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ORIGINAL ARTICLE

Behavioural plasticity in the monsoonal tropics: implications for thermoregulatory traits in sandy shore crabs

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Abstract

Behavioural time budgets of organisms reflect their reaction norms to environmental conditions and, as such, indicate their behavioural plasticity. In environments which limit the activity time of organisms, efficient organization of behaviours is critical to enhancing performance to achieve necessary functions and minimize time and/or energetic costs. We investigated variations in behavioural time budgets of a common deposit-feeding crab, *Scopimera intermedia*, to the spatio-temporal scales of environmental changes experienced on sandy shores in the monsoonal tropics, where activity times are restricted by the tides. Activity levels of the crabs varied strongly with air temperature, with crabs emerging from the sediments only when air temperature exceeded ~ 20 °C. Behavioural water uptake increased in frequency with both feeding rate and environmental temperature, and was often followed by waving displays. Water uptake and waving, therefore, appear to be multifunctional behaviours, as not only do the crabs replenish water for feeding and wave their chelipeds to court females, but these behaviours can also contribute to thermoregulation, enhancing cooling when taking up water from the sediment surface. Such plastic and multifunctional behavioural traits are likely a widespread solution for survival and reproductive success in harsh and dynamic environments, where specialized traits are energetically costly and time-inefficient to optimize performance.

Significance statement

Surviving in extreme and variable environments is challenging due to the potentially substantial energetic cost animals need to undertake in order to maximize performances under contrasting conditions. This study reveals a multitasking strategy adopted by the sand-bubbler crab to survive hot and variable temperatures within a limited activity time on tropical sandy shores. Behaviours of the crabs are strongly temperature dependent; and when active whilst the tide is out the crabs flexibly adjust their activity times to feed, stay cool and attract mates using a limited set of multifunctional behaviours. Specialized traits are therefore not necessary to achieve these critical functions and, as such, this study highlights the importance of this plastic, multitasking strategy as a common solution for animals to endure highly variable environments with minimal cost.

Keywords Sponging · Waving · Multifunctional behaviours · Seasonality · *Scopimera* · Robo-crabs

Introduction

The selection of different behavioural responses is critical in species' ecology and evolution, since the maximization of individual fitness depends on the expression of optimal behaviours at any given condition (Sibly and McFarland 1976; Mangel 1991). The expression of behaviours, however, not only varies spatially due to variations in microhabitat/environmental conditions but also over different temporal scales: hourly to daily periods (finding food, avoiding predators, interacting with conspecifics), seasonal cycles (finding mates during reproductive seasons, hibernating in physically harsh seasons) and ontogenetic shifts (reaching maturity, parenting, adopting more risky foraging options as individuals grow), which will all contribute to altering individual survival and/or reproductive success (Stephens and Krebs 1986; Lima and Dill 1990; Houston and McNamara 1999).

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Intertidal organisms, in particular, partition their behaviours throughout the tidal cycle (Palmer 1990; Williams and Little 2007), where behavioural processes for survival, growth and reproduction are often constrained to different tidal phases (Little 1989): during the immersion phase (e.g. barnacles, Trager et al. 1992), when awash (e.g. gastropods on tropical rocky shores, Garrity 1984; Williams and Morritt 1995; Davies et al. 2006) or when the tide is out and animals are emersed (e.g. intertidal crabs, Ansell 1988; Kennish 1998). Since the length of available activity periods will affect the possible optimal strategies (Houston and McNamara 1999), behavioural time budgets of intertidal invertebrates are, therefore, dependent on the tides which impose a strict time limitation on species' activities (Hughes 1988).

Rapid changes in on-shore environmental factors during different tidal phases result in a variety of temporal variations and trade-offs among behaviours of organisms (Kim and Choe 2003; Koch et al. 2007). Deposit-feeders on soft shores may, for instance, adjust their foraging times on a daily basis to match the temporal change in the abundance of their food (microphytobenthos) throughout the lunar cycle (Ribeiro and Iribarne 2011). Variations in temperature during tidal awash and emersion phases can severely impact the foraging duration of animals and, as many intertidal organisms are ectotherms, change in temperature plays a primary role in determining individual metabolism and thus behaviour (Garrity 1984; Darnell et al. 2015; Crickenberger et al. 2020). On tropical shores, where temperatures can be close to or exceeding the thermal tolerance of ectotherms, a large proportion of individuals' time budgets may be allocated for thermoregulatory behaviours, often with trade-offs between other behaviours such as feeding or mating (Munguia et al. 2017; Ng et al. 2017). Due to the dynamic changes in onshore environmental conditions during emersion, the ability to adjust behavioural time budgets is, therefore, critical for intertidal organisms to allocate time for activities most relevant to enhance performance under a particular set of environmental conditions (e.g. more time in foraging when food is available, seeking refuges under stressful temperatures, etc., see Hazlett 1988; Ng et al. 2017).

On sandy shores, most burrowing, deposit-feeding crabs are active on the sediment surface only during emersion periods (Ansell 1988), where they adopt a wide variety of behaviours depending on short-term variations in environmental conditions. In particular, variation in temperature during low tide can induce substantial behavioural responses in sandy shore crabs, where activity levels are limited at low temperatures (Nakasone 1982; Mat et al. 2017) and high temperatures often induce active, thermoregulatory responses (Allen et al. 2012). Fiddler crabs, for example, spend greater periods of time inside their burrows at noon when temperature increases rapidly, but more time foraging on the sediment surface as temperature decreases (Munguia et al. 2017). A common behaviour seen in some sandy shore crabs (e.g. dotillid, mictyrid and ocypodid crabs) is sponging, where the crabs press their abdomens onto the sediment surface in order to uptake interstitial pore water (Wolcott 1976; Thompson et al. 1989; Maitland 1990; Hui et al. 2019). Such behaviour is multifunctional, not only facilitating the flotation feeding process common in deposit-feeding crabs, but also contributing to maintaining hydration states (Wolcott 1976; Thompson et al. 1989) and potentially to thermoregulation by enhancing evaporative water loss when water moistens the crabs' carapaces (Hui et al. 2019).

Waving is another common behaviour in sandy shore crabs, in which the males wave to court females and engage in agonistic interactions (Backwell et al. 1999; Ohata et al. 2005; Kitaura and Wada 2006; How et al. 2007). In fiddler crabs such waving is performed using the major cheliped, which also functions as a heat sink and buffers changes in crabs' body temperatures during low tides (Darnell and Munguia 2011). When crabs wave, they raise themselves from the sediments (reaching cooler air above the boundary layer, see Denny and Miller 2011), and the sweeping cheliped action (see How et al. 2009) is likely to move the air, enhancing convective heat exchange. As such, similar to sponging behaviour, we hypothesize that waving is multifunctional and contributes to thermoregulation in addition to courtship/territorial defence, particularly for crabs inhabiting tropical shores.

Multifunctionality of traits is particularly advantageous in species living in harsh environments (Yao et al. 2010; Song et al. 2013; Hui et al. 2019), where energetic/maintenance costs can be reduced when multiple survival/reproductive processes are accomplished by a small number of multifunctional traits. Efficient time partitioning of behaviours can also minimize energetic and/or time costs by avoiding activities under unfavourable conditions when the energetic gain is unable to compensate for the cost, such as under stressful temperatures or sparse food availability. There is, however, a lack of detailed and accurate descriptions of how deposit-feeding crabs partition their behaviours at multiple temporal scales, as well as the inter-relationships between different behaviours that may act synergistically to enhance individual performance. To address this, we investigated the temporal partitioning and functions of different behaviours of a deposit-feeding, sand-bubbler crab in Hong Kong in different monsoonal seasons over 2 years, to determine how flexible behaviours can be expressed in response to dynamic environmental conditions at various scales. Specifically, we tested whether burrow number and behavioural time budgets of the crabs varied within or between seasons, and whether the crabs' behaviours varied with air temperatures throughout the study period. We further investigated the relationship between sponging, feeding (two major behaviours) and air temperature, and the inter-relationship between sponging and chelae waving via numerical simulations and biomimetic approaches to test if waving is associated with sponging and/or can contribute to thermoregulation. The potential multifunctionality of these behaviours highlights temperature as a key physical driver affecting behavioural traits on tropical shores, where the changing environmental and physiological constraints are likely to favour different sets of behavioural strategies over time.

Materials and methods

Seasonal patterns in burrow number and behavioural time budget

The behavioural patterns of *Scopimera intermedia* Balss, 1934 (Dotillidae) were measured at two sandy shores in Tolo channel, Hong Kong, from 2014 to 2016: Starfish Bay (SFB, 22° 25′ 55″ N, 114° 14′ 41″ E) and Three Fathoms Cove (TFC, 22° 25′ 43″ N, 114° 16′ 13″ E, see Table S1 for sediment properties), where the crab burrows from the mid to low high shore (average density ~ 40 burrows m^{-2}) at ~ 1.5–1.9 m above Chart Datum (C.D., maximum tidal amplitude ~ 2.5 m above C.D.). Two principal monsoon seasons (Kaehler and Williams 1996) were defined, with transition seasons in between, based on the average air temperatures measured at 0.5 cm above the sediment surface (assumed to be the most biologically relevant environmental temperature to the crabs, which are ~ 0.5–1 cm in height when active on the sediment surface). These four periods included the cool (temperature ≤ 25 °C, from Jan to Mar), hot (temperature ≥ 30 °C, generally from May to Oct), cool-hot transition (temperature ranging from 25–30 °C, from Apr to May) and hot-cool transition seasons (same temperature range as the cool-hot transition, generally from Oct to Dec). Since these seasons were defined based on empirical air temperatures over the study period, their onsets and durations were not necessarily temporally fixed but could shift slightly between years (see Table S2 and description in Williams et al. 2019).

Crab burrow number surveys were conducted from 2014 to 2016 in two haphazardly selected areas (~ 30 m^2 each, where crab burrows were abundant) in SFB, where the shore is sufficiently large to accommodate multiple areas for surveys. Crab burrows are fundamental to surface activities of deposit-feeding crabs, since they provide refuges against predators and stressful physical conditions on the sediment surface and are shelters for mating and embryo development (Gherardi and Russo 2001; Jennions et al. 2003; Reaney and Backwell 2007; Munguia et al. 2017). The number of burrows is not simply determined by the abundance of crabs but also varies according to whether the crabs emerge for surface activities during low tide periods as, if they remain inside the sediments, burrow openings are not formed. Burrow surveys were conducted along three 10-m transects set at 1.9 m (high), 1.7 m (mid) and 1.5 m (low) tidal heights above C.D. in each area, where burrows of *Scopimera intermedia* could be distinguished from other species by the distinctive lines of food pellets left when the crabs feed radially from the burrow entrances (Hui and Williams 2017). Surveys were conducted on 4–13 randomly selected days within each season during low tide periods, in which two to four surveys were conducted per month (on average ~ 12 days between surveys). In each survey, the number of burrows was counted hourly for four hours in five randomly positioned quadrats (55 × 55 cm^2) along each transect after transects were emersed by the tide, when burrow openings were formed by the crabs and increased in density as more crabs emerged. The maximum number over the four hours was taken to be the observed burrow number. The survey ran for 2 years to include temporal replication of seasons ($\sum n = 2$ (years) × 4 (seasons) × 4–13 (surveys) × 2 (areas) × 3 (tidal heights) × 5 (replicates) = 1860).

To investigate detailed behavioural time budgets, videos were taken of individuals (carapace width (CW) ~ 0.7 cm, max. CW ~ 0.9 cm) that emerged at ~ 1.7 m above C.D. (mid tidal height), where burrows were most abundant during low tide periods. Six to eight crabs from burrows of ~ 1 cm diameter were opportunistically selected in both SFB and TFC during each survey from 2014 to 2016. Approximately 20-min videos were recorded using digital cameras (Canon G12/15, Japan) fixed at ~ 30 cm above the sediment surface ($\sum n = 2$ (sites) × 2 (years) × 4 (seasons) × 2–5 (surveys) × 6 – 8 (replicates) = 324). After video recording, temperatures were taken at ~ 5 cm depth inside the individual's burrow, directly on the sediment surface, and 0.5 cm and 1 cm above the sediment surface, using K-type thermocouples (± 0.1 °C, TM-946 thermometer, Lutron, Taiwan). Temperatures on or above the sediment surface were averaged from three, haphazardly selected locations ≤ 10 cm from the burrow entrance. A surface sediment core (1.9 cm diameter, 0.2 cm deep) was taken next to the foraging tracks of the crabs to quantify the sediment water content (% weight), and the density of neighbouring crabs measured by counting the number of burrows within a 25 × 25 cm^2 quadrat centred at the studied crab's burrow. The CW of the crab was measured from the videos using the software CPCe 4.1 (Kohler and Gill 2006). Behaviours of the observed crabs were classified into ten categories (Table S3) and each category was timed to the nearest second for the total recording time in the video.

Seasonal patterns in burrow number and detailed behavioural time budgets of the crabs were analyzed via univariate and multivariate approaches respectively. To account for excess zeros and overdispersion in the burrow number, a generalized linear model (GzLM) with a zero hurdle and negative binomial error distribution (Lindén and Mäntyniemi 2011) was used to test for the variation in burrow number across seasons, tidal heights and survey days (see Fig. S1 and details in Supplementary Information). The proportion time spent in various behavioural categories, calculated by dividing the time spent in a specified behaviour by the total recording time, was used as a multivariate variable representing the behavioural time budgets of the crabs. The overall spatio-temporal variation in behavioural time budgets (across seasons, sites and survey days) and their dispersions (within seasons, sites and survey days) were investigated via a permutational multivariate ANOVA (PERMANOVA) and permutational multivariate dispersion tests (PERMDISP) in Primer 6 (Anderson et al. 2008, see Supplementary Information).

Relationships between burrow number/behavioural time budget and temperature

Both burrow number and behavioural time budgets of the crabs demonstrated strong seasonal variations (see below), in which air temperature appeared to be key in driving the observed plastic responses. To further assess the relationship between air temperature and burrow number of the crabs, the burrow number recorded in each survey at SFB was regressed against the maximum air temperature recorded at the nearest Hong Kong Observatory station (~ 9 km away from the study site, Hong Kong Observatory 2017) via a GzLM with negative binomial errors (to account for overdispersion in the count data, Lindén and Mäntyniemi 2011, using a log link function) and a zero hurdle, using the package 'countreg' in R (Zeileis et al. 2008).

The relationships between behavioural time budgets of the crabs and air temperature, as well as other environmental/biological variables, were investigated via a multivariate regression approach using a distance-based linear model (DISTLM) in Primer 6 (Anderson et al. 2008). Behavioural time budgets of the crabs were the multivariate responses with Euclidean distance set as the dissimilarity measure, whilst crab size, conspecific density, air temperature and sediment water content were treated as explanatory variables (with inter-correlations of, at most, 0.26; thus, these explanatory variables were not considered collinear). The model was visualized using a distance-based redundancy analysis (dbRDA). Spearman's rank correlations were used to further test for the inter-correlations between the proportions of time spent in different behavioural categories, as well as with air temperature, conspecific density and crab size (i.e. significant variables in the DISTLM). No multiple comparison corrections for P values were conducted for these correlations as each represents an independent test and no statistical inference was drawn by combining multiple test results.

Relationships between sponging, feeding and temperature

The relationships of feeding and sponging (the two most common activities, see below) to air temperature were analysed further. The numbers of food pellets produced and sponging events were counted from the videos (where a food pellet was defined as a clump of sediments produced and removed by the crabs after sieving through their buccal cavities, see Table S3), and the feeding rate was calculated by dividing the number of food pellets produced by the total time the crabs spent outside their burrows. A GzLM with negative binomial errors (and log link function) was used to test if the number of sponging events varied with the feeding rate, air temperature at 0.5 cm from the sediment surface, crab size and site. Negative binomial errors were used to account for overdispersion in the number of sponging events, where the variance in the number of sponging events was greater than the mean (Lindén and Mäntyniemi 2011). Since the crabs use a flotation mechanism to extract sediment food by diverting water to the buccal cavity and higher air temperature would enhance evaporative water loss (Thurman 1998), an interaction between feeding rate and the air temperature was included in the model. The time the crabs spent outside their burrows was treated as an offset variable, such that coefficients of the explanatory variables in the fitted model represent their effects on the sponging rate but not the number of sponging events per se. To test if a temperature gradient existed across the air–sediment boundary layer, differences between air temperatures at 0.5 cm and 1 cm above the sediment surface were tested across both sites using paired t tests.

Relationship between sponging and waving

The number of waves performed by individual crabs (counted from the ~ 20-min videos taken) was analysed using a GzLM (negative binomial errors with a log link function to account for overdispersion, see Fig. S1), to test if the number of waves differed among seasons (fixed, four levels) and crab size. Since the crabs spent different amounts of time outside their burrows despite the videos having similar durations, the number of waves within the video duration was therefore corrected by the time the crabs spent outside burrows, which was used as an offset variable in the GzLM. The probability of a crab waving after sponging was investigated more systematically by testing whether waving followed a random distribution in time. To achieve this, crab waving and sponging were quantified from the videos by counting the number of waving/sponging events that the crab performed within the entire video (the number of waving and sponging events ranged from 1–256 and 6–59, respectively), such that waving rates (WR, number of waves per second when the crabs were on the sediment surface) and the total number of sponging events (NS) were quantified for each individual. The number of sponging events followed by an immediate wave (within a second after sponging) was scored (denoted as O(NS)) and the observed proportion of sponging events followed by an immediate wave calculated as O(NS)/NS. Then, assuming waving is a random

Poisson event, the probability of waving (P_w) occurring within a second after sponging should follow an exponential distribution: $P_w = 1 - e^{-WR}$ and, therefore, the expected number of sponging events followed by an immediate wave (denoted as E(NS)) was $\sum_{i=1}^{\mathrm{NS}} i \binom{\mathrm{NS}}{i} P_w^i (1 - P_w)^{\mathrm{NS}-i}$, where $\binom{\mathrm{NS}}{i}$ represents the number of ways to draw i sponging events out of the NS sponging events without replacement. The expected proportion of sponging events followed by crab waving was thus calculated as E(NS)/NS. The expected and observed proportions were compared via linear regression to test if the slope and intercept differed from 1 and 0 respectively.

A biomimetic simulation of sponging, waving and body temperature

Due to the higher-than-expected chance of waving following sponging (see below), the effects of sponging and waving on the crab's body temperature were further investigated via a biomimetic approach in the laboratory. 'Robo-crabs' were constructed and programmed to wave at a specific frequency, followed by injections of seawater to simulate sponging actions. Each robo-crab was constructed from dried *Scopimera intermedia* exoskeletons (males, 0.84 ± 0.05 cm, mean ± SD, $n = 10$) collected from SFB, with freely rotatable claws and a body that could be programmed to wave and be lifted ~ 0.5 cm vertically (for details see Supplementary Information). To minimize stress, collected crabs were frozen upon return to the laboratory before being oven-dried to obtain the carapace. Whilst the use of robo-crabs does not factor in organismal physiology and metabolic heat production, which would be important in modifying body temperatures of ectotherms (Edney 1961; Heinrich 1974; Thurman 1998), the use of mimics with the same size and shape as the study animals (i.e. the exoskeleton of the crabs) enables realistic estimation of the operative environmental temperature (i.e. temperature of an object with the same morphology and radiative properties as the animal, see Gates 1980; Bakken 1992). This approach provides a comparative basis to investigate the effects of purely physical processes on the body temperature of a moving animal (e.g. conduction, convection and radiation) and, therefore, can enable comparisons between physical and physiological processes in modifying body temperatures.

To test if waving will reduce body temperatures compared to a non-waving posture, robo-crabs were firstly injected with natural seawater (~ 35‰ and 33 °C, a temperature comparable to the field body temperatures (mean ± SD = 34.4 ± 1.6 °C, $n = 20$) of *Scopimera intermedia* when they are inside the burrows during the hot season, T. Y. Hui unpublished data) through a small aperture between the eyestalks, to fully saturate them and then heated under heat lamps until their 'body' temperatures reached 34 °C. Natural seawater was then pipetted into the region between the legs and carapace of the robo-crabs (to simulate sponging) and the robo-crabs were set to either wave or remain still for 180 s, for three replicate trials haphazardly in time ($\Sigma\, n = 9$ (robo-crabs) × 2 (treatments, wave vs still) × 3 (trials) = 54). The waving rate was set at 0.53 waves s^{-1} to resemble the maximum rate demonstrated by crabs on the shore (median maximum rate = 0.4 waves s^{-1}, range = 0.01 to 0.83 waves s^{-1}, $n = 73$). The body temperature of the robo-crab was monitored every second by a Type-K thermocouple (± 0.1 °C, TM-947SD thermometer, Lutron, Taiwan) inserted into the 'body' through the carapace. To test if body temperatures will be affected by different amounts of water being sponged, the experiment was repeated with 0, 0.02 or 0.04 ml of water being sponged by the waving robo-crabs ($\Sigma\, n = 10$ (robo-crabs) × 3 (water amounts) × 3 (replicate trials) = 90). To test for the effects of waving/the amount of water sponged on body temperatures, linear mixed models were conducted with body temperature as the response variable and treatment (wave or still/the amount of water sponged) as the explanatory variable. Water temperature (used for sponging) and average air temperature (averaged between lifted and resting heights, see below) were also included in the model to control for their effects in modifying robo-crabs' body temperatures (see Supplementary Information). Robo-crab identity was treated as a random effect. Temperature variables were centred before fitting the models such that treatment effects could be assessed at the mean air and/or water temperature. Water temperature was not used in the analyses of the experiment investigating the effect of the amount of water sponged, as no water was sponged in one of the treatments (i.e. the zero water treatment). In both experiments, water temperatures were controlled at 32.9 ± 0.4 °C for sponging, whilst the air was warmed under heat lamps and thus was not controlled to a pre-set value. Water and air temperatures, therefore, were not considered collinear by design. Analyses were conducted separately for 10 s, 30 s, 60 s, 120 s and 180 s after sponging was simulated, and all linear mixed models were conducted using the package 'lme4' (Bates et al. 2015) in R, where coefficients of the fixed effects were tested using t-tests based on Satterthwaite's method.

Results

Seasonal patterns in burrow number and behavioural time budget

Seasonal variations in both the presence and number of burrows depended on tidal heights: whilst burrows were more likely to be present during the hot season at all tidal heights (Figs. 1 and S2), they were more likely to be absent during the cool season as compared to both transition periods along the mid and high heights but not the low tidal height. When crab burrows were present, they were less abundant during the cool-hot transition along the mid and high tidal heights and during the hot-cool transition along the low tidal height (Table S4).

Overall, both the multivariate dispersions and locations in behavioural time budgets of the crabs differed between days (dispersion: pseudo-$F_{45,278} = 6.19$, $P = 0.0001$; location: pseudo-$F_{38,278} = 3.93$, $P = 0.0001$), indicating between-day variations that could arise due to either variations between individual crabs within survey days (dispersion) or variations in the overall behavioural budgets of the crabs between days (location). Such between-day variations were likely to be averaged out when pooling survey days within seasons or sites, as the crab's behavioural budget did not vary in both dispersion and location between sites, seasons or their interactions (dispersion: P ranged from 0.1189–0.9285; location: P ranged from 0.1936–0.5258, Fig. 2).

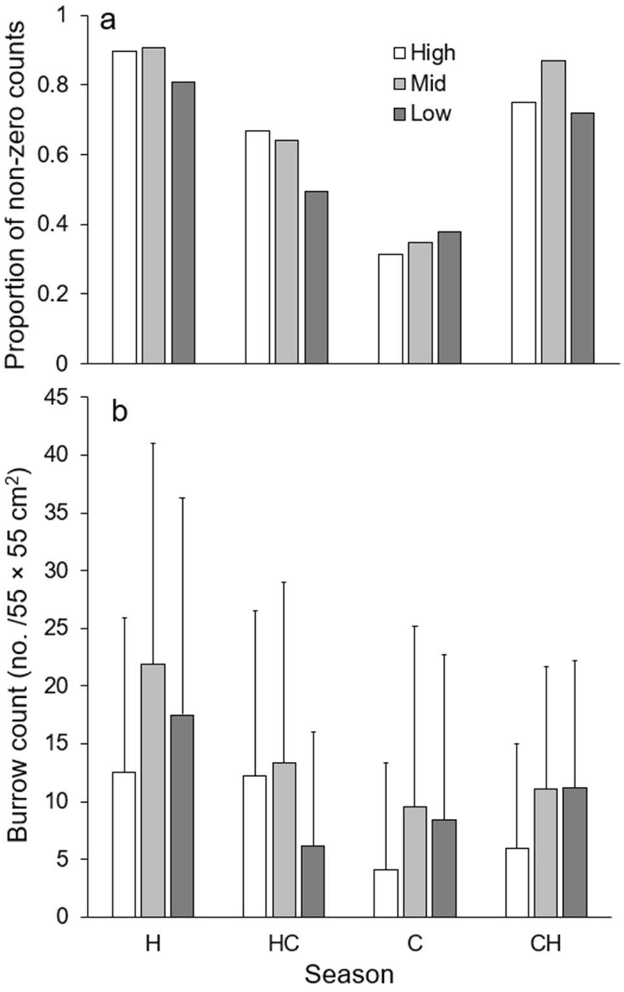

Fig. 1 Temporal variations in the presence (**a**) and mean burrow number (**b**) of *Scopimera intermedia* at Starfish Bay along the high, mid and low tidal heights (1.9, 1.7 and 1.5 m above Chart Datum, respectively) in two haphazardly chosen areas on the shore during the hot (H, $n = 240$), cool (C, $n = 130$), hot-cool transition (HC, $n = 150$) and cool-hot transition (CH, $n = 100$). Error bars are + SD. Both the presence and number of burrows varied between seasons, depending on tidal heights (significant season by tidal height interactions were detected using a negative binomial GzLM with a zero hurdle, presence of burrows: $\chi^2_6 = 22.7$, $P = 0.0009$; number of burrows: $\chi^2_6 = 53.9$, $P < 0.0001$, Table S4)

Relationships between burrow number/behavioural time budget and temperature

The probability of the occurrence of crab burrows increased with the maximum air temperature recorded during the survey period (zero hurdle of the negative binomial GzLM, $z = 21.3$, $P < 0.0001$, Fig. 3). When crab burrows occurred, however, their numbers were not affected by the maximum air temperature (count model of the negative binomial GzLM, $z = 0.1$, $P = 0.916$, Fig. 3).

The crabs' behavioural time budgets varied with air temperature at 0.5 cm above the sediment surface (pseudo-$F_{1,322} = 7.9$, $P = 0.0004$), as well as with conspecific density (pseudo-$F_{1,322} = 5.2$, $P = 0.0079$) and crab size (pseudo-$F_{1,322} = 3.0$, $P = 0.0431$), but not with sediment water content (pseudo-$F_{1,322} = 1.9$, $P = 0.1228$). Air temperature contributed the highest loading in the first dbRDA axis (0.77), with conspecific density being the second most important variable (loading $= -0.58$, Fig. 4). Specifically, the proportions of time spent feeding and sponging decreased and increased respectively with air temperature (Spearman's correlation with $n = 324$, feeding: $r_s = -0.19$, $P = 0.0007$, sponging: $r_s = 0.25$, $P < 0.0001$). Other activities such as walking, manipulating appendages and waving also increased with air temperature (r_s ranged from 0.47–0.54, $P < 0.0001$ in all cases). The proportion of time spent feeding, on the other hand, increased with conspecific density ($r_s = 0.21$, $P = 0.0001$), and the crabs spent less time being motionless when conspecific density was higher ($r_s = -0.15$, $P = 0.0074$). The crabs also spent more time sponging and waving when they were larger in size (sponging: $r_s = 0.14$, $P = 0.0117$; waving: $r_s = 0.22$, $P < 0.0001$).

Relationships between sponging, feeding and temperature

Air temperatures at 0.5 cm above the sediment surface were similar at both sites ($t_{322} = 0.2$, $P = 0.826$). The relationship between sponging rate and air temperature varied with feeding rate: at higher feeding rates, sponging rate was less dependent on air temperature as compared to lower feeding rates, when the crabs sponged more frequently with increasing air temperature (Table 1, Fig. 5).

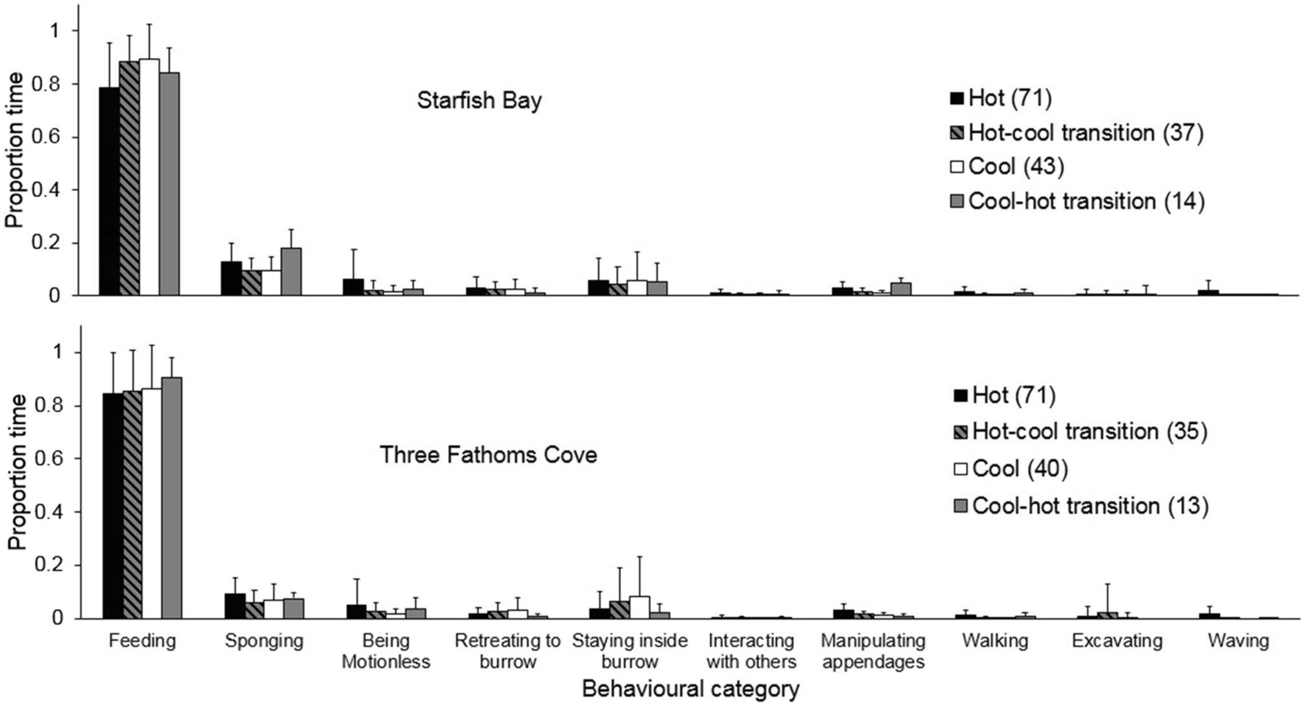

Fig. 2 Behavioural time budgets of *Scopimera intermedia* at Starfish Bay and Three Fathoms Cove during hot and cool seasons, and hot-cool and cool-hot transitions, pooled across 2014–2016 and expressed in terms of proportion time spent during video recordings (~ 20-min). Behavioural categories are defined in Table S3. Except for sponging, the time spent feeding correlated negatively with all other behaviours (significant Spearman's correlation r_s ranged from − 0.17 to − 0.68, Table S5). Error bars are + SD, and numbers in the legends indicate sample size

Relationship between sponging and waving

Crabs waved predominantly in the hot season as compared to no, or very few, waves observed during the cool season (analysis of deviance on the negative binomial GzLM, $\chi^2_3 = 148.4$, $P < 0.0001$, Fig. S3). Larger crabs waved more than smaller individuals (analysis of deviance on the negative binomial GzLM, $\chi^2_1 = 6.1$, $P = 0.0134$, Fig. 6), but the overall waving rate was variable, ranging between < 0.01 and 0.23 waves s^{-1} during the hot season (Fig. S3). Waving was not randomly distributed in time but appeared to follow sponging events, as a higher-than-expected proportion of sponging events were followed immediately by a wave (slopes between expected and observed proportions were > 1: SFB: slope = 3.3, $P < 0.0001$; TFC: slope = 2.7, $P < 0.0001$; at both sites, the intercept of the linear regression between expected and observed proportions was not different from 0, $P = 0.433$ and 0.973 for SFB and TFC respectively, Fig. 7). When the crab waves, its claws and body are raised to a higher position above the sediment surface. Air temperature at 1 cm above the sediment surface was slightly (− 0.3 ± 0.5 °C, range = − 2.0 to 0.7 °C) but significantly lower than 0.5 cm above the sediment surface during May–Sep 2014 and Jun–Oct 2015 across both sites (paired *t*-test, $t_{141} = -5.9$, $P < 0.0001$, Fig. S4).

A biomimetic simulation of sponging, waving and body temperature

After waving for 60 s, waving robo-crabs' body temperatures were 0.3–1.1 °C lower than still robo-crabs (Table 2, Fig. 8). Increasing the amount of sponged water reduced body temperatures by as much as 0.4 °C during the first 10–30 s after sponging (Table 2), but this effect was reduced to 0.2–0.3 °C after 60–120 s (Table 2), and was not present after 180 s. Waving robo-crabs without sponged water were, however, 0.2–0.9 °C cooler than still robo-crabs with sponged water after 60 s, although no statistical comparisons could be made due to these being two different experiments (Fig. 8).

Discussion

Seasonal patterns in burrow number and behavioural time budget

Scopimera intermedia demonstrated a marked seasonal pattern in activity, with a greater number of burrows and longer activity durations during the hot than the cool season (Figs. 1 and S5). Similar patterns have been recorded for other intertidal species in seasonal environments (Aagaard et al. 1995;

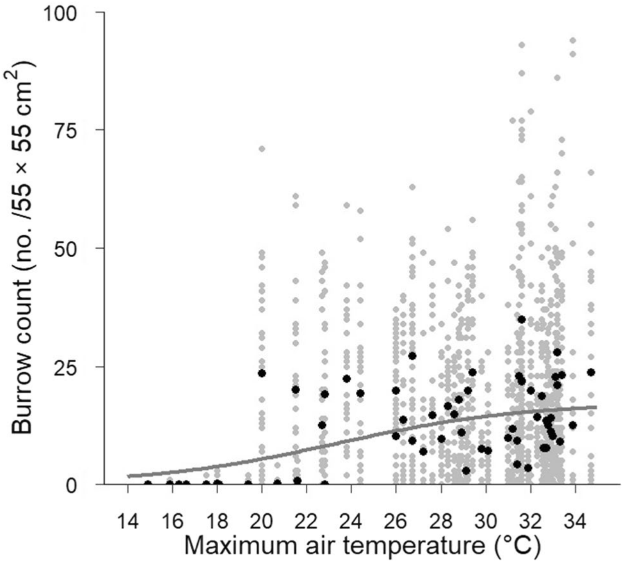

Fig. 3 Relationship between burrow number of *Scopimera intermedia* in Starfish Bay with the maximum air temperature recorded in a nearby weather station by the Hong Kong Observatory (~ 9 km from Starfish Bay). Grey dots are the burrow numbers ($n = 1860$), whilst black dots are the mean burrow numbers on each survey day. Grey line represents the best-fit zero hurdle negative binomial GzLM using maximum air temperature as the sole explanatory variable. Crab burrows were more likely to be present at higher air temperatures (zero hurdle of the negative binomial GzLM, $z = 21.3$, $P < 0.0001$), but, when they were present, their abundances were independent of the maximum air temperature (count model of the negative binomial GzLM, $z = 0.1$, $P = 0.916$)

Gray and Hodgson 1997; Ng and Williams 2006). Whilst such contrasting activity patterns between seasons could be attributable to greater food availability during the hot than cool seasons, the number of crab burrows increased with the local maximum air temperature and, specifically, the crab only emerges from its burrow when the air temperature is above a threshold at ~ 20 °C, as shown by the sudden rise in burrow number on warm days during the cool season (4 days during the cool season in 2015 and 1 day during the cool season in 2016, see Fig. S2). Although the increase in burrow numbers of the crabs during the hot season could be a result of newly settled juveniles, the fact that burrow numbers on warm days during the cool season were comparable to the hot season suggests that environmental temperature plays a dominant role in regulating crabs' activity level and hence emergence from burrows. Behavioural decisions of whether to excavate and emerge from burrows are, therefore, highly temperature dependent, and the reduction in burrow number during the cool season was likely driven by the reduced metabolic rates of crabs at low temperatures which has also been noted for fiddler crabs (Powers and Cole 1976). The number of burrows was, however, variable when air temperature exceeded 20 °C, possibly due to small-scale variations in local environments, such as sediment hydration states which influence burrowing and excavation decisions of *Scopimera* (Sassa and Watabe 2008).

Detailed behavioural time budgets and relationship with air temperature

Variations in environmental conditions, such as the amount of food, length of the activity period, presence of predators and thermal conditions have all been shown to alter optimal behavioural strategies (Caraco et al. 1990; Houston et al. 1993; Houston and McNamara 1999). In the case of *Scopimera intermedia*, the crab showed strong spatial and temporal variations in time partitioning of various behaviours according to local air temperature. In summary, the number of burrows increased, with the crabs devoting more time to conspecific interactions, sponging and waving, at warmer temperatures. Whilst the crabs emerge from the sediment only when the air temperature is > ~ 20 °C, temperatures > 30 °C impact the locomotor performance of the crabs (Hui et al. 2019), and at these warmer temperatures, the crabs spend more time sponging and waving. These multifunctional, thermoregulatory behaviours (see below) enable the crabs, whilst being active on the sediment surface, to maintain body temperatures lower than their lethal limits (~ 39 °C, Hui et al. 2019). The ability to flexibly adjust the time allocated for these behaviours is, therefore, important for the crabs to persist on shores with strong temporal variation in thermal conditions.

The crabs spent most of their time feeding (~ 80%), sponging (~ 10%) and staying inside their burrows (~ 5%) when they were active during emersion periods. It is logical that feeding is the dominant activity since the crabs are not only limited by the tides in their time to feed (as in most intertidal species, Williams and Little 2007) but they are also frequently interrupted by disturbances such as predators or wind, causing alarm or retreat behaviours (Jennions et al. 2003). The proportion of time feeding during the potential activity window was, however, variable between seasons in *Scopimera intermedia*. The crabs spent ~ 90% of their time feeding during the non-reproductive period (the cool season and transition periods when waving is not performed by the crabs), probably enhancing growth and body condition to promote courtship and reproductive success during future reproductive periods (as seen in other intertidal organisms, Martel et al. 1986; Santos et al. 1996). The crabs spent proportionally less time feeding at warmer temperatures during the hot season, however, when the time devoted to other activities such as waving, sponging and interacting with conspecifics increased (see Table S5 for the correlations between these behaviours). The increasing amount of time for these other activities may be driven by a combination of environmental and physiological factors, in which the frequency of conspecific interactions was

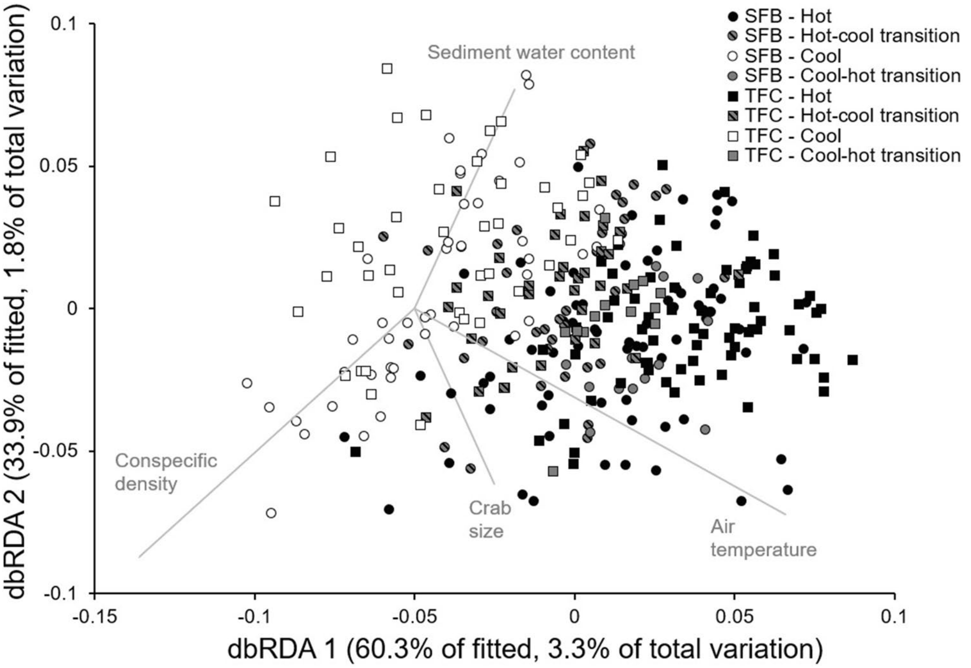

Fig. 4 Distance-based redundancy analysis (dbRDA) biplot of behavioural time budgets of *Scopimera intermedia* with the air temperature at 0.5 cm above the sediment surface, conspecific density, crab size and sediment water content as the explanatory variables in the distance-based linear model. Air temperature (pseudo-$F_{1,322}=7.9$, $P=0.0004$), conspecific density (pseudo-$F_{1,322}=5.2$, $P=0.0079$) and crab size (pseudo-$F_{1,322}=3.0$, $P=0.0431$) significantly altered the crab's behavioural time budget, which was independent of the sediment water content (pseudo-$F_{1,322}=1.9$, $P=0.1228$). In the dbRDA biplot, each point represents the modelled value of the behavioural time budget of an individual crab, ordinated using two principal dbRDA axes. The first axis represents 60.3% of the variation in the fitted model (3.3% of the total variation), with strong loadings of air temperature and conspecific density (0.77 and −0.58 respectively, as shown by the lengths of the overlaying vectors in grey), whilst the second axis represents 33.9% of the variation in the fitted model (1.8% of the total variation), where the loadings of air temperature and conspecific density are −0.48 and −0.58 respectively. $n=324$ across all four seasons in both Starfish Bay (SFB) and Three Fathoms Cove (TFC)

likely to be enhanced by the higher density of crab burrows at warmer temperatures. Warmer sea temperatures also facilitate pelagic larval development (Christy 1989; Suzuki and Kikuchi 1990) and, with the developed condition of the crabs' gonads (Koga 1995) and greater amount of sediment food available (Table S1), the crabs invest more time for reproductive activities and, consequently, less time in feeding during the hot seasons (Caravello and Cameron 1991; Koga 1995; Kim and Choe 2003; Bartolini et al. 2009).

Table 1 Results of the generalized linear model (negative binomial errors with log link) investigating the variation in the sponging rate of *Scopimera intermedia* with sites, air temperature at 0.5 cm above sediments, feeding rate, crab size and the interaction between air temperature and feeding rate. The number of sponging events was treated as the response variable and the time the crabs spent outside their burrows was treated as an offset variable. Coefficients and statistical significances of the model parameters are shown

Parameter	Coefficient	*z*	*P*
Site	−0.20	−4.72	<0.0001
Air temperature	0.07	5.16	<0.0001
Feeding rate	12.71	3.04	0.0024
Crab size	0.58	1.78	0.0766
Air temperature × feeding rate	−0.28	−1.98	0.0478

Possible functions of sponging behaviour?

Behavioural water uptake, such as the sponging behaviour in *Scopimera intermedia* and other deposit-feeding crabs, is critical to facilitate flotation feeding by supplying water to the buccal cavity (Quinn 1980; Maitland 1990). Flotation helps sort organic materials from sediment grains and a supply of water is thus essential for efficient ingestion, and so it seems logical that there is a positive association between feeding and sponging rates in the crabs (Hartnoll 1973; Vogel 1984).

The sponging rate in the crabs increased consistently with the temperature at both sites, indicating a common relationship between this behaviour and air temperature. The increase in sponging rate with temperature was more prominent when the crabs were feeding at a lower rate, suggesting that sponging of the crabs is more temperature dependent

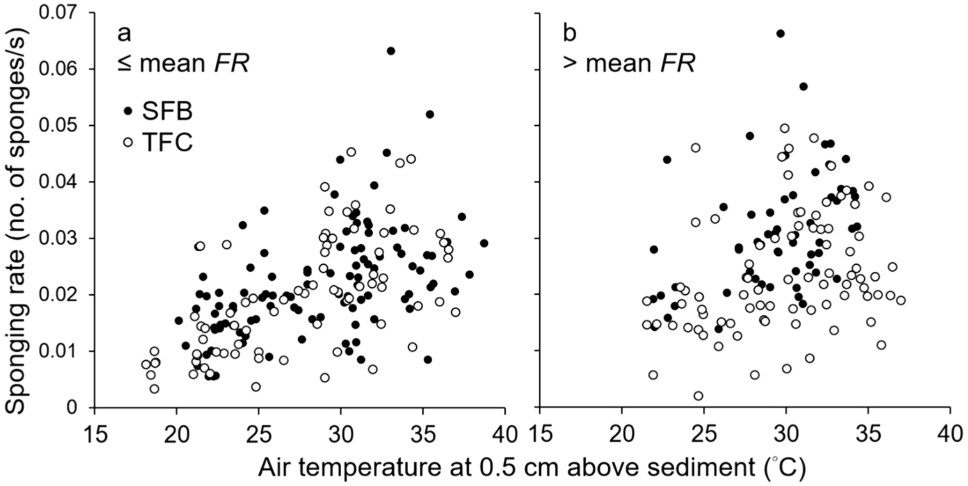

Fig. 5 Relationships between sponging rate (SR) and air temperature when feeding rate (FR) of *Scopimera intermedia* was (**a**) less than or (**b**) higher than the average FR in Starfish Bay (SFB) and Three Fathoms Cove (TFC). The increase in SR with air temperature was dependent on FR, where the positive relationship between SR and air temperature declined when FR increased (a significant air temperature by FR interaction was detected in the negative binomial GzLM, $z = -1.98$, $P = 0.0478$, Table 1). Samples were pooled across 2014–2016 (SFB: $n = 165$; TFC: $n = 159$)

when the absorbed water is replenishing lost water due to evaporation rather than just feeding. Whilst warmer sediment temperatures do not necessarily imply more dry sediments (which is also influenced by particle size, water table height, etc., see Table S6), Gherardi et al. (1999) observed an increase in the percentage of individual *Dotilla fenestrata* sponging at hotter periods of the day (noon and spring tides).

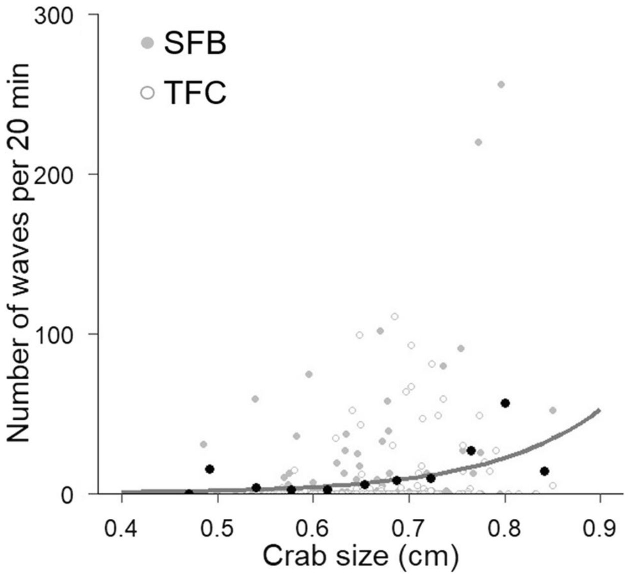

Fig. 6 Variation in the number of waves (during the 20-min video taken) with body size in *Scopimera intermedia* in Starfish Bay (SFB, grey-filled dots) and Three Fathoms Cove (TFC, grey open dots). Black dots represent averaged number of waves per 0.04 cm increment in size, whilst the dark grey line represents the best-fitting GzLM when the number of waves was regressed against size (using a negative binomial error distribution). When seasonal effects were taken into account, the number of waves still increased with crab size (negative binomial GzLM, $z = 2.3$, $P = 0.0241$)

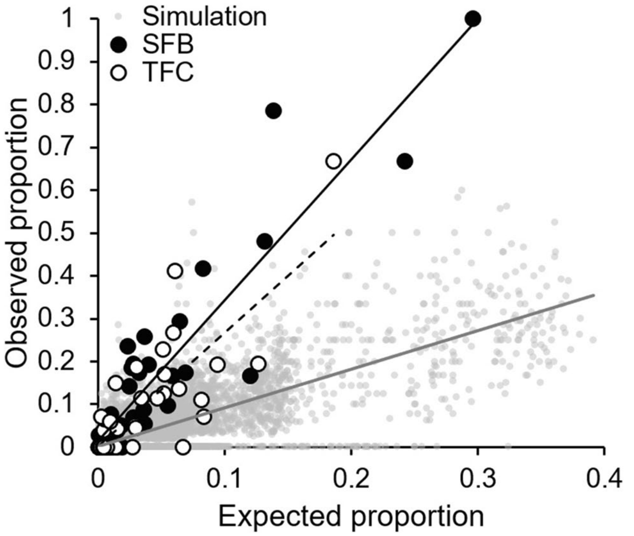

Fig. 7 Observed proportion of sponging followed by waving behaviour (within one second) in *Scopimera intermedia* at Starfish Bay (SFB) and Three Fathoms Cove (TFC), during May–Oct 2014 and Apr–Sep 2015, compared to expected proportion (assuming waving behaviours are random Poisson events). Solid black line represents the regression between observed and expected proportion in SFB ($n = 42$), whilst dashed black line represents such relationship in TFC ($n = 42$), where both slopes were significantly > 1: SFB: slope = 3.3, $P < 0.0001$; TFC: slope = 2.7, $P < 0.0001$). Grey line represents the linear regression between expected and observed proportions of the simulated behavioural data (grey dots), which were obtained using empirical sponging and waving rates ranging from 0.0069 to 0.0633 s^{-1} and 0.0009 to 0.3512 s^{-1} respectively, where sponging and waving were simulated to occur independently and randomly. 100 simulations were conducted for each empirical combination of sponging and waving rates ($n = 84$ combinations from the two sites in total)

Table 2 Linear mixed models testing whether body temperatures of the robo-crabs differed if they were waving or being still (a) or being simulated to sponge with different amounts of water before waving for 10–180 s (b). Treatment (waving or being still/amount of water sponged), air temperature and water temperature (water for sponging, used only for the waving vs being still experiment, see main text) were used as fixed explanatory variables in the model. Robo-crab identity was treated as a random effect. T_{water}, temperature of the water used for sponging; T_{air}, air temperature at ~ 2 cm from the robo-crab during the experiment; Crab, robo-crab identity. Numbers at 'treatment', 'T_{air}' and 'T_{water}' represent their effects (and the associated P values) on body temperatures of the robo-crabs, where the 'treatment' effects are either the temperature reductions of waving compared to still robo-crabs (a) or the temperature reductions when waving robo-crabs were sponged with 0.02/0.04 ml of water compared to waving robo-crabs without simulated sponging (b). Numbers at 'Crab' indicate the variance of the robo-crab identity effect, and the numbers inside parentheses indicate the ratio of such variance vs the residual variance. Numbers in bold indicate statistical significance ($P < 0.05$)

Parameter	Time since waving (s)				
	10	30	60	120	180
a. Effects of waving vs being still					
Treatment (waving)	0.04	−0.08	**−0.28**	**−0.84**	**−1.13**
P	0.530	0.191	**0.0003**	**< 0.0001**	**< 0.0001**
T_{water}	−0.05	−0.04	−0.18	0.00	0.03
P	0.485	0.660	0.0759	0.9798	0.8448
T_{air}	−0.03	0.00	0.06	**0.18**	**0.17**
P	0.259	0.992	0.2123	**0.0103**	**0.0437**
Crab	0.01 (0.25)	0.07 (1.58)	0.07 (1.04)	0.12 (1.52)	0.21 (1.61)
b. Effects of the amount of water sponged					
Treatment (0.02 ml)	−0.13	**−0.13**	**−0.17**	−0.05	−0.10
P	0.0754	**0.0382**	**0.0191**	0.4087	0.119
Treatment (0.04 ml)	**−0.41**	**−0.40**	**−0.33**	**−0.17**	−0.06
P	**< 0.0001**	**< 0.0001**	**< 0.0001**	**0.0108**	0.349
T_{air}	−0.05	**−0.08**	−0.05	**0.11**	0.07
P	0.0814	**0.0079**	0.1585	**0.0181**	0.199
Crab	0.04 (0.53)	0.01 (0.13)	0.01 (0.09)	0.06 (1.02)	0.07 (1.20)

During sponging events, not only does water flow from the sediment surface to the buccal cavity but a proportion of the water also wets the carapace by the 'shoogling' action of the crabs' legs (Maitland 1990). This is consistent with the observations that the proportion of time spent sponging in *Scopimera intermedia* correlated positively with the time spent manipulating its appendages (Table S5), and the crabs were often seen manipulating their appendages immediately after sponging. Such action is likely to enhance evaporation from the carapace and, in combination with the absorption of sediment water cooler than the crabs, individuals of *S. intermedia* able to sponge have lower temperatures compared to those unable to sponge (Hui et al. 2019). On the other hand, by maintaining hydration via sponging, locomotion performances of the crabs (walking, retreating to burrow, etc.) could also be sustained (Weinstein et al. 1994; Levinton et al. 2015). Whilst the crabs' burrows are cooler than the sediment surface and allow the crabs to replenish moisture (Bauchau and Passelecq-Gerin 1988), retreating to the burrow will compromise surface feeding time (Munguia et al. 2017) and, therefore, energy acquisition. Sponging behaviour thus provides an effective alternative for maintaining body temperature and hydration state in addition to retreating to burrows. Sponging is, therefore, a multifunctional behaviour for both feeding and thermoregulation and is a critical component in the behavioural time budgets of *S. intermedia* particularly during the hot season (Hui et al. 2019).

Occurrence and possible functions of waving behaviour

Waving in *Scopimera intermedia* occurred predominately during the hot season but not in the cool season. Apart from being an agnostic behaviour for burrow defence as suggested by Gherardi et al. (1999), waving has also been proposed as a courtship behaviour in sand-bubbler crabs (Henmi et al. 1993), suggesting a possible link to sexual selection, which has been well established in fiddler crabs (Salmon and Atsaides 1968; Backwell et al. 1999).

The occurrence of waving on a shorter temporal scale (seconds to minutes scales), however, was not random but followed sponging events more than would be expected by chance. One of the possible explanations for such postural changes after sponging is to facilitate the redistributions of haemolymph and cardiac outputs, as shown in land crabs (Burggren 1992). The fact that sponging serves a thermoregulatory function (Hui et al. 2019), however, and considering

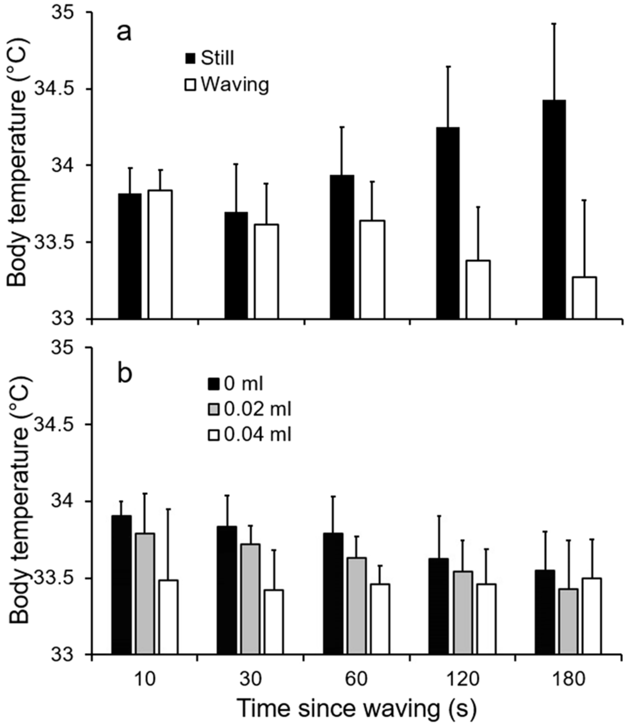

Fig. 8 Variation in body temperatures of biomimetic robo-crabs of *Scopimera intermedia* under different treatments. (**a**) The effect of waving (white bars) or being still (black bars) for 180 s on body temperatures of the robo-crabs after sponging was simulated using 0.02 ml of water. Waving robo-crabs were cooler than robo-crabs being still when waving occurred for > 60 s (linear mixed model, *P* ranging from < 0.0001–0.0003, Table 2). (**b**) The effect of the amount of water used to simulate sponging (0 ml: black bars; 0.02 ml: grey bars and 0.04 ml: white bars) on body temperatures of the waving robo-crabs for 180 s. Waving robo-crabs were cooler if more water was being sponged, until waving lasted for 120 s (linear mixed model, *P* ranging from < 0.0001–0.0382, Table 2). Values are expressed as mean + SD

the fact that temperature at 1 cm above the sediment surface is lower than at 0.5 cm above the surface (a boundary layer effect, Denny and Miller 2011) suggests waving might also be involved in modifying body temperature. Whilst constant muscle shivering/respiration can generate metabolic heat in invertebrates (Heinrich 1974; Pamatmat 1978; Southwick and Heldmaier 1987), the robo-crab experiments were unable to account for such an effect so the reduction in robo-crabs' body temperatures could only be attributable to purely physical, passive processes without any physiological regulation. Based on the observation that waving followed sponging events more than expected by chance, however, we hypothesize that waving can contribute to thermoregulation in living crabs by lowering their operative temperatures more than the metabolic heat they generate when they wave after sponging. This hypothesis is supported by observations in other species where positions/movements of body parts are suggested to reduce body temperatures via enhanced convection and evaporative cooling, such as the posing behaviour in semi-terrestrial crabs and gular flutter in birds (Bartholomew and Lasiewski 1968; Maitland 1990). Observation of females waving in some fiddler crab species (von Hagen 1993) could also be explained by this hypothesis, where such waving displays, in contrast to those carried out by males, are less likely to be involved in agonistic or courtship interactions (von Hagen 1993). Since waving is performed by a large number of soft shore crab species for courtship and territorial signals (notably fiddler crabs, Kitaura and Wada 2006; Murai and Backwell 2006), the potential thermoregulatory benefits of waving might be key to understand the evolution of such behaviour under multiple selection pressures driven by the need to multi-task within a limited activity window.

If waving is indeed involved in thermoregulation then such function questions traditional interpretations of the trade-offs between survival and reproductive success. The cost of sexually selected traits could, for example, be overestimated when the traits are also beneficial to survival or bear little cost compared to the functions they achieve (McCullough and Emlen 2013). In fact, higher survival and longevity have been found in males with more intense investment in sexually selected traits across a variety of taxa, suggesting that the ability to sustain more elaborate sexually selected traits may result in better body conditions which improve the chance of survival (Jennions et al. 2001) or pleiotropic effects acting on sexually selected traits resulting from other survival-related, phenotypic traits (Ducrest et al. 2008). As such, therefore, sexually selected traits may enhance/act as the precursor for the evolution of multifunctionality in variable environments (Candolin and Heuschele 2008), when the reproductive costs of such traits can be compensated by their benefits for individual survival.

In summary, behavioural time budgets of *Scopimera intermedia* vary both spatially and temporally at multiple scales, according to seasonal patterns and local environmental conditions. Whilst feeding is the dominant behaviour, contributing to most of the variation in the behavioural budgets, air temperature governs the overall activity level of the crabs, and the need to thermoregulate efficiently on tropical shores appears to drive the multifunctionality of sponging and waving behaviours. Sponging rate increased with both temperature and feeding rate and has been shown to be a multifunctional trait to aid both feeding and thermoregulation. Waving by the crabs in the hot season occurred immediately after sponging events more than expected by chance, and such behaviour physically lowered body temperature by ~ 1 °C. Though the costs and benefits of these behaviours were not quantified in the current study, any additional benefits achieved at minimal costs would be highly advantageous when activity periods are limited by environmental factors and, therefore, multifunctionality should be evolutionarily selected and possibly widespread in highly dynamic and harsh environments such as on tropical shores.

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Declarations

Ethics approval/consent to participate Not applicable.

Consent for publication All authors agree to publish this MS.

Competing interests The authors declare no competing interests.

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