Are "early birds" bolder? Early daily activity is not correlated with risk-taking behaviour in a major invasive species

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ABSTRACT

Daily behavioural rhythms provide ecological advantages with respect to exploitation of food resources and avoidance of predation and recent studies suggested that timing of activity could form a behavioural syndrome with risk-taking behavior. Moreover, the role of daily activity rhythms in biological invasions is unknown. Here, we investigated whether early nocturnal activity (the relative amount of locomotor activity displayed early in the night) and risk-taking behaviour (i.e. response to a scare stimulus) form a behavioural syndrome in a major invasive species, *Pacifastacus leniusculus*. We first characterized daily rhythms of locomotor activity over five days under controlled laboratory conditions and then scored the response to a scare stimulus across two different contexts (neutral and food) over two subsequent days. Crayfish displayed overall daily activity rhythms peaking in the first four hours of darkness. Both, early nocturnal activity and risk-taking behaviour showed consistent inter-individual differences with repeatability scores of 0.39 and 0.36, respectively. However, the two behavioural traits were not correlated as in a behavioural syndrome. We argue that a behavioural syndrome could be adaptive during the early stages of invasion but may lose importance once populations are established. By uncoupling early nocturnal activity and risk-taking tendency, individuals of established populations may be less susceptible to predation. We suggest that daily activity rhythms and risk-taking behavior can be important traits in understanding the adaptations underlying biological invasions or other processes of contemporary evolution.

Keywords: crayfish, *Pacifastacus leniusculus*, daily activity rhythms, personality, behavioural syndrome

INTRODUCTION

The behaviour and physiology of almost all animal taxa is characterized by daily activity rhythms (Dunlap and others 2004). Daily activity rhythms are usually synchronized to the day-night cycle, but other environmental or social factors can also play a role (Castillo-Ruiz and others 2012; Hut and others 2012). Daily behavioural rhythms provide ecological advantages with respect to exploitation of food resources and avoidance of predation (Helm and others 2017; Kronfeld-Schor and others 2013; Kronfeld-Schor and Dayan 2003). For example, in the desert golden spiny mouse (*Acomys russatus*) individuals that arrive earlier to a foraging patch gain more food than individuals that arrive later (Levy and others 2012). In zebrafish (*Danio rerio*), individuals displaying higher locomotion early in the activity period were also more risk-taking than individuals that were less active (Tudorache and others 2018). An increase of risk-taking behaviour is usually associated with an increased access to food resources and a decrease of survival towards predators (Lima and Dill 1990; Smith and Blumstein 2008). Therefore, the amount of locomotion displayed early in the activity period could be a fitness-related trait similar to chronotypes (Helm and others 2017).

Chronotypes are consistent inter-individual differences in the onset of activity with respect to a reference time point (Helm and others 2017), and they can have fitness consequences. For example, a recent study suggests that razorfish (*Xyrichtys novacula*) with early-active chronotypes could experience higher mortality from fisheries than late chronotypes (Martorell-Barceló and others 2018). However, daily activity rhythms may not only differ in the onset (i.e. chronotypes) but also in the relative amount of activity displayed at particular time periods. A recent study on zebrafish (*Danio rerio*) showed consistent inter-group differences in the relative amount of locomotion displayed early in the activity period (Sbragaglia and others 2019). Interestingly, elevated locomotion displayed early in the activity period was found to be linked to an increase of risk-taking behaviour in an evolutionary context (Sbragaglia and others 2019), suggesting an adaptive value for such combination of traits.

Animal behaviour plays a paramount role in biological invasions (Holway and Suarez 1999). Personality traits (i.e. consistent inter-individual differences in behaviour; Carere and Maestripieri 2013) such as risk-taking behaviour can determine the success or failure at different stages of biological invasions (Canestrelli and others 2016; Carere and Gherardi 2013; Chapple and others 2012; Juette and others 2015). By contrast, the role of daily activity rhythms in biological invasions is unknown. A key to the understanding of the process of biological invasion could be the finding that successful invaders often display correlation among a suite of consistent behavioural traits (i.e. behavioural syndrome; Chapple and others 2012; Sih and others 2004). For example, a behavioural syndrome between aggression and foraging activity is suggested to enhance the ability of the signal crayfish (*Pacifastasus leniusculus*), a major invasive species, to attain high densities and a negative impact on invaded communities (Pintor and others 2009).

Here, we test the hypothesis that early daily locomotor activity and risk-taking behaviour form a behavioural syndrome in *P. leniusculus*, a commercially harvested crayfish which is one of the most invasive species in Asia and Europe (Gherardi 2017; Larson and others 2012; Lodge and others 2000). We predict that early daily locomotor activity and risk-taking behaviour are consistent behavioural traits and that these traits are positively correlated.

MATERIALS AND METHODS

Sampling and acclimation

Signal crayfish (*P. leniusculus*) were sourced from a commercial supplier (Flowers Farm Lakes, Dorchester, UK). Prior to experiments, crayfish were kept in communal tanks (60x45x25 cm) in sex-segregated groups of 10-15 individuals. The light-darkness cycle was 12-12 hours and water temperature was kept at 15±1 ˚C. Crayfish were fed a mixed diet of prawns, peas and carrots.

We used a total of 48 male crayfish (cephalothorax length: 38.2 ± 3.2 mm). We conducted a total of six experimental trials from May to December. We ran each trial with 8 randomly-selected crayfish in an experimental room where light was under control (light-darkness cycle of 12-12 hours). Light was provided by fluorescent lamps at an intensity of 0.25 Klux. During the darkness period dim red light (0.01 Klux) was

provided by monochromatic LEDs to allow video recording. Water temperature was kept at 15±1 C.

The experimental setup consisted of 8 separated glass aquaria (45x30x25 cm). We equipped each tank with a recirculation pump (provided with a filter). We glued white opaque tissue at the bottom of the tank to create a suitable surface for the crayfish to walk on and the appropriate background to apply video imaging analysis (see below). We placed a shelter (12 cm long) in each tank, cutting transversally a PVC pipe of a diameter of 8 cm. We covered the sides of each tank with white fabric to eliminate any visual disturbance from neighboring tanks and we placed the tanks behind light proof curtains to eliminate any kind of light contamination.

Experimental trials

We left the crayfish undisturbed during the first stage of the experiment recording a time-lapse video (10 s frequency) that we used to track daily rhythms of locomotor activity (see below). Next, during the second stage we exposed crayfish to a scare stimulus in two different contexts (neutral and food contexts) to evaluate their level of risk-taking behaviour. We applied the scare stimulus during two consecutive days (one for each context) moving a plastic black board (15x15 cm) forward and back two times over the surface. During the neutral context nothing was changed in the experimental tank, while during the food context a small piece of prawn was added after light-off. The scare stimulus was applied within two hours after light-on only when the crayfish was moving or approaching the food (displacement for more than 1 body length), otherwise the stimulus was not applied. A full time 5-min video was recorded to manually score the risk-taking behaviour.

Data analysis of locomotor activity

We quantified daily locomotor activity rhythms of crayfish using video image analysis. 4 USB webcams (1 webcam for 2 aquaria) were placed behind light proof curtains on the top of the aquaria. We managed frame acquisition using open source camera security software (ispy: http://www.ispyconnect.com). The automated video image analysis was performed in Matlab 7.1 (The MathWorks, Natick, USA), adapting a compilation of a script with the image processing toolbox previously used in several

studies with decapods crustaceans (Sbragaglia and others 2013a; Sbragaglia and others 2015a; Sbragaglia and others 2015b). The final output was a time series of the movement of each crayfish (cm) at a frequency of 10 s.

Data analysis of individual behaviour

The total individuals used were 42 because some video recordings failed. A trained operator (VS) observed the 5-min full time videos to score the reaction of crayfish to the scare stimulus. Reaction to the scare stimulus was quantified as the time period (in seconds) that a crayfish spent moving (locomotion or evident movement of the chelae) after the introduction of the plastic board. Few animals remained in the shelter (6/42 in the neutral context and 5/42 in the food context) during the selected time period (two hours within light-off) in which we applied the stimuli. We scored this behaviour with a 0 because our interpretation is that remaining in the shelter implies a low level of risk-taking behaviour.

Statistical analysis

Time series of locomotor activity were binned at 10 min and Chi-square periodogram (Sokolove and Bushell 1978) was used to scan for periodicity and the percentage of variance (%V) was reported as a measure of rhythms' robustness (Refinetti 2006). Waveform analysis was carried out to quantify the amount of locomotor activity displayed within four hours after light-off (i.e. early nocturnal activity). Early nocturnal activity was calculated for each of the five days as the proportion between the percent of locomotor activity in relation to the percent of time (more details and examples are provided in Figure 1). This provides a quantitative measure of activity within a defined 4-hour time period respect to the overall activity (see also; Sbragaglia and others 2013b).

Although risk-taking measurements were count data (i.e. seconds spent moving), the range of values was overall high (0-280) and a power transformation can be used as alternative approach to stabilize variance with negligible effect on the parameter estimates (O'hara and Kotze 2010). Therefore, daily values of early nocturnal activity and the scores for risk-taking behaviour in each context were transformed by finding the exponent (lambda), which made the values of the response

variable as normally distributed as possible with a simple power transformation. Repeatability was calculated across time (5 days) for early nocturnal activity and across contexts (neutral and food) for risk-taking behaviour (Nakagawa and Schielzeth 2010). Model fitting was examined by checking normality of residuals and plotting theoretical quantiles vs. standardized residuals. The correlation among the average early nocturnal activity and risk-taking behaviour was calculated with the non-parametric Kendall's coefficient of concordance.

Periodogram and waveform analysis were performed using the software Eltemps (www.el-temps.com). All other analyses were conducted using R 3.3.1 (https://www.R-project.org/) and the following additional packages: rcompanion" (https://CRAN.R-project.org/package=rcompanion), "rptR" (Stoffel and others 2017). In all cases, we used a 95% confidence interval.

RESULTS

Locomotor activity of crayfish during the first stage of the experiment indicated robust daily activity rhythms (mean robustness ± standard deviation = 48±14 %; n = 42) with more activity concentrated during darkness (70±14%; Fig. 1a). Early nocturnal activity ranged from 1.09 to 3.36 (i.e. the crayfish displayed a 3.36 times more locomotor activity within 4-hours after light-off with respect to overall activity; fig. 1b). Early nocturnal activity was repeatable over time (R = 0.39 [0.24 – 0.53]; $p < 0.001$; n = 42; Fig. 1d). During the 5-min videos the time crayfish spent moving ranged from 0 to 280 s in the neutral context, while it ranged from 0 to 260 s in the food context. Risk-taking behaviour was significantly repeatable across contexts (R = 0.36 [0.07 – 0.59]; $p < 0.05$; n = 42; Fig. 1e). Early nocturnal activity did not show significant correlations with risk taking behaviour both in the neutral ($r_\tau = 0.16$; $p = 0.151$; Fig. 2) and food context ($r_\tau = -0.05$; $p = 0.664$; fig. 2). Finally, early nocturnal activity was not correlated with the central tendency of locomotor activity (mesor; $r_\tau = -0.07$; $p = 0.515$).

DISCUSSION

The importance of consistent inter-individual differences in the timing of activity has recently been highlighted with respect to the onset of activity ("chronotypes"; Helm and others 2017). In our study we provide evidence that the relative amount of

locomotion displayed early in the activity period can also show consistent inter-individual differences. Daily locomotor activity rhythms have a high degree of plasticity. For example, temporal niche switching (i.e. shifts in the timing of daily locomotor activity) has been suggested as a strategy to maximize survival in response to environmental changes both in endotherms and ectotherms (Chiesa and others 2010; Hut and others 2012; van der Vinne and others 2019). Our results suggest that consistent inter-individual differences could be an additional factor in shaping the ecological significance of biological rhythms. Indeed, behavioural ecologists have already recognized that both consistent inter-individual differences (i.e. personality) and individual plasticity must be considered as complementary aspects of individual phenotypes (Dingemanse and others 2010). It must be noted that the early nocturnal activity measured here does not correlate to the mean level of overall activity (i.e. the central tendency of locomotor activity; see Fig. 1a-c).

Our results provide the first in-depth characterization of daily locomotor activity rhythms of *P. leniusculus*, showing an overall peak of activity in the first hours of darkness (early nocturnal activity). Previous studies already showed that *P. leniusculus* is a nocturnal species (Edmonds and others 2011; Nyström 2005; Thomas and others 2016), but a clear daily activity pattern was never recorded for this major invasive species. The evolution of early nocturnal activity could possibly be related to foraging opportunities as demonstrated in other nocturnal decapod crustaceans (e.g. Aguzzi and others 2015; Sbragaglia and others 2013b). Interestingly, we showed that the consistent inter-individual differences in early nocturnal activity account for 39% of the phenotypic variance across time. Similarly, consistent inter-individual differences in risk-taking behaviour account for 36% of the phenotypic variance across contexts. The degree of consistency corresponds to personality traits of other species in a wide range of animal taxa (Bell and others 2009).

The main hypothesis of our study must be rejected because we did not find a behavioural syndrome between early nocturnal activity and risk-taking behaviour. Crayfish with a higher early nocturnal activity could have advantages in finding and exploiting food patches; however, higher activity could increase exposure to predators (Lima and Dill 1990). Indeed, *P. leniusculus* exposed to fish predators spent less time out of the refuge at night than individuals not exposed to predators (Nyström 2005).

Such trade-off could explain the adaptive value of the lack of a behavioural syndrome between early nocturnal activity and risk-taking behaviour, suggesting that a common architecture (e.g. pleiotropic genes or common neural pathways) between these traits is unlikely. However, previous results on zebrafish indicated an adaptive value of a behavioural syndrome between these two traits (Sbragaglia and others 2019; Tudorache and others 2018). Decapod crustacean are poorly represented in the studies on animal personality and behavioural syndromes in comparison to fishes, birds and mammals (Gherardi and others 2015). Therefore, we lack comparative studies to understand the general ecological significance of such behavioral syndrome in nocturnal crustaceans.

Biological invasions are often characterized by contemporary evolution (Colautti and Lau 2015; Reisinger and others 2017). For example, common gardens experiments with the rusty crayfish (*Orconectes rusticus*) indicated trait divergence between native and invaded range populations (Sargent and Lodge 2014). In particular, individuals from the invaded populations had faster growth rates and higher survival than individuals from the native range (Sargent and Lodge 2014). Similarly, our results could be explained according to an evolutionary scenario associated to the invasion process (Chapple and others 2012). Individuals used in this study were obtained from Dorset (Southern UK) where the presence of *P. leniusculus* was already reported more than 40 years ago (Guan and Wiles 1997; Holdich and others 1999). A behavioural syndrome between early nocturnal activity and risk-taking behaviour could have an adaptive advantage during the first stages of invasion, but may lose its adaptive value once crayfish populations are well established. For example, *P. leniusculus* collected at the invasion front in Croatian rivers showed lower level of intra-specific aggression than individuals from the core population, suggesting that a decrease in aggression is maladaptive once the population is established (Hudina and others 2015). Indeed, the sequential stages of invasion could have different selection landscapes that may erode behavioural syndromes (Chapple and others 2012).

A recent study, simulating fisheries-induced evolution, showed that life-history traits, early activity and risk-taking behaviour are under selection in population where smaller individuals are selectively harvested (Sbragaglia and others 2019). Although evolutionary adaptations in response to fisheries (Heino and others 2015; Uusi-Heikkilä

and others 2015) and biological invasions (Colautti and Lau 2015; Suarez and Tsutsui 2008) are well known, possible common patterns have seldom been explored. Future studies could benefit from integrating such fields in order to understand the underpinning mechanisms driving contemporary evolution of behavioral syndromes.

Ethical statement

All experiments were conducted at the University of Hull and were approved by the Ethics committee of the Department of Biological Sciences (approval number U035).

Data accessibility

Data will be available on Dryad (https://datadryad.org) upon acceptance of the paper

Authors' contribution

TB and VS conceived the idea; VS run the experiments and analyzed the data; VS led the writing of the manuscript with the inputs of TB. VS and TB agreed to be held accountable for the content therein.

Competing interest

We declare no competing interests

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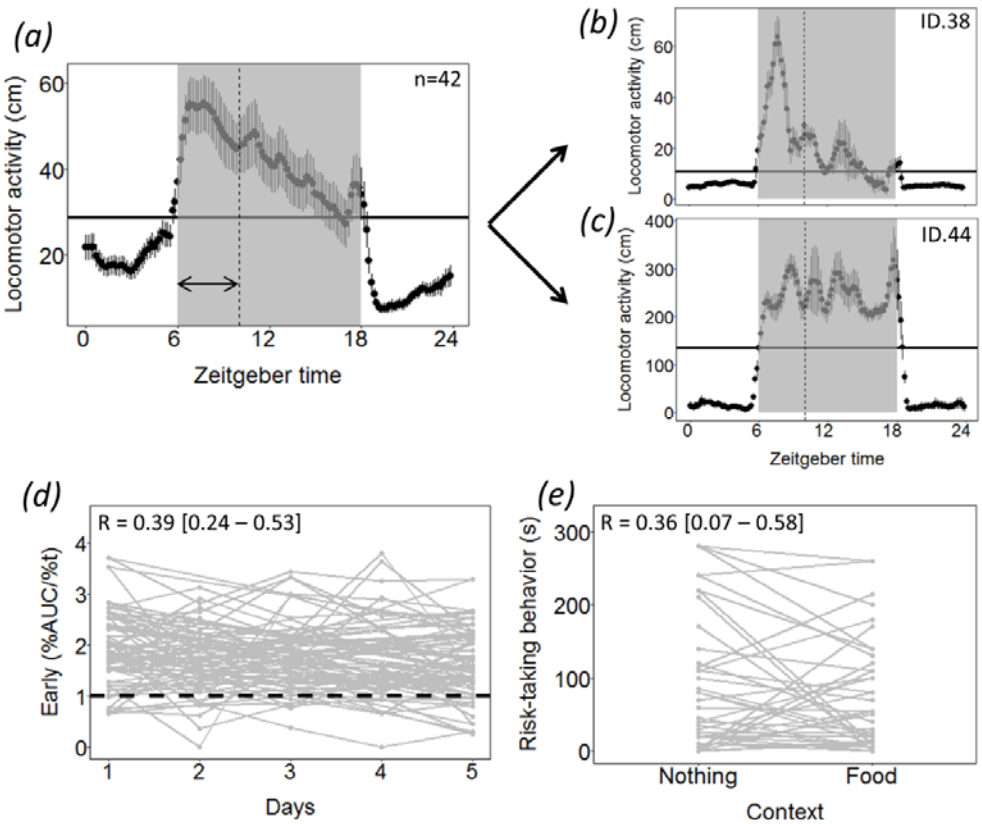

Figure 1 – Daily activity rhythms and risk-taking behaviour. (a): Average daily locomotor activity is presented for all individuals together with standard errors (vertical bars) and the midline estimating statistic of rhythm (i.e. mesor, the central tendency of locomotor activity; horizontal line). The vertical dashed line and the double-ended arrow represent the first four hours of darkness where we calculated the proportion between the percent of locomotor activity in relation to the percent of time (%AUC/%t). The grey areas represent darkness hours. (b-c): two representative examples of daily activity rhythms, ID38 (early %AUC/%t = 3.36) and ID44 (early %AUC/%t = 1.77). (d-e): Repeatability of early activity across five days and risk-taking behaviour across contexts (n=42). The horizontal dashed line represents a threshold and values above 1 indicate that locomotor activity is mainly displayed during the first four hours of darkness.

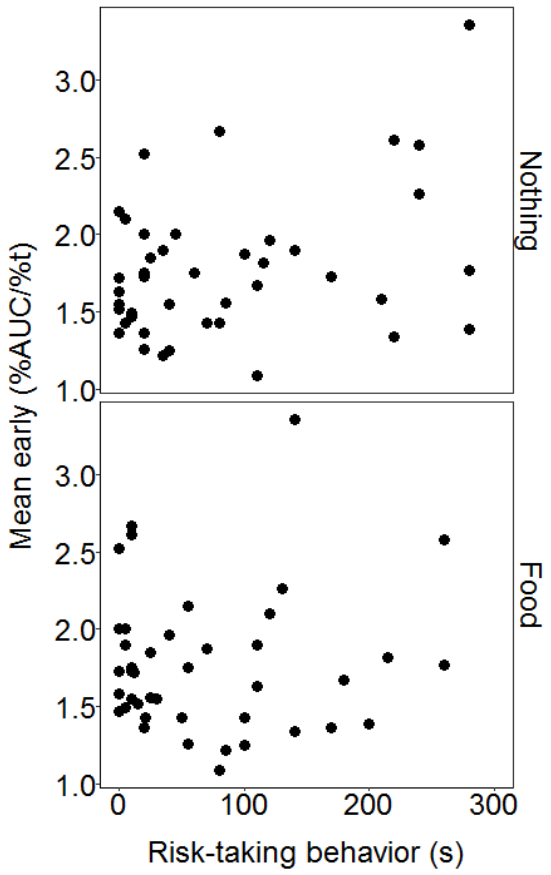

Figure 2 – Plot of risk-taking behaviour measured in two different contexts (Nothing and Food) against mean early-active phenotypes (n=42).