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Temperature variations affect postcopulatory but not precopulatory sexual selection in the cigarette beetle

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The ambient temperature varies on several timescales such as year, season and day and affects many reproductive traits of ectotherms. Thus, the direction and intensity of sexual selection should be affected by thermal conditions. However, the effects of temperature variation during mating events have sometimes been overlooked. We assessed traits associated with pre- and postcopulatory sexual selection in the cigarette beetle, *Lasioderma serricorne*, using three thermal mating conditions: 19 °C, 25 °C and 31 °C. Thermal conditions did not affect precopulatory traits (mating rate, mating latency and courtship intensity). Mating duration increased with decreasing temperature, whereas the number of sperm transferred and female fecundity were greatest at 25 °C. To investigate whether these thermal differences affected the risk of sperm competition (remating rate) and fitness consequences for both sexes, we conducted double-mating experiments using a black colour mutant. Females that had first mated at low or high temperatures were more likely to accept remating and exhibited higher fecundity compared to females that rejected remating; when females remated, the paternity of the first male was highest at 25 °C. Thermal conditions at the first mating event affected the fitness consequences for both sexes, irrespective of the females' remating acceptance. Changes to the thermal conditions for the female remating event caused no difference in the female remating rate or fecundity; however, the paternity of the second mate was highest at the intermediate temperature, and this could be attributed to the decreased sperm transfer at low and high temperatures. Our results suggest that temperature conditions during mating affect postcopulatory processes in *L. serricorne*. In particular, when females first mated at extreme temperatures, polyandry was promoted, potentially favouring males with higher sperm competitive ability through increased likelihood and intensity of sperm competition.
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The reproductive success of animals is often affected by sexual selection, which can be divided into pre- and postcopulatory processes. Precopulatory sexual selection occurs when males gain access to females via male - male competition and/or female mate choice (Andersson, 1994). Postcopulatory sexual selection occurs when females mate with multiple males, resulting in sperm competition and/or cryptic female choice (Eberhard, 1996; Simmons, 2001). Generally, sexual selection has the potential to impose strong, directional and consistent selection pressure (Andersson, 1994; Shuster & Wade, 2003). However, recent research has revealed that the direction and intensity of sexual selection are affected by biotic and abiotic environmental conditions, which vary spatially and/or temporally (reviewed in Miller & Svensson, 2014).

Temperature is one of the most important abiotic environmental factors. The ambient temperature directly affects behaviour, life history traits and physiological conditions (e.g. Abram, Boivin, Moiroux, & Brodeur, 2017; Angilletta, Niewiarowski, & Navas, 2002; Atkinson, 1996; Colinet, Sinclair, Vernon, & Renault, 2015). In particular, ectotherms, including insects, are impacted by the thermal environment. In these species, various behaviours such as

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foraging (Guarneri, Lazzari, Xavier, Diotaiuti, & Lorenzo, 2003), territorial (Ide, 2002; Wickman, 1985), flying (Samejima & Tsubaki, 2010; Taylor, 1963), and antipredator (Miyatake, Okada, & Harano, 2008; Mori & Burghardt, 2001; Weetman, Atkinson, & Chubb, 1998), are strongly temperature dependent (Chapman, 1998; Matthews & Matthews, 2010; May, 1979). Ambient temperatures also affect various reproductive behaviours of ectotherms, such as courtship display (Best, Lewis, Hurst, & Lizé, 2012; Jang & Gerhardt, 2007; Jiao, Wu, Chen, Chen, & Liu, 2009), male signals for conspecifics (Conrad, Stöcker, & Ayasse, 2017; Ord & Stamps, 2017), mating duration (Cook, 1994; Jiao et al., 2009; Katsuki & Miyatake, 2009), mate-finding tactics (Hedrick, Perez, Lichti, & Yew, 2002), mating frequency (Kindle, Johnson, Ivy, Weddle, & Sakaluk, 2006) and reproductive output (Chen, Jiao, Wu, Chen, & Liu, 2010).

Thus, one strong factor in sexual selection is hypothesized to be temperature variation (e.g. Best et al., 2012; Chen et al., 2010; Conrad et al., 2017; Cook, 1994; Hedrick et al., 2002; Jang & Gerhardt, 2007; Jiao et al., 2009; Katsuki & Miyatake, 2009; Kindle et al., 2006). However, with few exceptions, existing quantitative data on how mating behaviours and ultimate reproductive success are affected by temperature variation, which directly relate to sexual selection, are scarce (Miller & Svensson, 2014). Many studies have focused on changes in mating behaviours due to thermal variation, but our knowledge of the impact on fitness consequences with such behavioural changes is weak. Environmental temperature varies on temporal and spatial scales, for example diurnal, seasonal and annual temperature cycles, and differing levels of sunlight between microhabitats (Colinet et al., 2015). Thus, many animals experience temperature fluctuations or sudden changes, resulting in thermal variation, during mating events (Colinet et al., 2015; Zhang, Zhao, Hoffmann, & Ma, 2013). Fundamental aspects of mating behaviours and fitness may be affected by thermal conditions even if it is only a short-term variation such as diurnal fluctuations or cycles (Best et al., 2012). However, the potential impact of short-term variations can be overlooked, despite the obvious effects of the thermal environment on ectotherms.

Previous studies have investigated pre- and postcopulatory sexual selection in the cigarette beetle, *Lasioderma serricorne*. The female chooses whether to accept a male mating attempt based on male courtship intensity, that is, the number of courtship acts (fore- and midleg rubbing, antennae and genital licking) per s (Katsuki et al., 2017; Omae et al., 2012). Previous studies also used the time until copulation started (copulation latency) as an indicator of male attractiveness because females allow males with more intense courtship behaviour to mate sooner (Katsuki et al., 2017; Okada, Fuchikawa, Omae, & Katsuki, 2013). Okada et al. (2013) demonstrated that a single mating with an attractive male provides direct and indirect benefits to females: when females mated with attractive males, they laid more eggs and produced more attractive sons. Of those females that remate, approximately 40% mate with a single male the day after the first mating, and the proportion of offspring sired by this second mate (P_2) is approximately 0.80, irrespective of male attractiveness; that is, the last mated male has a higher rate of paternity (Katsuki et al., 2017). Attractive males have greater mating success regardless of the female's mating experience (virgin or nonvirgin); however, females that have mated with an attractive male readily remate with another male, owing to the smaller amount of sperm transferred to a female by an attractive male (Katsuki et al., 2017). Furthermore, the longevity of mated females is reduced by additional courtships, regardless of the outcome of male remating attempts, and this is costlier when the male is more attractive (Okada, Suzaki, Sasaki, & Katsuki, 2017). Therefore, previous studies on *L. serricorne* suggest that males and females are influenced by pre- and postcopulatory sexual selection and copulation latency, and that the number of sperm transferred to a female is one of the most important characters of sexual selection (Katsuki et al., 2017; Okada et al., 2013, 2017).

As shown above, pre- and postcopulatory sexual selection seem to be well studied in *L. serricorne*. However, these results are from studies conducted under constant environmental conditions. We predicted that thermal conditions, especially related to the time of reproduction, would directly affect the balance of pre- and postcopulatory sexual selection. Here, we examined how temporal temperature variation during mating events affects reproductive traits and the fitness consequences of pre- and postcopulatory sexual selection in *L. serricorne*. First, we compared mating performances at different temperatures: adults of *L. serricorne* that had been reared at 25 °C were transferred to environments at 19 °C, 25 °C or 31 °C. The temperature range of the present study was based on the mean temperature during the breeding season for *L. serricorne* being approximately 25 °C, and the minimum and maximum being 19 °C and 31 °C, respectively (Takaoka & Nakazawa, 1956). The fluctuation width of the present study is based on Takaoka and Nakazawa (1956). We measured reproductive traits (mating rate, mating latency, mating duration, courtship intensity, number of sperm transferred to the female and fecundity). Because most *L. serricorne* females mate with two males under laboratory conditions (Coffelt, 1975), we used two double-mating trials to investigate the thermal effect on paternity; one mating was observed at different thermal conditions (19 °C, 25 °C or 31 °C) and the other mating was observed at 25 °C. Based on these results, we discuss the effects of temperature variation on mating events and pre- and postcopulatory sexual selection in this beetle.

METHODS

Stock Culture

The culture of *L. serricorne* used in this experiment was derived from a strain that has been maintained for at least 100 generations in the laboratory of the Fuji Flavor Co., Ltd., Tokyo, Japan. We used two colour morphs to assess paternity of focal males (see below) in a double-mating experiment. Because the brownish-red colour is a dominant inherited trait, and the black body colour is recessive, the black colour was used as a genetic marker for paternity assessment (see Omae et al., 2012 for details).

We followed the method of Katsuki et al. (2017) to obtain virgin adults for our experiments. The larvae were reared in a larval medium of corn flour and corn bran (Sunny Maize, Shizuoka, Japan), enriched with brewer's yeast (Asahi Beer, Tokyo, Japan), at ratios (by weight) of corn flour: corn bran: yeast, 46:46:8. Each strain was placed in a plastic dish (diameter: 95 mm; height: 25 mm), with 54 g of larval medium as an oviposition substance, and was maintained in a chamber (2400 × 2400 × 2400 mm; CC-T3000, Sanyo, Osaka, Japan) at 25 °C, with 60% relative humidity and a 14:10 h light:dark photoperiod. Each strain was formed of 1000–1200 larvae per generation and maintained in the plastic dishes, with 250–300 larvae per dish; the regimes were continued for more than 50 generations.

The pupae were separated from the medium and sexed based on Halstead (1963). Males and females were housed in separate plastic dishes (diameter: 90 mm; height: 13 mm) after emergence. Because adults of *L. serricorne* are sexually mature at 1 week after emergence (Okada et al., 2013), 7-day-old virgin females and males were used for all experiments. All experiments in this study follow this maintenance protocol unless stated otherwise.

Experiment 1: Reproductive Behaviour

To investigate mating performance, we measured the mating rate, mating latency, mating duration, courtship intensity, number

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