



Micro-climate and incubation in a fiddler crab species



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ARTICLE INFO

Article history:

Received 4 March 2016

Received in revised form 11 August 2016

Accepted 16 August 2016

Available online 31 August 2016

Keywords:

Temperature
Larval development
Fiddler crab
Uca

ABSTRACT

Many tropical ectotherms will probably not survive climate warming without having access to thermal refugia. Temperature affects adult survival, but has just as strong an effect on larval stages, often due to its effect on reproductive timing and incubation duration. Intertidal animals usually have tight constraints on the timing of larval release since the planktonic larvae must be washed out to sea on the highest nocturnal spring tides. Can females behaviourally compensate for the effects of temperature over the naturally occurring temperature range by shifting the timing of mating and/or fertilisation or by adjusting the incubation duration? This experiment compares the timing of key reproductive events, as well as the size of eggs and larvae, in fiddler crabs that incubate over a 6 °C range of temperatures. There was no effect of temperature on the timing of reproductive events or the size of eggs or larvae produced. In other crab species, the effect of temperature on incubation duration is exponential, with smaller decreases in incubation duration at higher temperatures. Since the natural incubation temperatures are unusually high for this species, the effect of further increases in temperature may not have had as marked an effect as it does for species breeding in slightly cooler temperatures. Future climate warming may not have as strong an effect as may be expected for this species.

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1. Introduction

Tropical animals evolved in relatively constant thermal environments and tend to have narrow thermal tolerance ranges (Dillon et al., 2010). For tropical ectotherms, the primary challenge is to remain cool, and behavioural thermoregulation is one way to achieve this (Kearney et al., 2009). Behavioural thermoregulation includes body orientation (tropical butterflies, Bonebrake et al., 2014), increased heart and circulation rate (mushrooming in limpets, Williams et al., 2005), and - most importantly - retreating into the shade (Kearney et al., 2009). The ability of tropical ectotherms to survive climate warming will depend largely on the availability of shade (Kearney et al., 2009) and it has been predicted that most will not survive without having access to thermal refugia (Sunday et al., 2014).

Many studies document the effect of temperature on adults, but the effect is even more pronounced on larval stages. Temperature influences larval incubation duration (Hamasaki, 2003; Smith et al., 2015), and survival (Brillon et al., 2005). In a mosquito, for example, development rate and survival of the larvae were significantly reduced with a relatively small increase in temperature from 30 to 32 °C (Paaijmans et al., 2013). Females can control the temperature at which their eggs develop by selecting cooler micro-habitats. In the lark bunting, for example, nests that were exposed to solar radiation fledged fewer young

than nests that were protected from solar radiation (Pleszczyńska and Hansell, 1980); and females were more likely to mate with a male that has a nest site that was protected from solar radiation (Pleszczyńska, 1978; Pleszczyńska and Hansell, 1980).

Tropical intertidal ectotherms can experience extremely high temperatures. The banana fiddler crab, *Uca mjoebergi*, for example, lives on intertidal mudflats that reach 50 °C even though their critical thermal limit is 40 °C (Munguia et al., in prep). They are able to reduce their body temperature by retreating into their burrows (Smith and Miller, 1973) or by selecting cooler micro-habitats: they can live in the shade of the mangrove trees (Darnell et al., 2013; Powers and Cole, 1976; Smith and Miller, 1973; Thurman, 1998). Thermoregulatory micro-habitat selection may also affect the larval stages since females select the burrow in which she will incubate her eggs: if a female incubates in a burrow in the shade, her eggs would develop at lower temperatures than if she incubates in a burrow exposed to the full sun. Since the temperature in the burrow is much lower than on the surface, the incubation temperature is unlikely to affect larval survival, but it will very likely have an effect on incubation duration. In other fiddler crab species, even small increases in temperature decrease incubation durations (an increase of 2 °C can decrease incubation by ~1.5 days; Christy, 1982; Kerr et al., 2012). Faster incubation may not be problematic for many species, but it can have adverse consequences for intertidal species that have planktonic larvae (barnacles, anemones, starfish, crustaceans, sponges etc.). The most critical temporal constraint these species face is the timing of larval release: it is generally confined to ~3 nights of peak amplitude spring tides (Christy, 1982) so that the

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larvae are quickly washed out to sea and avoid the high levels of predation inshore.

There are very few studies that examine the effects of incubation temperature on the timing of larval release in tropical intertidal ectotherms. By examining how the naturally occurring range of temperatures affect the timing of larval release, and determining whether females can behaviourally compensate for these thermal effects, may allow us to predict the effects that climate warming may have on these species.

1.1. Study species

Uca mjoebergi is a small fiddler crab that lives in mixed-sex, high density populations on intertidal mudflats along the northern coast of Australia. Males have a single enlarged claw that is used as a weapon during territorial disputes and to attract females during courtship displays. Males and females each defend a territory that consists of a small area of mudflat surface where feeding and courting occur, and a central burrow used to access water, avoid extreme weather and predators, and where mating and incubation occur. The species live high in the intertidal zone and their habitat is covered by high tides of >6 m. For 5–10 days each semi-lunar tidal cycle (during the neap tides), the population is not inundated at all. It is in this period that females mate-search and males court them. Temperatures are high, with the sediment surface reaching >50 °C (Munguia et al., in prep). The population covers areas of mudflat that are open and in the full sun as well as areas that are partially or fully under mangrove trees and are shaded for part or all of the day. Males court in both the sun and shade areas, and mate-searching females freely move between the sunny and shaded areas.

When ready to mate, females leave their territories and wander through the population of courting males searching for a mate. A female visits multiple males by approaching them, briefly entering their burrows and then leaving (if the male or his burrow are rejected) or staying (if the male and burrow surpass a quality threshold; Reaney and Backwell, 2007). If the female accepts the male, she stays underground with him in his burrow. He seals the burrow entrance with a sand plug, and mating occurs within the next few hours. The female stores the male's sperm in a spermatheca and, 1–5 days later, she extrudes her eggs which are fertilised as they pass the spermathecal opening. The male remains underground, guarding the female until she fertilises and extrudes her eggs. He then leaves the burrow, resealing the female underground to incubate her eggs. The male wanders through the population, fighting with resident males to win a new territory. The female incubates her clutch for ~21 days before releasing her larvae into the water column at the highest amplitude nocturnal spring tide. The timing of larval release is critical if the larvae are to avoid the high levels of predation in the mangroves. By releasing the larvae at the ebbing, nocturnal highest spring tide, the female ensures the larvae get washed out to sea as quickly as possible (Morgan and Christy, 1995).

If a female selects a male with a territory in the sun, she will incubate her eggs at a higher temperature than females that select males with territories in the shade. Increased temperature decreases incubation duration (Sanford et al., 2006; Yamaguchi, 2001). This may affect the tight temporal constraint on the timing of larval release. In order to release her larvae during the highest nocturnal spring tide, females would need to compensate for a shorter incubation when selecting a male with a territory in the sun and the longer incubation duration when in the shade. Five non-mutually exclusive mechanisms that females could potentially use to compensate for this affect are: (i) they could select sun or shade males based on the timing of mate selection: early mating females could select males in the shade since this would slow down the development rate, and later mating females could select males in the sun since this would speed up larval development; (ii) they could select different size burrows when mating in the sun or shade: smaller burrows are warmer than larger burrows (Reaney and

Backwell, 2007) so females that mate in the shaded areas could select smaller burrows to compensate for the lower incubation temperatures and vice versa; (iii) females could adjust incubation temperatures by moving up or down the burrow shaft (Kerr et al., 2012): females that mate in the sun could move to the lower reaches of the burrow shaft while females that mated in the shade could sit higher up in the burrow shaft; (iv) they could alter the time between mating and fertilisation. The female could delay fertilising her eggs if she is in a warmer burrow, and fertilise them earlier if she is in a cooler burrow; (v) females could slow the rate of egg development by adjusting the size of eggs they produce. There is a strong negative relationship between egg size and temperature in many crustaceans (Kobayashi and Matsuura, 1996; Sheader, 1996) including fiddler crabs (Christy, 1982; Kerr et al., 2012). Egg size varies according to the amount of yolk laid down (Sheader, 1996). Crustaceans are unusual in that they can rapidly produce yolk using several sites for its production: hepatopancreas, ovaries and hemolymph (Quackenbush and Keeley, 1988). This allows females to alter yolk content shortly before fertilisation. The incubation period of *U. mjoebergi* females could potentially be extended or decreased by producing larger/smaller eggs.

The following terminology is used to describe the stages of the mating process: 'Mating day' is the day on which the female approaches a male, enters his burrow and the male seals the pair underground (mating occurs within a few hours of burrow sealing). 'Fertilisation day' is the day on which the male leaves the burrow, resealing the female underground (the male leaves as soon as the female has extruded her eggs – fertilising them as they move past the spermatheca). 'Mate guarding period' is the time between the mating day and the day of fertilisation (the male remains underground with the female, preventing her from re-mating until her eggs have been fertilised). 'Larval release day' is the day on which the eggs hatch into the water. 'Incubation period' is the time between fertilisation and larval release day.

1.2. Aims

Natural incubation temperatures that females would experience when selecting a male that has a territory in the sun or shade was determined. The fourth and fifth mechanism above (the first three mechanisms are the topic of an earlier study: Kerr and Backwell, in prep) were then explored to ascertain their role in managing micro-habitat induced temperature variation. It was then determined whether the naturally occurring range of incubation temperatures affect the timing of mating, fertilisation and/or larval release. An examination of eggs produced by females at different temperatures was conducted to determine whether females adjust yolk size in order to control incubation duration; and whether larvae produced at different temperatures differ in size.

2. Methods

Field work was conducted at East Point Reserve, Darwin, Australia (12°24'31.89"S 130°49'49.12"E) and laboratory work was conducted at the North Australian Research Unit, Darwin (12°22'11.81"S 130°52'17.31"E) between September and December 2012.

Incubation temperatures that females would experience if they selected a male with a territory in the sun or in the shade were ascertained. Four iButtons were buried at a depth of 20 cm (which is the average depth of the incubation chamber in a male's burrow: Clark and Backwell, 2016), two in the open area of mudflat that gets full sun during the day; and two in the shaded part of the mudflat where the mangrove trees protect the surface sediment from the full impact of the sun. The iButtons logged temperatures at hourly intervals for 44 days (22 October–4 December 2012).

Mate-searching females were located and watched as they moved through the population of courting males and were followed until they selected a male, remained in his burrow, and he sealed the burrow

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