

Ranging behaviour of the invasive crayfish, *Procambarus clarkii* (Girard)

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The spreading of the invasive crayfish *Procambarus clarkii* throughout the world is attributed to human introductions; however, the rapid and widespread diffusion of the species following its establishment is the result of its dispersal capabilities. This study aimed to provide further information for the comprehension of the invasive potential of this crayfish by underlining some aspects of its behavioural flexibility. Radio-telemetry was used to analyse locomotion, home-range faithfulness and dispersal of the species in an Italian irrigation ditch system. Space was used differently by the two sexes, females being more nomadic in their ranging behaviour probably due to their reproductive phase. In addition, an inter-individual variability was found in both speed of locomotion and dispersal pattern. By applying a simulation model, it was shown that (1) both sexes disperse, and (2) ranging behaviour is not the result of a passive dispersion, but that the occupancy of burrows may affect the rate of dispersion. Finally, an intra-individual variability is related to the occurrence of two spatial strategies within the same population.

KEYWORDS: *Procambarus clarkii*, invasive crayfish, ranging behaviour, dispersal, radio-tracking.

Introduction

The red swamp crayfish, *Procambarus clarkii* (Girard), native to north-eastern Mexico and south-central USA, is one of the world's most invasive species (Huner, 1977; Huner and Avault, 1979; Gherardi and Holdich, 1999). Several traits of its life history, e.g. polytrophism, rapid growth, high fecundity and disease resistance (Huner and Lindqvist, 1995; Lindqvist and Huner, 1999; Holdich, 2001), make its cultivation commercially feasible and its invasion of the wild successful.

This crayfish provides an excellent opportunity to analyse the question of how behaviour contributes to the invasive potential of species. Analyses of behaviour

have been relatively neglected when compared with studies on ecological, genetic and life-history characteristics of invasive species (Lodge, 1993; Sakai *et al.*, 2001). More recently, given the enormous ecological problems and economic costs associated with biological invasions, efforts have been directed to determine how behavioural mechanisms contribute to invasion success (Holway and Suarez, 1999). In addition, the awareness is growing that successful control of an invasive species requires a detailed knowledge of the dynamic of invasion.

The spreading of *P. clarkii* throughout the world is attributed to introductions by humans. The rapid diffusion of this species following its establishment has been related to its active dispersal capabilities (Gherardi and Barbaresi, 2000). Previous studies on the movement patterns of *P. clarkii* have revealed differences in both the use of space and the extent of dispersal among populations inhabiting different European habitats (Gherardi and Barbaresi, 2000; Gherardi *et al.*, 2000, 2002a, b). These results support the idea that ranging behaviour is flexible similarly to other behavioural patterns of the species (Gherardi *et al.*, 2001; Hazlett *et al.*, 2003). Although behavioural flexibility is characteristic of invasive species which exploit novel ecological opportunities and have broad ecological niches (Gherardi, 2000), this phenomenon has been poorly described and its role in invasions simply hypothesized (Grosholz and Ruiz, 1996).

Radio-telemetry was used in the present study to describe the ranging behaviour of *P. clarkii* in an Italian irrigation ditch system with the main object of providing further information on the rate of active dispersal in this species. While previous studies have been conducted at the population level only, our interest here was directed to the analysis of variations at both sex and individual levels of complexity in locomotion, home-range faithfulness and dispersal. Our expectation was to contribute to the debate on the behavioural flexibility of this invasive species.

Materials and methods

Radio-tracking was carried out during September 2000 in an irrigation ditch in the neighbourhood of Florence, Italy. The irrigation system consisted of a net of similarly sized canals (mean width 1.50 m), with permanent water connections and inhabited by an abundant population of *P. clarkii* (Gherardi *et al.*, 1999). During the study period, water depth averaged 17–25 cm, oxygen content ranged from 12.4 to 54.6% and the pH was 6.5–8 (see Gherardi *et al.*, 1999).

Five mature, non-berried females (cephalothorax length: 49.4–63.9 mm) and five Form-I males (cephalothorax length: 46–53.9 mm) were individually tagged by radio-transmitters (type TW-4, Biotrack, Wareham, UK). The transmitters were powered by an Ag392 battery and emitted a pulsed signal at a frequency between 150.034 and 150.147 MHz, spaced by a minimum of 10 KHz. Each tag was 18 mm in diameter (plus a 16-cm long whip antenna) and 7 mm in height, with an overall mass of not more than 1.2 g, corresponding to about 2% of an adult specimen's mass. The tag-weight : body-weight ratio was lower than the value reported for studies on river crabs (Gherardi *et al.*, 1988b), lobsters (Smith *et al.*, 1998), the white-clawed crayfish *Austropotamobius pallipes* (Lereboullet) (Robinson *et al.*, 2000) and previous studies on *Procambarus clarkii* (Gherardi and Barbaresi, 2000; Gherardi *et al.*, 2002a, b).

Transmitters were attached to the cephalothorax using a rapid-set epoxy resin. Specimens were captured using baited traps and retained in a water tray for about

20 min until the epoxy was dried, before returning them to the site of collection. On release, all tagged crayfish moved freely and behaved similarly to untagged individuals, hiding inside burrows and under covers. Crayfish were tracked using a radio-receiver (RX-98, Televilt International, Sweden) supplied with a foldable directional antenna attached to the housing. The position of each crayfish was recorded at 6-h intervals over 10 days using a grid system placed in the study area. Error in detecting crayfish position averaged 50 cm. The first day of recording was not included in the analysis to exclude the initial 'fright' reaction in response to capture as described in other crayfish (Robinson *et al.*, 2000).

Air and water temperatures, and the temperature of a reference burrow were recorded by mercury thermometers during each visit. Changes in water level were recorded using four reference marks placed along the canals, and oxygen level was measured by an Ati Orion 810 Dissolved Oxygen Meter.

Over the study period, sunrise and sunset occurred, respectively, at around 05:00 h and 19:00 h. We defined those records taken between 05:00 h and 19:00 h (or 19:00 h and 05:00 h) as occurring at day- (or night-) time.

The behaviour of individual crayfish was modelled as a uni-directional random walk using a Monte Carlo simulation technique (Rohlf and Davenport, 1969). Each simulated bout consisted of a sequence of 40 steps, whose length was randomly drawn from the frequency distribution of the observed distance between two subsequent fixes. Each step had a constant probability (0.5) of being left- or rightward orientated and no relationship was assumed between successive steps. A total of 500 individual bouts was simulated.

Parametric statistical techniques were used when data appeared to be drawn from a normally distributed population (Zar, 1984). Otherwise, statistical inference was made through non-parametric tests (Siegel and Castellan, 1988). Repeated measures ANOVA was used to correct for the temporal autocorrelation that arises from repeated measurements through time and to prevent temporal pseudo-replication (Winer, 1991).

Text and figures give mean values \pm standard error. The level of significance at which the null hypothesis was rejected is $\alpha = 0.05$.

Results

Locomotory speed

Table 1 provides sex, size, the total distance travelled (TDT) and the mean locomotory speed (range: 37.9–115.9 and 9.9–138.1 cm h⁻¹ in females and males, respectively) for individual crayfish, numbered on the basis of the transmitting frequency.

Locomotory speed significantly differed among individuals (repeated measures ANOVA: $F_{[8,390]} = 4.52$, $P < 0.001$) while no difference was found either between sexes (females: 55.6 ± 7.2 cm h⁻¹, $n = 5$; males: 47.8 ± 15.5 cm h⁻¹, $n = 5$; $F_{[1,8]} = 0.08$, NS), or among hour classes ($F_{[3,8]} = 0.27$, NS).

A negative correlation was found between locomotory speed and water temperature ($r_{[178]} = -0.21$, $P < 0.05$) in the females. On the contrary, no correlation was found between locomotory speed and abiotic parameters of the habitat in the males.

Table 1. Details of radio-tagged crayfish, numbered on the basis of their transmitting frequency.

Crayfish	Sex	CL (mm)	Total distance (m)	Mean speed (cm h ⁻¹)	SE	<i>n</i>
034	M	52.4	62.60	29.01	9.36	36
045	M	46.6	54.60	25.28	5.46	36
055	M	53.9	21.53	9.97	3.01	36
066	M	46	308.79	138.14	74.65	36
087	M	47	78.65	36.42	10.80	36
097	F	63.8	276.72	115.95	21.35	36
117	F	57.9	104.68	38.56	18.23	36
126	F	50.5	97.70	45.24	10.41	36
138	F	50.7	87.42	40.47	14.29	36
147	F	49.4	82.08	37.99	10.33	36

CL, cephalothorax length; *n*, number of records used for the analysis.

Movement patterns

When locomotory speed was plotted against the time passed since the release, one or more peaks of higher locomotory activity were found to alternate with longer periods of slow or null speed (four examples are shown in figure 1).

To describe sequences of movements with different length, displacements were arbitrarily split into two categories, on the basis of the frequency distributions of movements performed within 6 h: 'short-range' (SR) or 'long-range' (LR) movements, if the distance travelled per fix was lower or higher than 3 m, respectively (figure 2). SR movements were more frequent in both sexes (Wilks test, males: $G_{[1]}=80.826$, $P<0.001$; females: $G_{[1]}=36.728$, $P<0.001$); however, the females covered distances longer than 3 m more often than the males ($G_{[1]}=5.117$, $P<0.05$).

The transition analysis from one category of movement to the other showed that the sequence was not random. The probability that a LR followed another LR was higher than expected by chance in both the males ($G_{[1]}=3.87$, $P<0.05$) and the females ($G_{[1]}=3.85$, $P<0.05$). In the latter sex, the transitions LR–SR, and *vice versa*, occurred less frequently than expected (LR–SR: $G_{[1]}=4.15$, $P<0.05$; SR–LR: $G_{[1]}=4.25$, $P<0.05$). Comparison between sexes in the frequency distribution of transitions showed that both SR–SR and LR–LR sequences were respectively lower and higher in the females than in the males ($G_{[3]}=14.247$, $P<0.01$).

Home-range faithfulness

An estimate of the crayfish's faithfulness to its home range provides complementary information to the evaluation of its dispersal. On the basis of the frequency distributions of the movements performed within 6 h, home range was here defined as the 3-m² surface surrounding each crayfish.

The crayfish's faithfulness to its home range was estimated by computing the frequency of returning to the same area and the time of permanence in it. On average, females returned to an area they had previously occupied more frequently than males (females: 11 ± 1.1 times, males: 5.2 ± 2.0 times, $F_{[1,8]}=6.42$, $P<0.05$). Crayfish mostly remained in the same home range for 6 h ($G_{[6]}=243.107$, $P<0.001$) (figure 3), but the two sexes significantly differed in their mean time of permanence

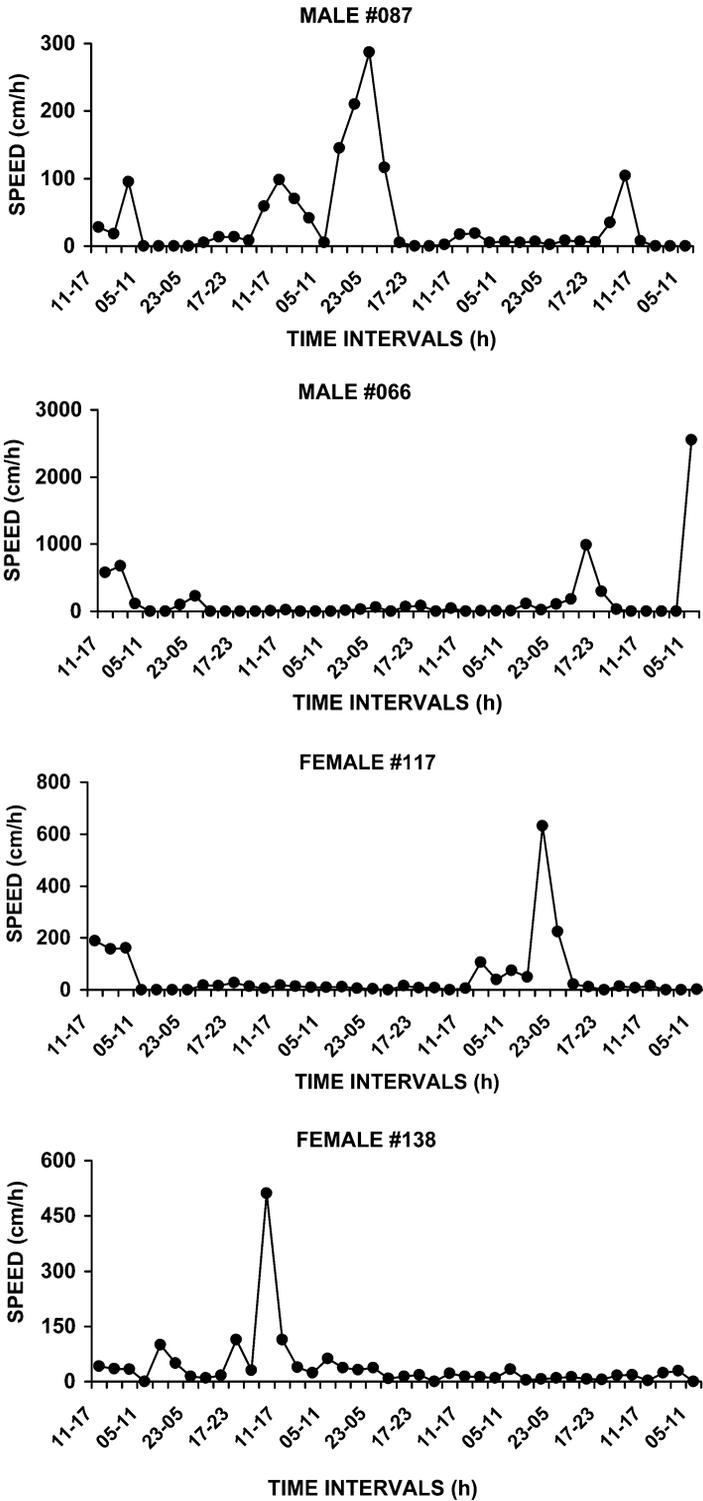


FIG. 1. Locomotory speed plotted against time: four examples.

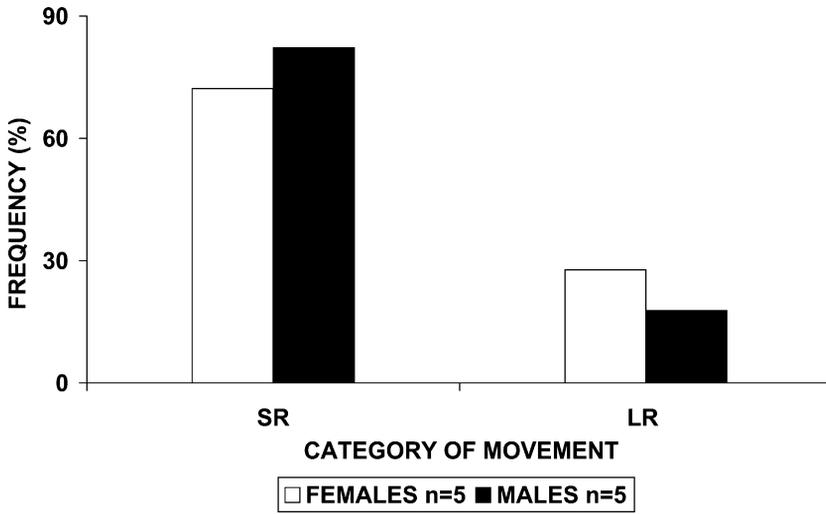


FIG. 2. Frequency distribution of movements performed within 6 h in the two sexes. SR, ‘short-range’ movements (≤ 3 m); LR, ‘long-range’ movements (> 3 m).

(after log–log transformation: $F_{[1,177]}=9.581$, $P<0.005$), which was longer in the males (females: 10.4 ± 0.8 h; males: 18.5 ± 3.2 h).

Dispersal

Figure 4 shows the relationship between the distance from the release site and the time passed from release for each radio-tracked crayfish. A positive correlation

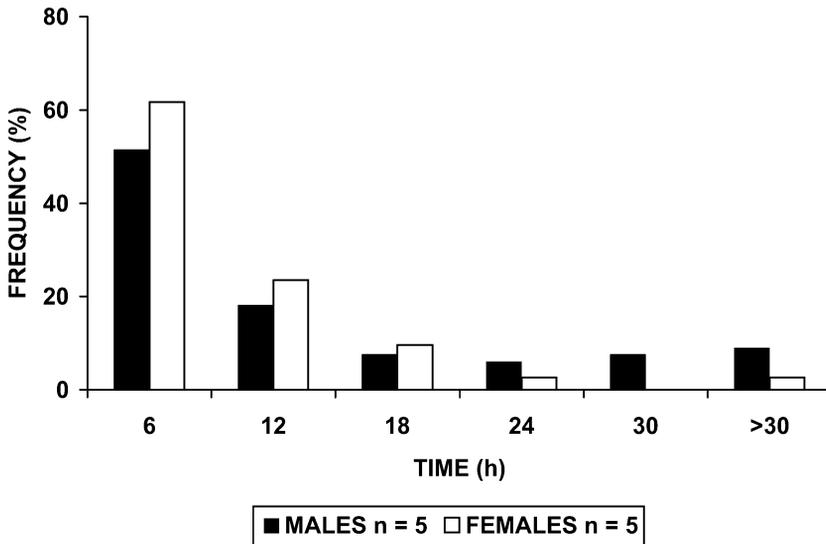


FIG. 3. Time of permanence in each 3-m² home range compared between sexes.

was found in four females and two males, while it was negative in male 045 (after Pearson correlation test; table 2).

At the end of the study, both the TDT and the final distance from the release point (FD) were similar in the two sexes (Mann-Whitney U -test: TDT, females: 129.7 ± 36.97 m; males: 105.2 ± 51.7 m, $W_x = 20$, NS; FD, females: 39 ± 7.6 m; males: 32.8 ± 23.6 m, $W_x = 22$, NS).

A uni-directional random walk was simulated, assuming as unitary steps the frequency distribution of the distance covered between subsequent fixes (see Materials and methods section). Expected and observed data were compared for the TDT, FD and dispersal.

No difference between observed and expected TDT and FD was found in either females (TDT: $G_{[1]} = 1.213$, NS; FD: $G_{[1]} = 3.759$, NS) or males (TDT: $G_{[3]} = 1.213$, NS, FD: $G_{[3]} = 2.202$, NS).

A comparison between the expected and observed dispersal was made for each individual separately (table 3; figure 4). In crayfish 034, 097, 117, 126 and 147 the observed distance from the release point increased faster than expected. On the contrary, dispersal of crayfish 055 was slower than expected.

Discussion

The study of ranging behaviour in the crayfish *P. clarkii* is of interest to the growing discipline of biological invasions, revealing the need for ethological observations. A distinction among levels of complexity has both theoretical and practical implications. In fact, a multiple-level analysis of behavioural patterns is relevant to a better comprehension of the spreading potential of invasive species and, consequently, to the development of control and management programmes.

Although recorded from a few individuals, our radio-telemetric data are sufficient to reveal a variability in ranging behaviour and in the use of space between sexes, among individuals and by the same individual.

Features of ranging behaviour

Crayfish speed was slow ($0.3\text{--}76.5$ m day⁻¹), if compared with the massive use of space (up to 4 km day⁻¹) recorded using the same technique in a population inhabiting rice fields of the Lower Guadalquivir, Spain (Gherardi and Barbaresi, 2000). The locomotion rate recorded in our study, however, is similar to that found in a long-term mark-recapture study performed in the same water body under study here (estimated speed: $0.6\text{--}1.5$ m day⁻¹; Gherardi *et al.*, 2000) and in a short-term monitoring carried out through radio-telemetry in a temporary stream of southern Portugal (estimated speed: $1\text{--}11$ m day⁻¹; Gherardi *et al.*, 2002b).

The locomotion rate differed among individuals, differences being independent of sex, size and hour of records. That crayfish, typically defined as nocturnal species (Gherardi, 2001), make long displacements by day as well as by night may be related to the low risk of predation observed in the study habitat. However, the same pattern has been revealed in other habitats where the pressure exerted by diurnal predators was high, possibly because the benefits of an easier and quicker orientation through visual landmarks outweighed predation risks (Gherardi and Barbaresi, 2000).

The relationship between speed of locomotion and some environmental parameters differed between the two sexes. Females moved to a lesser extent

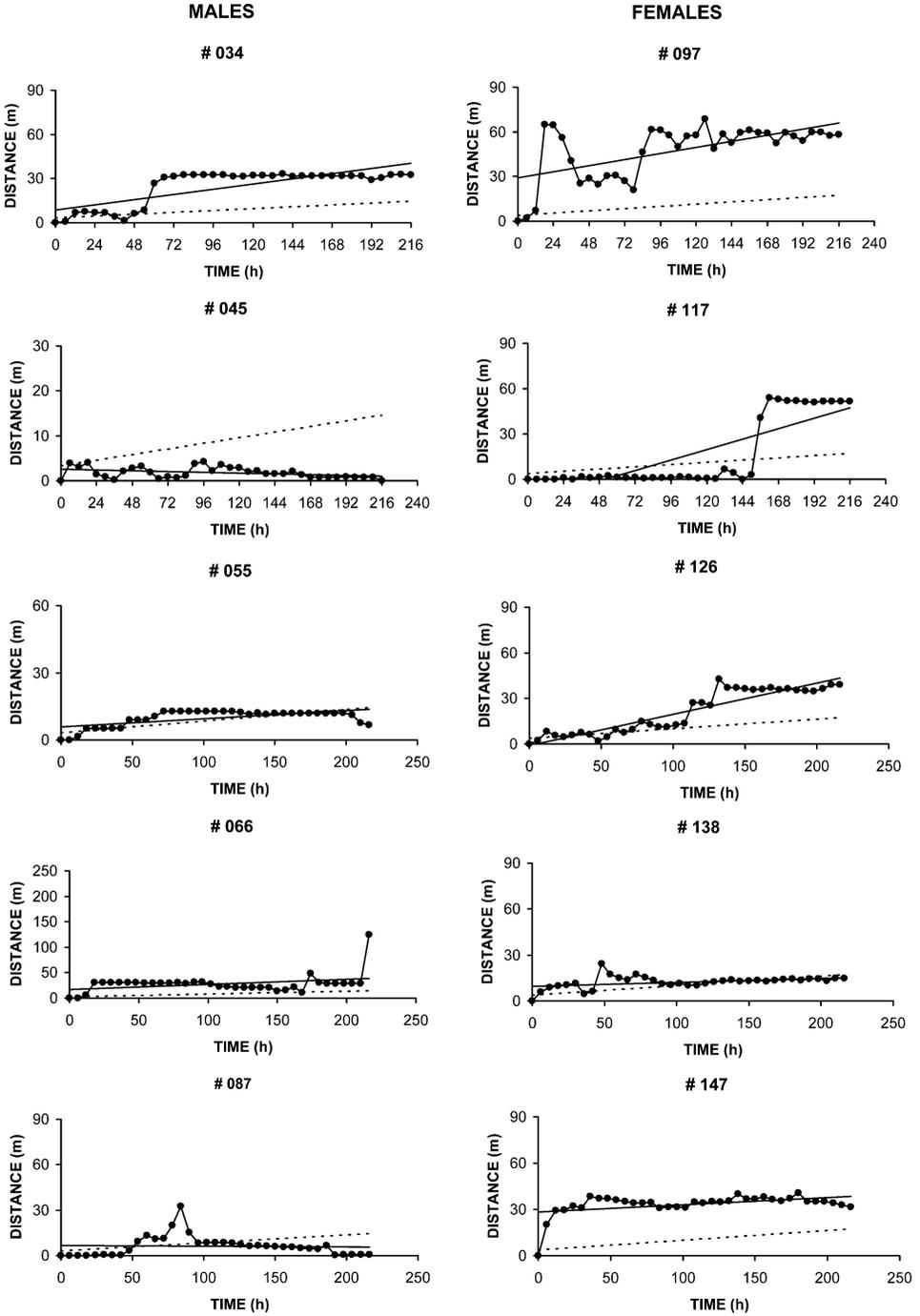


FIG. 4. Individual dispersal of radio-tagged crayfish. Solid line, observed; dashed line, expected.

Table 2. Relationship between distance from the release point and time in individual radio-tagged crayfish, numbered on the basis of their transmitting frequency, after Pearson correlation test.

Crayfish	<i>r</i>	<i>b</i>	<i>a</i>	<i>P</i>
034	0.753	0.139	9.702	<0.01
045	-0.484	-0.009	2.815	<0.01
055	0.569	0.031	6.548	<0.01
066	0.300	0.088	18.385	NS
087	-0.095	-0.099	7.398	NS
097	0.591	0.159	30.697	<0.01
117	0.813	0.299	-16.745	<0.01
126	0.922	0.299	-1.188	<0.01
138	0.317	0.017	10.795	NS
147	0.421	0.024	31.652	<0.02

r, correlation coefficient; *b*, slope of the regression line; *a*, elevation of the regression line.

Table 3. Comparison between observed and expected dispersal in individual radio-tagged crayfish, numbered on the basis of their transmitting frequency.

Crayfish	$t(b_{\text{obs}} \neq b_{\text{exp}})$	df	<i>P</i>
034	4.283	68	<0.01
045	18.391	68	<0.01
055	2.371	68	<0.01
097	2.674	68	<0.01
117	6.531	68	<0.01
126	9.798	68	<0.01
147	3.835	68	<0.01

t, *t*-test statistic resulting from the comparison between the slopes (*b*) of the regression line for the observed (obs) and expected (exp) data. For b_{obs} see table 2; b_{exp} : males=0.049, females=0.059.

with increasing water temperatures. This behaviour could be explained by considering the species' life cycle in the studied habitat; in September, females spawn and carry the hatchlings under their abdomen (Gherardi *et al.*, 1999). In this period, females could respond to an increase in temperature by spending a longer time in favourable (lower temperature) microhabitats with a consequent reduction in their speed of locomotion. Although the radio-tagged females were not ovigerous, we did not know their reproductive state immediately before or after the study period.

The locomotion rate showed an intra-individual variability through consecutive days. Individuals alternated peaks of higher locomotor activity with longer periods of slow or null speed, during which they moved less than 3 m, or found refuge inside burrows or under vegetal cover. Our data confirm the results from previous studies (Gherardi *et al.*, 1999, 2000, 2002b; Gherardi and Barbaresi, 2000) that showed the coexistence of two spatial strategies. A similar pattern has been found in other freshwater decapods, such as the river crab, *Potamon fluviatile* (Herbst) (Gherardi *et al.*, 1988b), and several crayfish species, such as *Orconectes rusticus* (Girard) (Merkle, 1969), *O. virilis* (Hagen) (Hazlett *et al.*, 1974), *Astacus astacus*

(L.) (Schütze *et al.*, 1999) and *Austropotamobius pallipes* (Lereboullet) (Gherardi *et al.*, 1998; Robinson *et al.*, 2000).

Conservative/dispersive use of space

A sexual difference in the use of space emerged from the analysis of home-range faithfulness. In fact, females were faithful to one area for less time than the males and covered longer excursions, displaying a more nomadic behaviour than males. In contrast, a radio-telemetry study conducted in the same area during October to November (Gherardi *et al.*, 2002a) found no evidence for a sexual difference in the use of space. Similarly to *Potamon fluviatile* during the breeding season (Gherardi *et al.*, 1988b), in the period of study females might have required a more abundant or different diet that could be supplied by the use of a larger or diversified foraging area (Gherardi *et al.*, 1988a, 1988b).

The extent of dispersal varied among individuals, with some crayfish that do not disperse at all. The application of a uni-directional random walk simulation to our data furnished contradictory results: a comparison between observed and expected FD (distances from the release point recorded at the end of the study) suggested that both sexes disperse randomly. On the contrary, a comparison between observed and expected data at the individual level showed that crayfish do not follow a random walk movement and that they disperse faster than expected, with the exception of crayfish 055.

This apparent contradiction can be resolved by assuming that (1) both sexes disperse in the habitat, and (2) the ranging behaviour of *P. clarkii* is not the result of a passive dispersal. As hypothesized in the river crab, *Potamon fluviatile* (Gherardi *et al.*, 1988a), some factors can either slow down or accelerate dispersal. Occupancy of burrows could have an effect on the rate of dispersion. Burrows are primary resources, allowing *P. clarkii* to withstand environmental extremes (Gherardi *et al.*, 2002b). Since burrow availability may be limited in time and space, it is possible that crayfish maintain an ‘ephemeral home range’ (Robinson *et al.*, 2000) in relation to the attachment to one burrow and that each individual adopts a different spatial strategy.

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