). Over the course of winter, females cease to feed but continuously groom their eggs to prevent the growth of pathogenic fungi, a behavior crucial to reproductive success (Boos et al., 2014; Diehl et al., 2017). This species is native to Eurasia but has reached nearly worldwide distribution as an invasive species, for example in North America and the Falkland Islands (Langston and Powell, 1975; Maczey et al., 2016). This widespread occurrence suggests that the species is able to adapt to a variety of winter conditions, but little is known about the effects of winter phenology. Additionally, seasonality is expected to affect reproduction in this species, as females can produce a second clutch in spring and the likelihood of producing a second clutch is generally higher in populations from warmer climates (Meunier et al., 2012; Ratz et al., 2016).

In our experimental setup, earwig clutches were experimentally kept under winter conditions (5 °C) for either 33 or 47 days to reveal whether winter duration has any subsequent effect on important life history traits in the offspring upon reaching adulthood. The difference in cold period length represents recorded phenological shifts in the study animals' home range between 1950 and 2001 (Linderholm, 2006). Specifically, we were interested in whether winter length determines 1) the hatching date of the eggs, 2) the developmental speed of the juveniles (called nymphs) into adults, 3) the mass of the adults, and 4) the immune-competence of the resulting adult offspring. Because a recent study revealed that resistance against pathogens of earwig adults at least partly relies on their social environment (Kohlmeier et al., 2016), exploring the effects of winter length on earwig immunity

required us to control for their social environment. To this end, the adult females were exposed to different social environments consisting of females being maintained in groups with either constant or changing group members, or suddenly isolated after long-term group living. Note that we chose to only investigate females because immune expression in males of this species may be affected by their tendency to engage in combat, as well as by reported trade-offs with their conspicuous weaponry (Körner et al., 2017). Female immune-competence was measured using three key components of insect immunity: phenoloxidase activity (PO), prophenoloxidase activity (PPO; which is measured together with PO as total-PO), and hemocyte concentration (Gillespie et al., 1997; Körner et al., 2017; Lavine and Strand, 2002; Strand and Pech, 1995). In insect immunity, PO mediates the melanization of foreign objects and the release of cytotoxic agents through the activation of PPO, its inactive precursor mostly stored in the hemolymph and the hemocytes (Cerenius and Söderhäll, 2004). Hemocytes are immune cells suspended in the hemolymph that are involved in recognizing and encapsulating pathogens (Lavine and Strand, 2002).

We expected that long winters would slow down egg development, as low-temperature conditions can arrest development in insect eggs (Tatar and Yin, 2001). Phenological shifts during early life-stages may not necessarily carry over to later stages (Salis et al., 2017), so we predicted no difference in developmental time from nymph to adult, which typically takes two months but can vary slightly between populations (see Ratz et al., 2016). While insect immunity is known to vary with season and temperature and can directly trade-off with cold responses, these relationships seem largely species dependent, and how these trade-offs affect developing insects in the long-term is yet unclear (Ferguson and Sinclair, 2017; Linderman et al., 2012). Given the importance of early development for life history traits, we expected adults' immune competence to reflect any development trade-offs compensating for the phenological shift between the two winter treatments. Finally, in line with previously shown immune-sensitivity to changes in the social environment (Kohlmeier et al., 2016), we expected adults to reflect challenged immunity when living in changing group compositions compared to constant groups.

## 2. Materials and methods

### 2.1. Animal origin & winter treatments

We caught *F. auricularia* adults in July-August 2015 in Mainz, Germany (49°58'20.5"N 8°11'42.3"E). Immediately after field sampling, we distributed these field-caught individuals among 36 plastic terraria (37 × 22 × 25 cm), which were grounded with moist sand and cardboard shelters and kept at 18–20 °C dark: light. These animals were allowed to mate freely from August 15th to November 12th. After that time, each female (approx. 1500 individuals) was isolated in a Petri dish (ø 9 cm) to mimic natural dispersion and encourage egg production (Lamb, 1975). The Petri dishes were setup with moist sand and maintained in constant darkness. Each female was provided with an ad libitum amount of food (artificial diet mainly consisting of pollen, cat food, wheat germ, and agar; see details in Kramer et al., 2015), renewed once per week. Immediately after isolation, temperatures were sequentially decreased to initiate winter conditions: 7 days at 15 °C, 7 days at 10 °C, 7 days at 8 °C and finally, 33 days at 5 °C. At this point, we haphazardly selected half (~650) of the females ("short winter") to immediately enter the sequential warm-up phase (7 days at 8 °C, 7 days at 10 °C, and then maintained at 15 °C until egg hatching), while the other half ("long winter") spent an additional 14 days at 5 °C prior to entering the warm-up phase (for an exact timetable see Fig. 1). From the day of egg laying, each clutch was monitored daily to check for emerged offspring. Egg hatching is generally well synchronized within a clutch and all offspring typically emerge within a day (Meunier and Kölliker, 2013). The hatching date for each clutch was noted. Following egg hatching, females and their offspring were moved to a climate

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