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Shelter use of the Red-Swamp Crayfish (*Procambarus clarkii*) in dry-season stream pools

Maria Ilhéu[1], Patrizia Acquistapace[2], Chiara Benvenuto[2] and Francesca Gherardi[2]

With 4 figures and 1 table

Abstract: Patterns of shelter use of the red-swamp crayfish, *Procambarus clarkii*, were studied in a temporary stream of the south of the Iberian Peninsula during the summer of 1999. By shelters, we mean both excavated burrows and natural refuges, such as crevices under rocks, boulders, and stones. Both crayfish shelter use and faithfulness, and the relationship between the use of shelters and some abiotic parameters of the habitat were analysed. Five main issues were raised. (1) Crayfish did not hide exclusively inside excavated burrows, but regularly used natural refuges. The low burrowing activity recorded might be related to the large particles of the sediment and to the scarce presence of free water. (2) Burrows were mostly found either empty or occupied by a single individual, while refuges had a higher rate of occupancy. Shelters were often used by both females and smaller individuals. (3) A role played by burrows and refuges was to help crayfish to withstand high environmental temperatures; in fact, the number of specimens inhabiting the same shelter increased with the air temperature. Shelters also provided protection against predation and cannibalism. Burrows seemed more efficient shelters, since crayfish more often moved from a refuge to a burrow than vice versa. (4) Crayfish were found outside the shelters mainly at night and dawn, while they were mostly hidden in burrows during the day. (5) *Procambarus clarkii* seemed not to be faithful to a unique shelter; thus this species seems to have "ephemeral home ranges" with a shelter as the core. Although refined orienting capabilities have been reported in several decapods, in this case, crayfish did not exhibit a "homing behaviour", which may be related to the fact that burrows were used mostly for protection purposes.

Key words: invasive crayfish, burrow, home range, heat protection, refuge.

[1] **Address for correspondence:** Department of Ecology, University of Évora. Colégio Luis Verney, 7000-726 Évora, Portugal. E-mail: milheu@uevora.pt

[2] Department of Animal Biology and Genetics, University of Florence, Italy

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Introduction

The nearly cosmopolitan distribution of the red-swamp crayfish, *Procambarus clarkii*, has been related to several biological features that make this species a good colonizer (HUNER & BARR 1984, HUNER & LINDQVIST 1995), one of them being its ability to withstand environmental stresses, such as desiccation (GHERARDI et al. 2002) and extreme temperatures (GHERARDI & BARBARESI 2000).

During the summer, numerous streams in the south of the Iberian Peninsula are partially dry, and only a few isolated pools remain. Most pools dry up and are characterized by harsh environmental conditions. Despite this scenario, crayfish can reach high densities in many of these water courses (ADÃO & MARQUES 1993, BRAVO et al. 1994, BERNARDO & ILHÉU 1994). *P. clarkii* survival and success in such environments may be related to the great physiological resistance of this species, and may also depend on certain behaviour, such as the burrowing activity, that allows it to avoid harsh conditions induced by abiotic factors and other environmental stresses, such as predation.

Procambarus clarkii is considered a tertiary burrower (HOBBS 1942), spending most of its life in open water and constructing burrows to avoid environmental constraints, or to reproduce (HOBBS 1981, ILHÉU 1996, GHERARDI 2001). This species can also behave as a secondary burrower, mostly inhabiting burrows, but frequently moving into open waters, especially during the rainy season (HUNER & BARR 1984). *Procambarus clarkii*'s burrows generally present a simple morphology, typically extending downward in an undulating channel (ILHÉU 1996). More complex burrows, with many tunnels and entrances, have also been reported (CORREIA & FERREIRA 1995). Tunnels are commonly covered with a mud plug or a chimney at the top, and end in an enlarged chamber that is normally below the water table (JASPERS & AVAULT 1969, HASIOTIS 1995, ILHÉU 1996).

Considering the crucial importance of burrows to *P. clarkii* survival and recruitment, the aim of this study was to contribute to the understanding of this species' shelter ecology, and specifically to describe: (1) patterns of burrow and refuge use (both indicated as shelters) during summer, (2) crayfish faithfulness to shelters, and (3) the relationships between shelter use and environmental conditions.

Materials and methods

Study area

This study was carried out in August–September 1999, along a 150-m stretch of the temporary stream Ribeira dos Alamos at an altitude of about 165 m in Alentejo region, southern Portugal. This stream is a second order tributary of the Guadiana River. Temporary streams are here defined as lotic systems that cease to flow for periods exceeding three months (modified from GILLER & MALMQVIST 1998). Ribeira dos Alamos is located in a granitic zone with rather flat slopes, but shows some erosion effects. The riparian corridor is discontinuous, with some degree of degradation. At the reach level, the substratum is composed of large boulders (around 30 %), gravel and pebble (around 40 %), and mud or silt (around 30 %).

In the study area, the annual average precipitation is 560 mm, and rainfall is concentrated from November to April. During the winter, the stream is composed mostly of pools that seldom exceed 150-cm depth, interspersed with shallow riffles. Occasional floods occur. During summer, no surface flow is observed, and the stream comprises long dry reaches with some isolated pools. During this period, the aquatic fauna inhabiting the shallower pools is subject to extreme environmental conditions. The fieldwork coincided with the drought phase, when few pools persisted. Pools were shallow, exceeding no more than 50 cm.

Sampling methods

Excluding those burrows found sealed with a mud plug, all shelters (25 burrows and 7 natural refuges) occupied by crayfish within the studied area were identified and marked. By refuges we mean those crevices under rocks, boulders and stones where individuals were observed sheltering. Refuges were all terrestrial.

On August 25, 1999, about 98 adult crayfish were carefully extracted from the shelters, avoiding alteration to their structure. The crayfish were sexed, measured and their moulting condition was recorded. The ovigerous status of females was also evaluated. Each individual was marked, using plastic tags glued to the first half of its cephalothorax, and then released inside the shelter of provenience. Individuals found outside shelters were not marked.

On the day following the initial sampling, crayfish and shelter were monitored for 8 consecutive days, every six hours, at 06:00 (dawn), 12:00 (day), 18:00 (dusk), and 00:00 (night). The number and identity (when marked) of those crayfish that inhabited burrows and refuges were recorded without disturbing the animals. Whenever possible, physical contact was avoided. Only opened burrows were checked. In burrows, both the state of the entrance and traces of recent digging activity (mostly, scrape and scratch marks, HASIOTIS 1995) were evaluated. The position of marked crayfish was recorded, distinguishing whether crayfish were outside shelters, inside burrows or inside refuges.

Air, water and shelter temperature, dissolved oxygen, pH and water conductivity in pools were recorded, following the same time schedule as that used for the collection of crayfish and shelter data. A mercury thermometer and a multivariable probe (WTW Instruments) were used. Both the sediment (grain size and % of water content) and the soil depth, as well as the water level table, were examined in areas with high densities of burrows. For the wet sieving, grain-size analysis samples were dehydrated and homogenised and, once weighed, were sieved, using an ATSM with quadrangular nets (19.0 mm, 9.51 mm, 4.76 mm, 2.00 mm, 0.841 mm, 0.420 mm, 0.250 mm, 0.105 mm, 0.074 mm). Water was used to help the sample pass through the sieves. The retained parts in each net sieve were collected, dried at a temperature of 60 °C and weighed separately.

In this study, nonparametric statistical tests were used. Apart from X^2 test, used to compare frequencies, nonparametric tests (Mann-Whitney U-test, Friedman two-way analysis of variance, Kruskal-Wallis one-way analysis of variance, and Spearman rank correlation test) were considered more appropriate than parametric ones when the assumptions of normality of distribution and homogeneity of variance were not met or were violated, as in our case. All statistical analyses followed Zar (1984) and Siegel & Castellan (1988). The level of significance under which the null hypothesis was rejected was $\alpha = 0.05$.

Results

Crayfish burrows were found concentrated around the water pools in wet or moist sediment. Burrows were made mainly of clay (84.4 %) and had an average water content of 32 % (SD = 11.1). Ground water table depth varied from 2.5 to 15 cm, and the soil was, on average, 10 cm deep (SD = 3). All burrows consisted of a single downward tunnel, ranging from 4 to 15 cm deep. Around 85 % of the examined burrows contained water. Refuges, where individuals

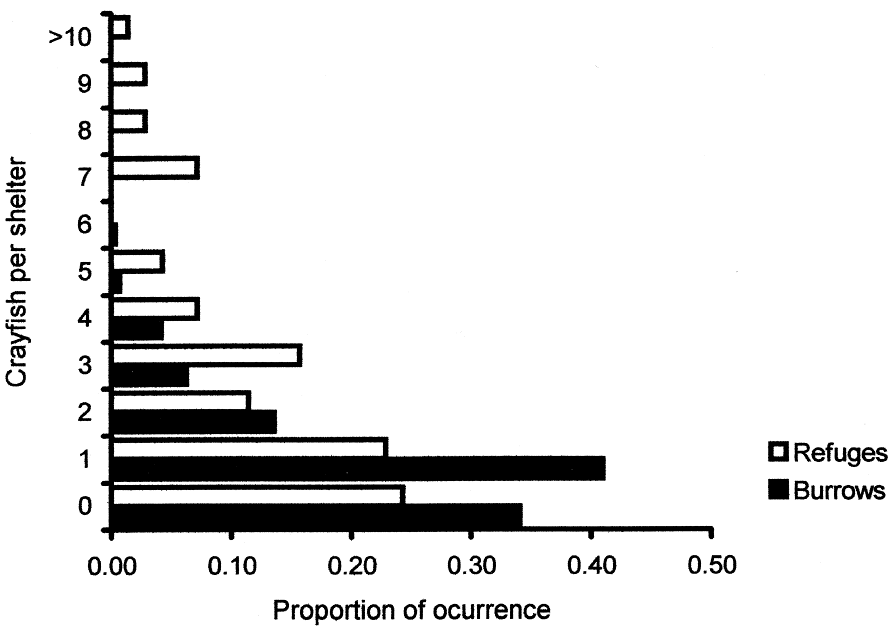

Fig. 1. Frequency of occurrence of *Procambarus clarkii* per shelter, comparing burrows and refuges.

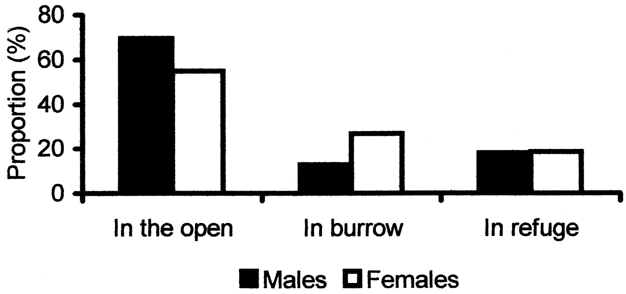

Fig. 2. Sex ratio of *Procambarus clarkii* in burrows, refuges and outside shelters (males n = 212, females n = 135).

were observed sheltering, varied from crevices under rocks, boulders and stones to wood debris outside water. Their distance from the water border was erratic, ranging from a few centimeters to several meters (maximum 15 m). The inner area of refuges ranged between 4 and 100 cm^2.

On average, each burrow was occupied by 1.6 crayfish (SD = 0.07, n = 190; maximum 6) and refuges by 4.8 (SD = 0.89, n = 53, maximum 12). Burrows were more often occupied by a single crayfish, followed in a hierarchical sequence by no crayfish, two crayfish and more than two crayfish (after Friedman two-way analysis of variance for related samples, $X^2 = 62.482$, df = 5, $P < 0.0001$) (Fig. 1). The number of inhabitants per refuge appeared more uniformly distributed and within a higher range. During the period studied, each marked burrow and refuge was on average occupied by 3.64 (SD = 2.61) and 13.3 (SD = 16.5) different crayfish, respectively.

The female-male distribution among habitats differed significantly ($X^2 =$ 192.118, df = 5, $P < 0$). Males tended to occur more frequently outside shelters, while females prevailed inside burrows (Fig. 2).

Crayfish found outside shelters were significantly larger than those in burrows and refuges (outside shelters-outside water: CL = 48.0 mm, SD = 1.4, n = 4, outside shelters-in water: CL = 47.4 mm, SD = 0.9, n = 6; in burrows: CL = 46.0 mm, SD = 0.5, n = 4; in refuges: CL = 44.6, SD = 2.6, n = 3; after Kruskal-Wallis one-way analysis of variance, H = 8.314, df = 3, $P < 0.05$).

When shelters were occupied by more than one crayfish, the sex ratio (i.e. the percentage of males over the whole population) did not differ between groups of two or more than two crayfish and was 57.14 % and 42.86 % ($X^2 =$ 0.457, df = 1, $P > 0.05$), respectively. Couples were mostly composed of one male and one female. No ovigerous female or moulting crayfish were ever found.

About 78 % of the 98 marked crayfish were recaptured at least once. On average, each marked individual was located 4.12 (SD = 2.9) times. About 10 % of the marked crayfish were recorded dead outside the shelters while in-

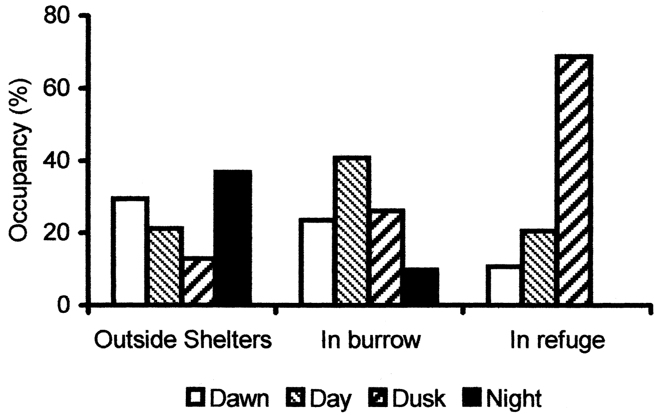

Fig. 3. Habitat use among phases of the 24-h cycle (Dawn, n = 110; Day, n = 141; Dusk, n = 111; and Night, n = 38).

side shelters mortality was about 3.5 %. During the study period, 166 dead unmarked individuals were also found outside shelters, mostly at the pool margins, and 18 inside refuges and burrows.

During the monitored periods, most marked crayfish were observed outside the shelters (56 %), both in water and on land. However, proportionally, during diurnal hours, they were mostly hidden under shelter, particularly in burrows ($X^2 = 175.386$, df = 11, $P<0.001$). Crayfish were mostly found in refuges at dusk. At night, burrows showed a very low occupancy, and no crayfish were found in refuges (Fig. 3).

Although a high frequency of empty burrows (0.40) occurred during the night, both the average number of crayfish per burrow and indices of burrowing (opened/closed entrance and freshness) did not result in significant differences throughout a 24-h cycle (after Kruskal-Wallis, $P>0.05$).

The mean time spent by marked crayfish in each habitat was variable. However, the time spent outside shelters (82.3 h, SD = 39.9, n = 68) significantly exceeded the time spent in burrows (25.6 h, SD = 34.7, n = 28 h) and in refuges (35.7 h, SD = 36.4, n = 36 h) (after Friedman two-way analysis of variance for related samples, $X^2 = 14.38$, df = 2, $P<0.002$). The percentage of time spent in and outside shelter was obtained by assuming that crayfish located in the same habitat for two consecutive records, spent at least 6 hours in that habitat. This assumption was confirmed by a radio-telemetric study conducted in the same study area and period (GHERARDI et al. 2002).

Crayfish did not show any shelter faithfulness. Only one crayfish returned to a previously occupied burrow (after 40 hours) and one to a previously occupied refuge (after 70 hours). On average, the time spent by each crayfish in both the same burrow and the same refuge was 12.7 hours (SD = 5.8, n = 52)

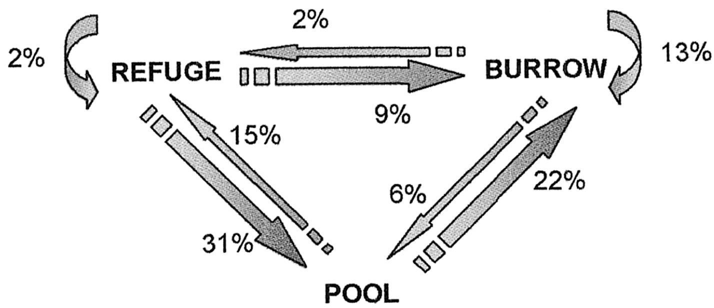

Fig. 4. Proportions of *Procambarus clarkii* movement between shelters and the pool (refuge to burrow and vice-versa, refuge to refuge, burrow to burrow and from burrow and/or refuge to the pool).

Table 1. Air, water and burrow temperature, dissolved oxygen, pH and conductivity along 24 h-cycles (mean ± SD).

	Dawn (6:00 h)	Day (12:00 h)	Dusk (19:00 h)	Night (1:00 h)
Air temperature (˚C)	22.8 (±5.3)	34.4 (±2.6)	22.6 (±1.9)	18.8 (±1.7)
Water temperature (˚C)	20.9 (±2.5)	30.5 (±2.5)	22.6 (±1.5)	21.7 (±0.5)
Burrow temperature (˚C)	19.4 (±1.7)	24.4 (±2.4)	22.4 (±1.0)	20.7 (±1.5)
Dissolved oxygen (mg/l)	14.1 (±8.7)	16.3 (±8.0)	2.1 (±3.0)	0.5 (±0.1)
PH	8.8 (±0.4)	9.2 (±0.4)	8.5 (±0.6)	8.6 (±0.5)
Water conductivity (µS/m)	3900 (±700)	4260 (±935)	4336 (±878)	3900 (±400)

and 14.4 hours (SD = 8.2, n = 19), respectively, without significant differences between both shelters (after Mann-Whitney U-test, U = 542, n = 33,40, $P > 0.05$). During the study period, 47 % of the marked individuals that were followed for more than 3 days inhabited two different shelters ($X^2 = 10.082$, df = 2, $P < 0.01$).

The frequency of the transitions that occurred between the shelters and the pools significantly prevailed over the other analysed transitions ($X^2 = 32.22$, df = 7, $P < 0.001$) (Fig. 4). About 62 % of individuals were seen in the pools between the occupancy of two different shelters. Crayfish movements to burrows, either from refuges, from pools or from other burrows, represented about 44 % of all transitions. The frequency of crayfish movements from burrows to other environments was very low (8 %) compared to movements from refuges (40 %). Only about 9 % of the marked crayfish dug a new burrow.

Temperature, dissolved oxygen and pH varied through the 24-h cycle (Table 1), with a similar pattern within the study period. With the exception of water conductivity and pH, the analysed variables presented significant daily variation (after Kruskal-Wallis one-way analysis of variance, air temperature: H = 44.5, df = 3, $P < 0.001$; water temperature: H = 19.7, df = 3, $P < 0.001$; burrow temperature: H = 37.7, df = 3, $P < 0.001$; dissolved oxygen: H = 21.4, df =

3, $P < 0.001$). The mean number of crayfish inhabiting a shelter per inspection increased significantly with the increase in air temperature (after Spearman rank correlation, $r_s = 0.386$, $n = 44$, $P = 0.01$), but did not increase with an increase in water temperature ($r_s = 0.125$, $n = 35$, $P = 0.475$). This may be related to extreme daily variations observed in air temperature (15 to 39 °C in the same day). Although extreme daily variation did also occur for the dissolved oxygen content (about 25 to 0.29 mg/l within 9 hours), no significant relation was observed between shelter occupancy and the minimum oxygen water content ($r_s = 0.324$, $n = 32$, $P=0.071$).

Discussion

Crayfish did not hide exclusively inside excavated burrows, but also in natural crevices under rocks, boulders and stones. Only a few crayfish were seen constructing a new burrow, the number of burrows being nearly constant throughout the study period. This low burrowing activity might be related to the type of sediment of the area under study. As extensively reported in the literature (see, Grow & Merchant 1979, Grow 1982, Rogers & Huner 1985, Hobbs & Whiteman 1991, Burras et al. 1995), crayfish are unable to construct permanent burrows in soils with large particles (i.e. sand, gravel, and cobbles) and without water or with scarce free water. Another reason may be related to drought processes. Due to the high temperatures, the water level in the shrinking pools decreased about 2–3 cm during 24 hours. Under these conditions, the margins of the pools became completely dry within a few hours, affecting crayfish burrowing. According to Burras et al. (1995), *P. clarkii* is largely unsuccessful in initiating burrows without the presence of standing water. In this study, many crayfish occupied wet sediment depressions with no free water.

Most burrows were simple, with a single short tunnel no deeper than 10 cm, and most morphological characteristics were quite similar to those previously described (Jaspers & Avault 1969, Huner & Barr 1984, Correia & Ferreira 1995, Ilhéu 1996). The low depth of the burrows may be related to both the high water table level (a few centimetres from the surface) and the low depth of soil. According to several authors (Tarr 1884, Hobbs 1942, Jaspers & Avault 1969), the depth of the burrows varies considerably with the different characteristics of the habitat, and is mainly dependent on the water table fluctuation.

Most burrows were occupied by a single individual or were found empty. Similar data were obtained by Correia & Ferreira (1995) in rice fields. When couples inhabited shelters, they mostly comprised a male and a female. Several studies (e.g. Huner et al. 1990, Ilhéu 1996) have reported that burrows were more often occupied by a male and a female (ovigerous or not), the former being in the front, if the female was berried or carrying young (HUNER 1992). HUNER & BARR (1984) reported that *P. clarkii*'s burrows with a complex architecture were able to host up to 50 individuals. Burrow use seems to be dependent on some habitat characteristics, strictly related to the hydrological cycle, and some phases of crayfish life history, such as reproduction (ILHÉU 1996). Although the study period coincided with the reproductive period of *P. clarkii* in the south of Portugal (ILHÉU & BERNARDO 1996), no ovigerous female or hatched young-of-the-year (YOY) were found in burrows. Thus, apparently, no immediate direct reproductive function seemed to be associated with burrow use.

Refuges were more crowded than burrows, with an average of 4.8 crayfish and a maximum of 12 individuals per refuge. Shelters were more often occupied by both females and smaller individuals. This suggests a role played by shelters in protecting more vulnerable individuals from predators. Predation on crayfish in temporary streams is strong, particularly in this region. The otter (*Lutra lutra*) is very abundant and feeds mainly on crayfish populations (DELIBES & ADRIEN 1987, M. ILHÉU, pers. obs.). During the drought period, the aquatic fauna becomes more vulnerable to predators (SCHWARTZ & JENKINS 2000), and the use of refuges, including burrows, may be of crucial importance for the individual's survival.

One further role played by shelters is to keep the crayfish temperature below the maximum environmental extremes (GHERARDI et al. 2002), as suggested by the increased number of specimens inhabiting the same shelter as the air temperature increased. This is in accordance with the hypothesis that the success of invading species depends on their ability to adjust to the new thermal environments occupied (MUNDAHL & BENTON 1990). However, further studies will be required to examine the thermal tolerance of *P. clarkii* and its relation to crayfish behaviour.

Crayfish left refuges more frequently than burrows, and passed from a refuge to a burrow more often than vice versa. Apparently, burrows were more efficient in providing protection, particularly against desiccation, as crayfish moved from refuges to the water more frequently than from burrows. Although some of the refuges provided a certain degree of cover/shadow, most of them did not assure a good protection against the environmental constraints, because of their location in dry sediments. Refuges near the margins of the pool showed higher humidity but had a low depth with no top protection. The high frequency of crayfish movements between refuges and pools could also be associated with foraging activity (ILHÉU 1996).

In accordance with previous observations (ILHÉU 1996, GHERARDI et al. 2002), crayfish were found outside the shelters mostly during the night and at dawn, while they were mostly hidden in shelters during the day. Contrary to our expectations, the indices of burrowing (opened/closed entrance and freshness) did not differ significantly throughout the 24-h cycle, which may be related to the low burrowing activity observed. According to BURRAS et al. (1995) *P. clarkii* burrowed only at night-time, while, during the day, individuals remained attentive to activities external to their chamber.

Although territorial behaviour has been reported on *P. clarkii*'s burrows (securing and defending) (BURRAS et al. 1995), in this study, individuals seemed not to be faithful to a unique shelter, since they used the same burrow and refuge no longer than, respectively, 30 hours and 24 hours. As shown in a radio-telemetry study (GHERARDI et al. 2002), crayfish may maintain "ephemeral home ranges" (ROBINSON et al. 2000), with a shelter as the core. As also recorded in other environments (e.g. in an irrigation ditch system in Italy, S. BARBARESI, pers. obs.), crayfish tend to occupy the first "best" shelter at the end of either their wandering phase or their foraging movements. A similar phenomenon was described in the river crab, *Potamon fluviatile*, in central Italy, and it was related to a surplus of excavated burrows available in the habitat (GHERARDI et al. 1987). Refined orienting capabilities have been reported in decapods (VANNINI & CANNICCI 1995), including crayfish species (BASIL & SANDEMAN 2000). However, in this study, crayfish did not exhibit "homing behaviour", probably due to both its costs in terms of energy and time and the environmental constraints.

The high number of crayfish found outside shelters indicates a certain degree of activity, which may be related to the crayfish feeding behaviour (ILHÉU 1996) and also to the burrowing process, including restoring and modifying the initial burrow (BURRAS et al. 1995). Furthermore, the low burrowing activity (new dug burrows) and the absence of an evident pattern of burrow use, could result from a considerable number of environmental constraints (e.g. low availability of adequate substrate for burrowing, harsh dry conditions, and predators) which may have conditioned the crayfish life cycle, including their "reproductive" burrowing behaviour.

In contrast to reservoirs or marshes, which present free water throughout the year, the ecological success of the crayfish is more precarious in temporary streams, and depends mostly on its ability to adapt to and resist harsh conditions during the summer season, particularly in dry years. In this scenario, crayfish seem to use burrows mainly for protection purposes against predators and from harsh environmental conditions.

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