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Habitat use and dispersal of the invasive crayfish *Procambarus clarkii* in ephemeral water bodies of Portugal

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Abstract
We used radio-telemetry to analyze habitat use and dispersal of the invasive crayfish *Procambarus clarkii* in the extreme environmental conditions of a temporary river in southern Portugal. The rationale of this study was that an understanding of the properties that make this species a successful invader can be of help for the conservation of freshwater biodiversity. The results showed that: (1) crayfish displaced at a similar rate (ranging 2.5–38 $m\,d^{-1}$) as other European populations; (2) movement was faster at night; (3) crayfish movement had no clear environmental correlates, except for water temperature; (4) peaks of more intense locomotion were intercalated with longer periods of slow or null speed; and (5) *P. clarkii* did not excavate burrows in the study habitat, but took refuge under boulders and most often occupied complex microhabitats (e.g., vegetated sections of the river). The conclusion was that, notwithstanding their extreme conditions, ephemeral water bodies in southern Europe are highly susceptible to invasion by *P. clarkii*.

Keywords: *Invasive crayfish, dispersal, habitat use, ephemeral water bodies,* Procambarus clarkii, *southern Europe*

Introduction

Much attention is directed today to the changes induced worldwide by species introduced by man outside their natural range. Although, in some cases, non-indigenous species can be beneficial to man, several behave as invaders (Holdich 1988) provoking a loss of biodiversity (Diamond and Case 1986, Vitousek et al. 1996, Sala et al. 2000) and an increased "biotic homogenization" of the invaded habitats (Lodge 1993). Due to the strong affinity of humans to water for commercial, transportation or recreational reasons, and the

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relative ease of dispersal of aquatic species, freshwater biota are particularly vulnerable to non-indigenous and invasive species (Lodge et al. 1998, Beisel 2001).

The red swamp crayfish, *Procambarus clarkii* (Girard 1852), is a paradigmatic example of a freshwater invader (Gherardi and Holdich 1999), its invasive potential being related to a number of biological, ecological, and ethological features that include early maturity, rapid growth rate, high fecundity, disease resistance, plastic life history traits, omnivory, and active dispersal capability (Lindqvist and Huner 1999). The dynamics of invasion by this species has been thoroughly documented by several authors (reviewed, e.g., in Gutiérrez-Yurrita et al. 1999). Once translocated for different reasons (e.g., aquaculture, commerce of live crustaceans, baits, pets) from its natural range (north-eastern Mexico and south-central USA; Hobbs 1989) to as many as 15 states in the USA and 25 other countries (Huner 1977, 1988, Huner and Avault 1979, Hobbs et al. 1989), crayfish have often escaped from farm ponds and colonized natural water bodies. Today, this species is one of the major threats to indigenous crayfish species (Gherardi and Holdich 1999).

P. clarkii was successfully introduced into Spain in 1974 and first recorded in Portugal at the end of the 1970s (Gutiérrez-Yurrita et al. 1999), its natural dispersal across the border with Spain being facilitated by translocation by Spanish fishermen (Gutiérrez-Yurrita et al. 1999). By the middle of the 1980s, the species was found throughout the entire hydrographic basin of the Guadiana River (south-eastern Portugal) (Adão 1992), including several temporary rivers and streams of the area.

Previous studies (Gherardi et al. 2002, Ilhéu et al. 2003) have shown that several behavioral traits of *P. clarkii* made its colonization of extreme environments possible. It was suggested that crayfish did not aestivate during the dry period. Their activity appeared to be intercalated with sedentary phases, when crayfish hid inside burrows. These studies underlined that burrows are fundamental resources in their function of keeping crayfish body temperature below lethal limits (other functions in Huner and Barr 1991). However, an analysis of the distribution of this species in southern Portugal (M. Ilhéu, unpubl. rep.) revealed that several water bodies colonized by dense populations of *P. clarkii* have sediment soil composition that limits burrow construction (Correia and Ferreira 1995, Barbaresi et al. 2004a, b).

In the present study, we gathered information about habitat use and spatial behavior of this species in extreme environments characterized by high temperatures and low water levels. The purpose was to increase our understanding of the properties that make *P. clarkii* a successful invader with the rationale that such a knowledge could help conserve freshwater biodiversity. Radio-telemetry was used to analyze dispersal capability and habitat occupancy of a population of *P. clarkii* inhabiting a temporary river in southern Portugal.

Methods

Study area

The study was conducted at the beginning of the dry period (June 29–July 8, 2001) in a pool (800 m^2 10–60 cm deep) of the Degebe River, a first-order tributary of the Guadiana River in south-eastern Portugal. The Degebe is a temporary river that flows over metamorphic rocks of lower Palaeozoic origin. By temporary rivers, we mean "lotic systems that cease to flow for periods exceeding three months" (Giller and Malmqvist 1998). A preliminary analysis of the substratum of the study area showed that its composition varies from large boulders on exposed bedrock to cobbles, sand (79%), and gravel (20%), silt and clay being practically absent in the sediment (less than 1%). As a consequence, the ratio measured

between Sc/Sg (weight of silt plus clay divided by weight of sand plus gravel) was on average lower (0.046, SE = 0.004, $n = 8$) than the critical value for crayfish to excavate burrows (0.1–0.2) (Correia and Ferreira 1995).

The pool under study was surrounded by pasture-land and was characterized by several common species of aquatic macrophytes, such as *Paspalum paspalodes*, *Scirpus lacustris*, *Juncus* sp., *Thypha latifolia,* and *Carex* sp. Before the study commenced, the pool was mapped by an experienced surveyor for the distribution of aquatic macrophytes, of boulders and of other possible refuges for crayfish, as well as of open substrata. In the study area, potential predators of crayfish were the otter (*Lutra lutra*), the genet (*Genetta genetta*), the polecat (*Mustela putorius*), the beech-marten (*Martes foina*), and the white stork (*Ciconia ciconia*) (M. Ilhéu, personal communication).

Radio-telemetry data

Five mature, non-berried females (cephalothorax length: 56.5–60.5 mm) and five Form I males (cephalothorax length: 51–62 mm) were tagged with individual radio-transmitters (Televilt International, Sweden). The transmitters (type TW-4, Biotrack, Wareham, UK), powered by one Ag392 battery and encapsulated in electrical resins, emitted a pulsed signal at a frequency of 150–151 MHz spaced by a minimum of 10 KHz that allows for individual identification of crayfish. Transmitter size was 18 mm in diameter (plus a 16 cm long whip antenna) and 7 mm in height. The overall mass was 1.2 g, corresponding to about 5% of an adult mass. This is a lower tag weight: body weight ratio than used in other telemetry studies on, e.g., river crabs (Gherardi et al. 1988), lobsters (Smith et al. 1998), *P. clarkii* (Gherardi and Barbaresi 2000, Gherardi et al. 2002) and other crayfish species (Robinson et al. 2000, Bubb et al. 2004). Epoxy resin was used to attach the transmitters to the crayfish cephalothorax. Specimens were retained in a tray of water for about 15 min until the epoxy set, and then were returned as close as possible (<0.5 m) to the site of capture. We are confident that the equipment did not interfere with crayfish activity; in fact, on release all tagged crayfish moved freely, behaving similarly to untagged individuals. Moreover, radio-tracked crayfish were able to hide inside shelters and under rocks.

The radio receiver (RX-98) had a 2-MHz band width and was supplied with a foldable directional antenna attached to the housing. The position of every crayfish was recorded using a grid system superimposed on the study area by an experienced observer wading in the river. To obtain an estimate of diurnal and nocturnal movement, records were taken twice a day, i.e., at sunrise (at about 06:00) and at sunset (at about 21:00), obtaining a total of 22 radio-fixes per individual over 10 days. A preliminary test had shown that the error in detecting the position of a crayfish averaged 50 cm and that wading did not affect crayfish behavior. During each visit, we also noted whether crayfish were in/out of the water, and the microhabitat occupied (among vegetation, under a boulder or in the open). We recorded water temperature (using a mercury thermometer) and dissolved oxygen concentration (using an Ati Orion 810 Dissolved Oxygen meter).

For each individual, we computed diurnal and nocturnal displacements (i.e. the distance covered between sunrise and sunset and between sunset and sunrise, respectively), the total displacement (TD) (i.e., the sum of diurnal and nocturnal displacements performed during the whole tracking period); and the final displacement (FD) as an estimate of crayfish dispersal (i.e. the distance between the release and the end points). To compare displacements between day (15 h) and night (9 h) we analyzed the ratio between diurnal/nocturnal displacement and time (relative displacement). Relative displacement was also used to compare TD among animals and between sexes and to analyze the relationships between

displacement and temperature or dissolved oxygen concentration. In fact, the intervals between subsequent fixes differed, even if slightly, among animals. Signals from two individuals (1 male and 1 female) ceased after two days of recording due to transmitter failure; therefore, data from these two crayfish were excluded from the analysis.

Statistical analyses

We followed the recommendations and the procedures found in Zar (1984) and Siegel and Castellan (1988). We applied Repeated Measures ANOVA (statistic: F) to locomotion speed data to correct for the temporal auto-correlation that arises from repeated measurements and to prevent temporal pseudo-replication (Milliken and Johnson 1992). Measures of dispersal were compared between independent samples by Mann-Whitney tests (statistic: U) and Student's t-tests (statistic: t). G-tests adjusted by William's correction (statistic: G) were used for frequency data and Pearson tests (statistic: r) for parametric measures of correlation for distance vs. time and speed vs. abiotic parameters of the habitat. For every individual, the occupancy of different microhabitats was assessed using Bonferroni simultaneous confidence intervals (Neu et al. 1974, Byers et al. 1984). Text gives mean values $\pm$ standard error. P values of less than 0.05 were considered statistically significant.

Results

Total displacement

Table I shows the absolute and relative TD of each crayfish, numbered on the basis of the transmitting frequency. Relative TD did not differ either among specimens ($F = 1.871$, $df = 6$ and 166, NS) or between sexes (females: $34.4 \pm 7.3\,\mathrm{cm\,h^{-1}}$, $n = 4$; males $32.3 \pm 8.5\,\mathrm{cm\,h^{-1}}$, $n = 4$; $F = 0.160$, $df = 1$ and 6, NS). However, we found a significant difference in the relative displacement between diurnal and nocturnal hours ($F = 6.499$, $df = 1$ and 6, $p < 0.05$), on average all crayfish dispersing further at night ($45.0 \pm 9.8\,\mathrm{cm\,h^{-1}}$) than during the day ($21.6 \pm 3.9\,\mathrm{cm\,h^{-1}}$). The relative TD in females was negatively correlated with water temperature (20.2–30.0°C) ($r = -0.229$, $df = 82$, $p < 0.05$; in males: $r = -0.110$, $df = 82$, NS). No correlation was found on the contrary between the relative TD and the dissolved oxygen concentration (31.6 and 82.8% saturation) (females: $r = -0.215$, $df = 82$, NS; males: $r = -0.101$, $df = 82$, NS).

Table I. Details of radio-tracked crayfish. # = Frequency of radio-transmitters (in kHz). CL = Cephalothorax length. TD = Total displacement. Radio-fixes were 22.

#	Sex	CL (mm)	Absolute TD (m)	Relative TD ($\mathrm{cm\,h^{-1}}$)
034	f	57.6	50.3	20.7
055	f	56.5	29.5	13.6
087	f	56.9	83.0	36.7
126	f	60.5	153.4	66.5
045	m	62.0	63.0	24.9
066	m	53.5	39.8	15.6
117	m	57.0	71.2	30.1
138	m	49.2	136.0	58.6

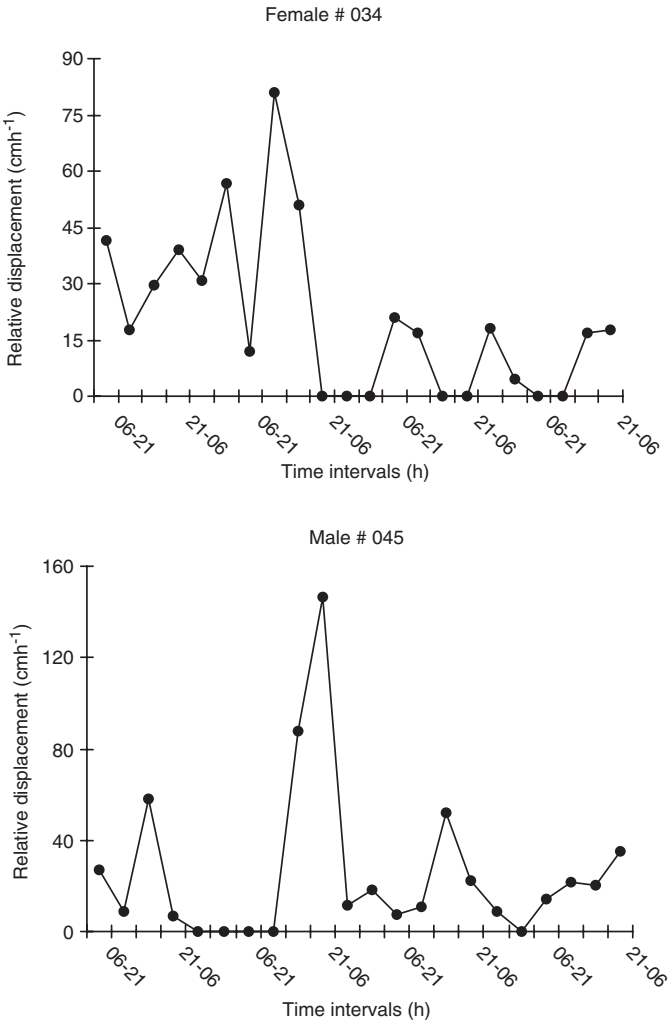

Figure 1. Relative displacement (in $\mathrm{cm\,h^{-1}}$) with time in two radio-tracked crayfish (numbered from the frequency of their radio-transmitters, in kHz).

Movement patterns

We found peaks of high activity and periods with slow or null activity (two examples in Figure 1). Figure 2 shows the frequency distributions of classes of distances between two subsequent radio-fixes. These did not significantly differ between sexes ($G = 1.716$, $df = 3$, NS), movements of 0–3 m being most frequent (males: $G = 87.083$, $df = 3$, $p < 0.001$; females: $G = 84.451$, $df = 3$, $p < 0.001$).

Dispersal

FD was positively correlated with the time elapsed from the release for two females and four males, while no correlation was found in females #034 and #126 (Table II). At the end of the radio-tracking session, both TD and FD were similar in the two sexes (TD, females: 35.7 ± 17.3 m; males: 51.4 ± 39.7 m; $U = 4$, NS; FD, females: 79 ± 24.1 m; males: 77.5 ± 24.1 m; $U = 5$, NS).

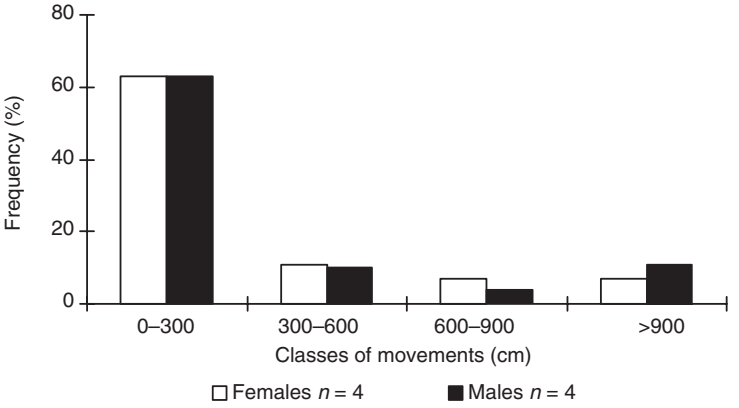

Figure 2. Frequency distributions (in %) of classes of movements (in cm) in the two sexes between two subsequent radio-fixes.

Table II. Relationships (after Pearson correlation test) between the distance from the starting point and the time elapsed from the release for each radio-tracked crayfish (#). *b* and *a* are slope and elevation, respectively, of the regression lines obtained by plotting distance against time.

#	Sex	*r*	*b*	*a*	*P*
034	f	−0.231	−9.6546	150.451	NS
055	f	0.531	12.942	1.480	<0.05
087	f	0.890	4.3209	24.876	<0.01
126	f	−0.315	−1.745	155.579	NS
045	m	0.899	13.750	−4.010	<0.01
066	m	0.711	21.523	−16.232	<0.01
117	m	0.811	8.5758	15.6137	<0.01
138	m	0.713	2.656	15.002	<0.01

We simulated a unidirectional random-walk, assuming as unitary steps the frequency distribution of the distances covered between subsequent fixes. Females #034 and #126 that did not show any significant dispersal were excluded from the analysis. The comparisons of frequency distributions between observed and expected TD and FD did not reveal significant differences (TD: $G = 1.617$, $df = 3$, NS; FD: $G = 0.722$, $df = 3$, NS). However, crayfish (Table III and Figure 3) showed a clear interindividual difference in dispersal, individuals #087, #117, and #138 dispersing faster, and individuals #045, #055, and #126 lower, than expected, and female #045 at the same rate as expected.

Habitat use

Often crayfish were recorded under boulders and among vegetation (42.7% and 43.2% of records, respectively); they were never found out of the water and were seldom seen on open substrata (7.9%) or on the banks (6.2%). Due to its limited use by crayfish, the microhabitat "on the banks" was excluded from the following analysis.

The two sexes significantly differed in their microhabitat occupancy ($G = 21.678$, $df = 2$, $p < 0.001$): males hid more frequently under boulders ($G = 41.532$, $df = 2$, $p < 0.001$), while females were found more often among the vegetation ($G = 13.598$,

Table III. Comparisons using Student's *t*-test between the slopes (*b*) of the regression lines describing the observed and the expected dispersals for each radio-tracked crayfish (#). Females #034 and #126 were excluded from the analysis because they did not show any significant dispersal (see Table II). Values of the observed *b* are in Table II. The expected *b* is 4.469. The regression line describing the expected dispersal was obtained by applying a unidirectional random-walk model. +, −, and = indicate that the observed dispersal is higher, lower, and equal, respectively, than expected.

#	Sex	*t*	*df*	*P*	obs vs. exp
055	f	4.264	40	<0.01	−
087	f	6.653	40	<0.01	+
045	m	1.713	40	NS	=
066	m	4.709	40	<0.01	−
117	m	2.194	40	<0.05	+
138	m	2.969	40	<0.01	+

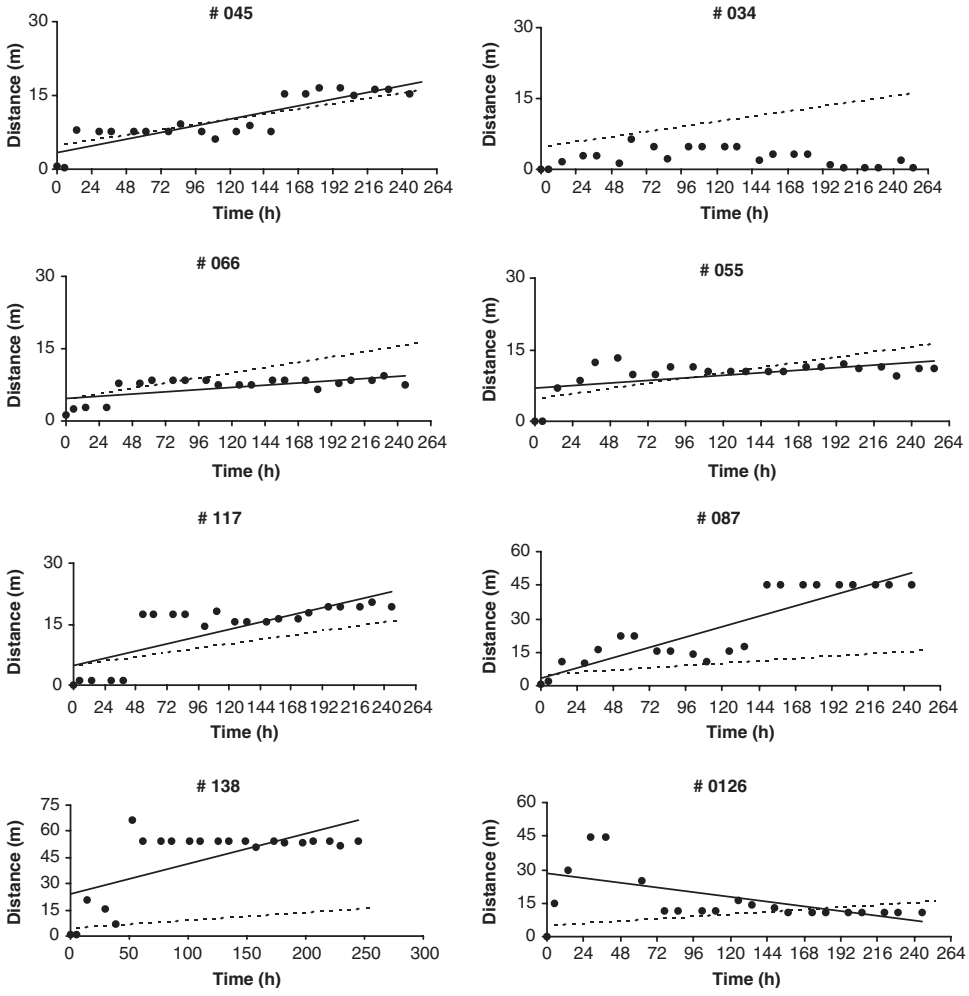

Figure 3. Observed (continuous lines) and expected (dashed lines) dispersal (distance in m from the starting point vs. time in h) for every crayfish (numbered from the frequency of its radio-transmitter, in kHz). See Table III for details.

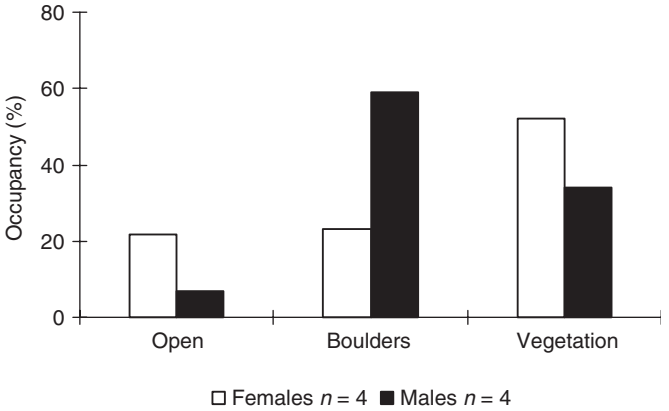

Figure 4. Frequency distributions (in %) of occupancy of three microhabitats (open, boulders, and vegetation) by the two sexes.

Table IV. Comparisons between the occupancy of three microhabitats by each crayfish (#) and their availability. The analysis was done using Bonferroni simultaneous confidence intervals followed by G-test (statistic: G; $df = 3$; P always < 0.01). +, −, and = indicate a higher, lower, and equal occupancy of the microhabitat, respectively, than expected from its availability.

#	Sex	Open	Boulders	Vegetation	G
034	f	−	+	+	64.423
055	f	−	=	+	57.377
087	f	−	=	+	28.495
126	f	−	+	+	49.774
045	m	−	+	+	77.560
066	m	−	+	=	98.590
117	m	−	+	+	69.883
138	m	−	+	=	97.155

$df = 2$, $p < 0.001$) (Figure 4). However, both sexes used the habitat in the same fashion during at both sunrise and sunset (females: $G = 1.610$, $df = 2$, NS; males: $G = 0.773$, $df = 2$, NS).

Using Bonferroni simultaneous confidence intervals, we found that the occupancy of every microhabitat was not related to its availability (Table IV). Crayfish were recorded under boulders and among vegetation more often than expected but less frequently on open substrata.

Discussion

Obviously, our results obtained from a small sample of individuals should be interpreted with caution and more general conclusions can be only drawn after additional studies. However, the information gathered in the Degebe River provides some interesting suggestions about the spatial behavior and the habitat use of the invasive *P. clarkii* in ephemeral water bodies.

Crayfish relative displacement ranged between 2.5–38 m d^{-1} independently of the sex. These values are similar to those previously reported in other radio-telemetric studies

that, however, were based on 4–6 radio-fixes per day (1–11 m d^{-1}, Gherardi et al. 2002; 1.1–38.1 m d^{-1}, Barbaresi et al. 2004), but differ highly from the displacement of up to 4 km d^{-1} recorded during the mating period (September; Fidalgo et al. 2001) in the rice fields of the lower Guadalquivir, Spain (Gherardi and Barbaresi 2000).

Crayfish displacement was longer during nocturnal hours. Previous studies have not reported strong evidence for an exclusive nocturnal activity by *P. clarkii* (Page and Larimer 1972). For instance, Gherardi et al. (2000) showed that, at least in spring, more than 50% of *P. clarkii* collected by baited traps in an irrigation ditch system in Tuscany were active at daytime, a finding confirmed in a laboratory study in which locomotion did not show a substantial difference in its occurrence between day and night. A similar pattern was recorded in southern Spain (Gherardi and Barbaresi 2000) by the contemporary use of both baited traps and radio-telemetry. The expression of nocturnal activity is usually considered adaptive, because it minimizes the risks of being preyed upon by species (mostly fish and birds) that largely depend on vision for hunting (Flint 1977, Cukerzis 1988, Maitland and Campbell 1992). However, the effect of predatory pressures on modeling the timing of crayfish locomotion has never been proved and other factors, equally plausible, may exert an influence (e.g., the crayfish matching nocturnal habits of its prey). In the Degebe River, documented crayfish predators are both nocturnal (otters) and diurnal (storks).

There were no clear environmental correlates with the crayfish movement except for the negative relation found between the relative displacement in the females and water temperature. Other studies indicated that air and water temperatures exert an obvious influence on the movement of freshwater decapods. In fact, the rise of water temperature within the range 5–25°C was associated in the laboratory with the increase of *P. clarkii*'s locomotion activity (Gherardi et al. 2000), observed also in *Austropotamobius pallipes* using the same experimental protocol (Barbaresi and Gherardi 2001). In summer, radio-tracked river crabs showed a significant reduction in the distance traveled with the increase of the mean daily air temperature (Gherardi et al. 1988), while dispersal appeared faster with the rise of air temperature in *P. leniusculus* in a temperate climate (Bubb et al. 2004). On the contrary, water depth seemed to be the main correlate of *P. clarkii*'s movement when air and water temperatures were constantly high (Gherardi et al. 2002).

The patterns of movement resemble those recorded in previous studies on *P. clarkii* (Gherardi et al. 1999, 2000, 2002, Gherardi and Barbaresi 2000) and on other crayfish species (*Orconectes rusticus*, Merkle 1969; *O. virilis*, Hazlett et al. 1974; *Austropotamobius pallipes*, Gherardi et al. 1998; *Pacifastacus leniusculus*, Bubb et al. 2004). They all indicate that crayfish alternate peaks of higher locomotion activity with longer periods of slow or null speed, during which they move within a range of 3 m, or take refuge under vegetation cover or boulders.

Overall, adult crayfish dispersed in the pool of study. The extent of such dispersal showed a clear interindividual variability, some individuals dispersing more quickly and others more slowly than predicted by a random-walk model. As hypothesized for the river crab, *Potamon fluviatile* (Gherardi et al. 1988), the rate of dispersal in the habitat can be the result of an interplay among different mechanisms, including the occupancy of refuges that function as cores of "ephemeral home range" (Robinson et al. 2000).

In the Degebe River, crayfish do not excavate burrows due to the prevalence of coarse sediments in the soil which inhibit burrowing activity (Correia and Ferreira 1995). Nevertheless, males most often took refuge under boulders and females were often found in complex microhabitats, such as vegetated sections of the study pond. As shown in other crayfish species (Garvey et al. 1994), microhabitats characterized by higher plant biomass

provide safer refuges. For instance, Jordan et al. (1996) found that the population density of *Procambarus alleni* decreased with water depth and increased with plant biomass: higher depths were associated with fish predators of large size, whereas plant biomass reduced the ability of wading birds to detect and capture their prey, crayfish included (Heck and Crowder 1991).

In essence, this study clearly proves that ephemeral water bodies like the Degebe River are highly susceptible to the invasion by *P. clarkii*. First, we found that crayfish did not enter aestivation at the onset of the dry period; on the contrary, most of them continued to disperse in the study pond, following the pattern described for other populations and conditions. The second result was that crayfish movement mostly occurred at night, possibly to avoid diurnal predators, but seemed to be relatively independent of environmental parameters, like water depth. Finally, and more interestingly, the inability to construct burrows did not seem to decrease the survival of this species, crayfish making use instead of other abundant refuges in the habitat (crevices under boulders and vegetated sections of the river).

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