Chapter · October 2018

DOI: 10.5772/intechopen.76191

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Chapter 3

Behavioral and Reproductive Strategies of *Porcellio* Species (Oniscidea) in Tunisian Pre-Desert Ecosystems

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Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/intechopen.76191

Abstract

Oniscids inhabiting xeric habitats are of particular interest because these habitats may be one of the important agents for desert soil fertility. Although numerous studies have examined the relationship between the environment and population ecology in woodlice that live in mesic habitats, very little is known about these desert species. Tunisia is known for its arid regions south of the Tunisian Dorsal, habitats in which several species of terrestrial isopods are well adapted. *Porcellio* is the most widely represented within these habitats: their species richness reaches eight in arid bioclimatic stage. The most widespread of the *Porcellio* is *P. buddelundi*, and the least widespread is *P. albicornis.* Behavioral and reproductive studies carried out in Zarat and Matmata on the two species *P. albinus* and *P. buddelundi* showed that the xeric *Porcellio* species are mainly active at night and they shelter from the extreme heat and dryness of their habitats either in burrows they dig or by vertical migration. The reproductive pattern is seasonal with two breeding seasons. Life history traits allow *P. buddelundi* to be an r-strategist and *P. albinus* a k-strategist. The latter displays a fairly developed social behavior, which allowed him to be the most evolved of *Porcellio.*

Keywords: terrestrial isopods, xeric species, arid environment, reproductive traits, behavior, abiotic factors

1. Introduction

Soil is a dynamic and complex system: its physical and chemical nature, with a porous structure, immense surface area, and extremely variable supply of organic materials, food, water, and chemicals, provides habitats for many living beings among which arthropods that make up an essential component. Five groups are chiefly represented: Isopoda, Myriapoda, Insecta, Acari, and Collembola [1]. The oniscoids (Oniscidea) with more than 3600 species belonging to 5 major taxonomic groups—Diplocheta, Tylida, Microcheta, Synocheta, and Crinocheta [2]—are an important component. Isopod species composition and diversity were studied in several habitats within the Mediterranean region. Terrestrial isopod community structure differs across habitat types (natural area, seminatural area, agroecosystems, and protected area), vegetation structure, and altitude [3–12].

During the last 30 years, great efforts have been made to understand the role of isopods as well as other invertebrates in soil processes and their interactions with the abiotic factors of soil function. These isopods are involved in the process of maintaining soil fertility. They are both "litter transformers" and "ecosystem engineers" [1]. First, these detritivores, like other invertebrates such as Myriapoda and Collembola, contribute to nutrient cycling through mechanical breakdown of plant litter, through biochemical changes in organic matter during digestive transit, and by regulating soil microbial activity [13]. Second, these ecosystem engineers as many other arthropods affect the structural properties of soils ensuring adequate nutrient retention, aeration, and water-holding capacity below ground, facilitate root penetration, and prevent surface crusting and erosion of topsoil. However, most of the studies concerning the contribution of isopods to nutrient cycling have focused on soils in mesic habitats of temperate regions [13–15]. In drier warmer areas of the world, particular attention was addressed to termites and ants as well as to their constructions which affect soil processes by increasing soil porosity and infiltration, reducing or increasing bulk density, altering soil erosion by depositing subsoil on the surface, and altering the concentration and spatial distribution of soil nutrients [1, 16]. Among desert isopods, the role of the burrowing species *Hemilepistus reaumurii* in maintaining soil fertility in arid regions has been well studied. The results of field observations and feeding experiments in the laboratory show that annual ingestion was 3–12% of the available dead organic matter [17] and soil turnover 2–41 g m^{-2} depending on the soil type and site conditions [1]. *H. reaumurii* by ingestion and defecation of organic matter and inorganic soil particles alters the structure of the decomposition substrate and increase the rate of decomposition in the desert ecosystem [17].

Besides their importance in maintaining ecosystem integrity, woodlice represent a remarkable group of crustaceans due to their high degree of terrestrialization [18]. These Oniscidae originally arising from the aquatic environment became terrestrial during the second half of the Paleozoic era [19]. They have evolved into a wide diversity of terrestrial species that have successfully colonized a wide range of habitats ranging from supralittoral levels (*Ligia* [20]) to mountains (*Porcellio djahizi* [21]) and desert ecosystems [22–24].

According to Sutton et al. [25], the successful colonization of the entire terrestrial globe by Oniscidea is explained by their flexible reproduction (onset and duration of the reproduction period) and its demographic parameters (longevity, age at sexual maturity, number of brood, etc.) that help them overcome the influence of the biotic and abiotic environmental factors to which they are subjected. Temperature, precipitation regime, and photoperiod are important factors regulating the reproduction of terrestrial isopods [26, 27], resulting in temporal coincidences of the release of the mancae with favorable conditions for growth and survival. This could explain the different reproductive patterns observed in terrestrial isopods: the majority of tropical and subtropical species have continuous reproduction [28–30], while temperate has a seasonal breeding followed by a period of sexual rest. The information available on terrestrial isopod reproduction patterns in temperate regions is largely for species occupying mesic habitats [31–42]. The reproductive phenology of xeric species in temperate regions has been studied extensively only for populations in the Middle East desert [32, 43–45]. These desert species that are well adapted to an arid environment differ considerably in their breeding seasons and strategies [46]. The burrowing species *Hemilepistus reaumurii* and *Hemilepistus klugii* are semelparous and reproduce during a very short time of the year: April and May for *H. reaumurii* and April for *H. klugii*. The other xeric species, which do not live in the burrows, are iteroparous. These are *Porcellio ficulneus* and *Porcellio barroisi*, which breed in spring, and *Armadillo albomarginatus*, which breeds in autumn. Both *Porcellio olivieri* and *Agabiformius obtusus* show continuous reproduction under laboratory conditions. Reproductive success in these terrestrial isopods depends on the largest size and number of offspring a female may have. The females of terrestrial isopods produce eggs and develop, following a parturial molt, a marsupium, which is not only a pouch for carrying eggs but plays the same role as a uterus that provides a transfer of substances between the female and its brood [47]. These activities require high energy costs for its offspring [48] that limit the future reproductive potential of the female. Given these constraints, better reproductive success can be achieved by extending care to offspring. Investing in already expensive offspring may be a better choice [44]. This hypothesis seems to explain the high parental investment of some terrestrial isopods in arid regions. The semelparous and burrowing species *H. reaumurii* shows two-parental care with sustainable family cohesion [2]. Indeed, the parental energy investment continues for several months after mancae release, until the young isopods disperse.

Oniscoids have succeeded, thanks to a number of adaptations noted above, to become the only large group of crustaceans to be completely terrestrial. Among them, Species that do not have effective protection against desiccation have been restricted to mesic habitats [49]. However, other species have managed to colonize semiarid and arid habitats, and some have even managed to thrive in the desert. These adaptations have made the nine species of *Hemilepistus* the most abundant detritivores of the macrofauna of many arid areas of Asia Minor [26, 45, 50]. All of them are burrowing species. The model species *H. reaumurii*, widely distributed in North Africa, is an isopod, physiologically and morphologically, well adapted to terrestrial life with its respiratory organs [51], its water balance, and its resistance to temperature [52, 53]. However, based solely on these adaptations, the species could not exist in the current biotopes. His great success is due, firstly, to his behavioral adaptations—his social character [44, 54] and his orientation [55]—and secondly to his reproductive strategy: *H. reaumurii* as *H. klugii* is semelparous and reproduces during a very short time of the year, April and May for the first species and April for the second [44, 45].

In the case of Tunisia, *H. reaumurii* can occupy the same xeric habitat as many other Oniscidea such as *Porcellio* species. In this genus, several studies have been conducted only on widely distributed and very frequent species. These studies focused on morphology [21, 56, 57], reproductive cycles [28, 40, 41, 58], enzymatic polymorphism [59], and Infection with the feminizing *Wolbachia* bacterium [60]. Little is known about xeric species.

Knowledge about the xeric species of *Porcellio* is still limited to their systematic [61–64], and only partial information is available on their reproductive and behavioral strategies

[44]. Based on the results obtained by the different studies carried out on the reproductive phenology of the desert species of the Middle East and based on the knowledge acquired in the *H. reaumurii* model terrestrial species, it is envisaged:

- To closely study the reproductive model of the semidesert species *P. buddelundi* and desert *P. albinus*.
- To verify the hypothesis of a single breeding season observed in Middle East desert species.
- To analyze the burrowing behavior of *P. albinus* and to identify its locomotor activity rhythm, in order to understand the behavioral mechanisms of adaptations of this species to the xeric conditions.

2. Desert *Porcellio* species and their geographical distribution

Despite its small size (163,610 km^2), Tunisia has 1300 km of coast on the Mediterranean Sea and is characterized by climatic, geological, and relief diversity. It is comprised of wetlands (5%), cultivated land (32%), nearly 13% forests, and about 40% desert lands. The arid regions

Figure 1. Geographical distribution of *Porcellio simulator* and *Porcellio albicornis* in Tunisia.

extend south of the Tunisian Dorsal from Sfax to Douiret in Tataouine. The climate of pre-Saharan Tunisia is located in the Mediterranean isoclimatic zone which can be defined, from an ecological point of view, as a climate of temperate zone, thus with seasonal and daily photoperiodism and with rainfall concentrated during the cold or relatively cold season (less than 200 mm/year), summer being dry [64].

This great ecosystem diversity has allowed the installation of several species of terrestrial Isopods, and the most recent assessments point to more than 40 species of oniscoids (Charfi-Cheikhrouha et al., unpublished). The *Porcellio* list, assessed by Medini-Bouaziz as 12 species in 2002 (*P. laevis*, *P. variabilis*, *P. dominici*, *P. marginenotatus*, *P. spatulatus*, *P. albicornis*, *P. lamellatus*, *P. djahizi*, *P. simulator*, *P. buddelundi*, *P. olivieri*, and *P. albinus*), was enlarged by the discovery of a 13th species *Porcellio wagneri*, which was first reported in Tunisia by Hamaied et al. (unpublished). The high species richness of *Porcellio* is reached in arid bioclimatic stages (eight species). The xeric species are quite numerous, representing more than a third of all *Porcellio* reported in Tunisia. These pre-desert and desert species belong to two distinct geographical groups of *Porcellio*: the North African group or laevis group and the group bético-rifain or group Hoffmanseggi. The former is represented by four of the five species reported in Tunisia (*P. simulator*, *P. olivieri*, *P. albicornis*, and *P. albinus*) and the last one by species *P. buddelundi* [64].

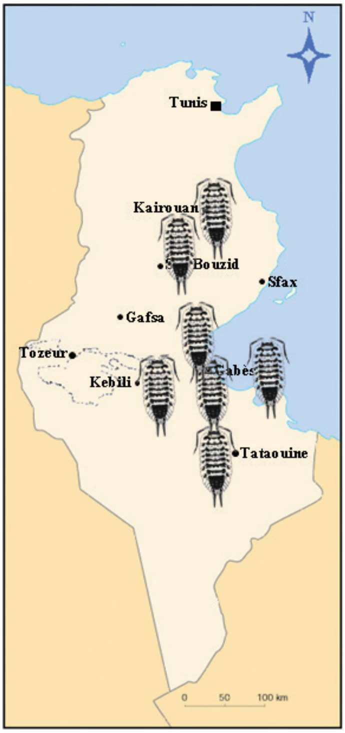

Figure 2. Geographical distribution of *Porcellio buddelundi* in Tunisia.

2.1. Geographical distribution in the world and in Tunisia

Xeric species, confined to the pre-Saharan Tunisia, are spread south of the Tunisian Dorsal corresponding to the eastern extension of the Saharan Atlas, as follows:

- *Porcellio simulator* is a North African species; its populations cover the center of Algeria [50] and occupy the center-west sector in the region of the high steppes in Tunisia [57] (**Figure 1**).
- *Porcellio buddelundi* and *Porcellio albicornis* show a narrow distribution area that is restricted to Sicily and circum-Sicilian islands in Italy [62] and in Tunisia [23, 64]. In Tunisia, the distribution of *P. buddelundi* covers Jeffara, the plains of Kairouan, and the high Tunisian steppes, while the presence *of P. albicornis* has been reported in the regions of Gabes and Kebili (**Figure 2**).
- *Porcellio olivieri* has a wide geographical distribution area that covers North Africa including Morocco [63], Algeria [65, 66], Libya [63, 67] as well as Egypt [49, 63, 65], and the Middle East [65, 68]. Described as an eastern desert species, *Porcellio olivieri* is found in Tunisia, in the Jeffara regions, in the southern lowlands, and in the southern Sahel (**Figure 3**).

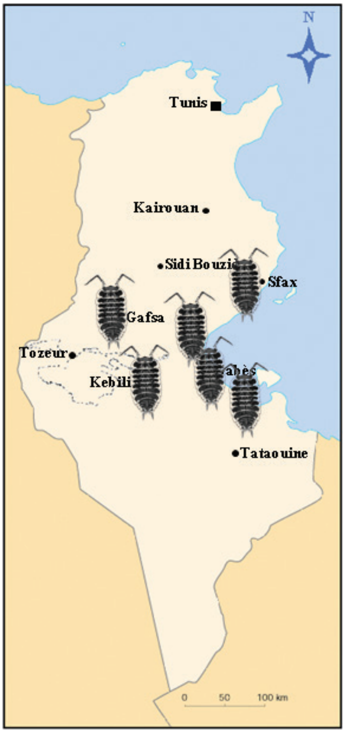

Figure 3. Geographical distribution of *Porcellio olivieri* in Tunisia.

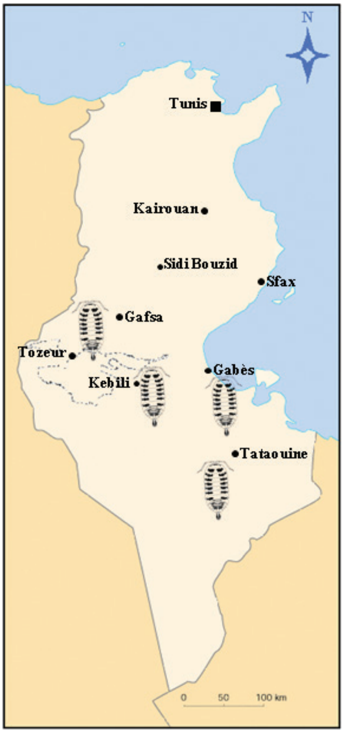

Figure 4. Geographical distribution of *Porcellio albinus* in Tunisia.

Figure 5. *Porcellio buddelundi.*

Figure 6. *Porcellio albinus.*

- The distribution area of *P. albinus*, the only burrowing species of the genus in Tunisia, is less extensive than that of *P. olivieri*. Its geographical distribution covers the North African Sahara, the Canary Islands [67], and the Niger Sahara [44]. In Tunisia, *P. albinus* occupies the regions of Jeffara and Nefzaoua and the southern lowlands. The expansion of this species to the north stops south of the Gafsa region (**Figure 4**). *Porcellio albinus* as *P. albicornis* is one of the rare species adapted to arid and Saharan habitats [64, 69].

2.2. Biotopes

The distribution of the xeric species correlates to stone coverage with the exception of both species *Porcellio albicornis* and *Porcellio albinus*, which live in sandy soil irrespective of stone coverage. The three pre-desert species *P. simulator*, *P. buddelundi*, and *P. olivieri* dwell in rocky areas (reg) which is home to various types of garrigue vegetation, including *Artemisia, Rosmarinus, Stipa,* and *Lygeum*; they rarely share the same habitat. The other two species, *P. albinus* and *P. albicornis*, were found in sandy nebkhas covered by desert vegetation species such as *Stipagrostis pungens*, *Astragalus armatus*, *Zygophyllum album*, and *Calicotome villosa*. However, *P. albicornis* may occupy another type of biotope that corresponds to a dry wadi rich in *Limoniastrum monopetalum* and *Peganum harmala* where he lives in sympatry with *Hemilepistus reaumurii*.

The two *Porcellio* we investigated in this chapter are *P. buddelundi* and *P. albinus* (**Figures 5** and **6**). Both species were collected at two different sites.

The population of *P. buddelundi* was collected at Oued El Jir, Matmata (Gabès), in the southeast of Tunisia (33°31′34″N, 10°7′19″ E (DMS)) (**Figure 7**). The habitat corresponds to a bare stony "reg" (**Figure 8**), and the soil is silt-clay type. This silt-clay structure is characterized by its high water

Figure 7. Sampling sites.

retention capacity and consequently high residual moisture content. In fact this criterion and the slightly alkaline pH of the soil (pH = 7.83) favor the survival of this species in a desert environment. Oued El Jir homes various types of garrigue vegetation, including *Artemisia*, *Rosmarinus*, *Stipa*, and *Lygeum*. The Köppen-Geiger climate map classified Matmata climate as BSh type. The climate in this area is characterized by an annual mean temperature of 18.9°C and a moderate annual temperature range (9–28.6°C) (**Table 1**). The total annual rainfall is 209 mm, and the variation in the precipitation between the driest and the wettest month is 34 mm (**Table 1**).

For *P. albinus*, the sampling site was the coastal area of Zarat, South of Gabes, Tunisia (33°40′N, 10°21′E (DMS)) (**Figure 7**); it corresponds to a marine sebkha environment [70]. The habitat is dominated by nebkhas corresponding to an accumulation of sand brought by the wind and trapped by vegetation (**Figure 9**). The vegetation was mainly composed of desert-adapted species

Figure 8. Biotope (Reg) of *Porcellio buddelundi.*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Mean temperature (°C)	9	10.6	13.7	17.7	21.2	25.3	28.6	28.4	25.9	21.1	15.3	10.2
Minimum temperature (°C)	4.2	5.2	8	11.7	15.1	19.2	21.8	21.7	19.8	15.5	9.9	5.3
Maximum temperature (°C)	13.9	16.1	19.5	23.7	27.3	31.4	35.4	35.1	32.1	26.7	20.7	15.2
Rainfall	28	24	35	16	11	3	1	3	13	24	28	23

Table 1. Matmata temperature and precipitation.

Figure 9. Biotope (nebkhas) of *Porcellio albinus.*

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Mean temperature (°C)	11.7	12.9	15.3	18.3	21.8	25.1	27.7	28.1	26.3	22.2	16.9	12.8
Minimum temperature (°C)	7	7.7	9.9	12.8	16.2	19.6	21.6	22.1	20.7	17	11.8	8.1
Maximum temperature (°C)	16.4	18.1	20.8	23.9	27.4	30.6	33.9	34.2	31.9	27.6	22.1	17.6
Rainfall	19	17	20	15	7	2	0	1	16	35	23	23

Table 2. Zarat temperature and precipitation.

restricted to arid areas such as *Stipagrostis pungens*, *Astragalus armatus*, *Zygophyllum album*, and *Calicotome villosa*. The climate at Zarat is considered to be BWh by the Köppen-Geiger climate classification. Zarat climate is characterized by an annual rainfall of 178 mm and a difference in precipitation between the driest and the wettest month of 35 mm (**Table 2**). The average annual temperature is 19.9°C, and the annual temperature range is about 16.4°C (**Table 2**).

3. Reproductive traits comparison of *Porcellio albinus* and *Porcellio buddelundi* in pre-desert habitats

In North Africa, only the xeric species *Armadillo officinalis* from Libya [71] and *Hemilepistus reaumurii* from Tunisia [72, 73] have been the subject of study on reproductive phenology. These studies confirmed seasonal reproduction of temperate region species. Considering this element and what has been reported for the xeric Oniscidea of the Middle East in the introduction, two *Porcellio* species from the arid regions (*P. buddelundi* and *P. albinus*) were chosen on the basis of their geographical distribution in Tunisia (quite large in the case of *P. buddelundi* and more restricted in *P. albinus*) and their burrow digging (non-burrow digging *P. buddelundi* and *P. albinus* burrowing species). Both species are expected to have seasonal breeding, based on studies of reproductive phenology performed on temperate oniscoids.

3.1. Breeding phenology

The two *Porcellio* we investigated on Tunisia area were studied in the field. To study the breeding pattern of both species, a sampling of almost 100 specimens of *P. buddelundi* and about 60 specimens of *P. albinus* took place during 12 consecutive months for the former and 17 months for the latter. See Medini-Bouaziz et al. [22, 23] for further details on material and methods.

Sexual maturity was reached at about 14 mm in size during the first year of life (9 months) in females *of P. albinus* and at 41.1 mg of body mass in those of *P. buddelundi*. Considering this and the mean ovigerous female size (17.38 ± 1.8 mm), females of *P. albinus* cannot reproduce until the second year of their life. Those of *P. buddelundi* reproduce when they reach or exceed 70 mg body mass.

For both species, breeding starts in March and two breeding activities are defined (**Figure 10**). The first and the most important one was in spring, from March to June in the Zarat population of *P. albinus* and from March to May in Matmata population of *P. buddelundi*. The second was in the fall during the month of September in the first population and from September to October in the second one.

3.2. Fecundity, fertility and reproductive allocation

Fecundity estimated by the number of marsupial eggs was lower in *P. albinus* (36.3 ± 13.8 eggs) than that in the *P. buddelundi* species (60.9 ± 3.5 eggs). In the latter species, Medini-Bouaziz et al. [22] have shown that fecundity increases more with increasing ovigerous female body mass in spring than in autumn. A positive correlation between ovigerous female size and fecundity is noted in both species [22, 24].

Based on the study of fertility (number of mancae released from the marsupium) and the energy allocated to reproduction for each of the two species (**Table 3**), different tradeoffs were highlighted. The pre-desert species *P. buddelundi* generates a large number of small progeny (53.13 ± 3.2 mancae; newborn body mass = 0.44 ± 0.21 mg), whereas *P. albinus* produces few large offspring (19 ± 9 mancae; newborn body mass = 1.44 ± 0.75 mg).

3.3. Care of progeny

Of the two species studied, only *P. albinus* is able to provide care to his offspring. As reported by Medini-Bouaziz et al. [22], the study of the population dynamics of *P. albinus* in Zarat revealed, in all samples taken at night outside the burrows, predominance of larger specimens due to the absence of individuals whose size is smaller than 8 mm. Indeed, after the mancae release and during the first 2 months of life, newborns do not leave the family burrow. During this sensitive period, they depend on their brood-caring mother who provides

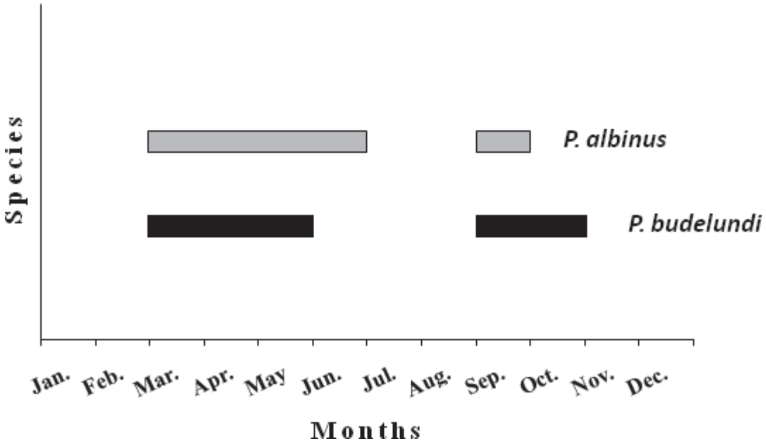

Figure 10. Reproductive activities of *Porcellio albinus* and *Porcellio buddelundi.*

them with food and defends them against predators. At the age of 2 months (size 8 mm), the young emerge for the first time from the burrow to forage.

Besides these results, the digging of about 30 burrows during the spring breeding season, carried out during the day when the animals are inside their burrows, revealed that these burrows contain either adults over 14 mm in size (one or two males/burrow, one female/burrow, a couple/burrow) or an adult female with several mancae or juveniles less than 12.5 mm in size. The number of these young in the burrows ranges between 3 and 35 individuals with an average number of 15 ± 10 pulli or juveniles/burrow. This indicates that the young of *P. albinus* remain in their natal burrow and do not disperse until they reach sexual maturity.

3.4. Life history traits comparison of *Porcellio albinus* and *Porcellio buddelundi*

The study of life history strategies integrates physiological, morphological, and behavioral traits to explain how organisms allocate finite resources to maintenance, growth, and reproduction, under predictable and unpredictable environments [74]. Thus life history patterns, evolved by natural selection, represent an optimization of tradeoffs between growth, survival, and reproduction. One major tradeoff could be between the number of offspring produced and the amount of energy allocated to each one. The timing of the first reproduction is another tradeoff; early reproduction reduces the chances of dying without offspring, but late reproduction can provide healthier offspring or better care. Members of some species breed only once (semelparity), while members of other species can breed several times (iteroparity). The choice of the appropriate strategy may be related to the degree of habitat specialization. Habitat specialists have often shown K-selected traits, while habitat generalists have shown r-selected traits. The xeric species *P. albinus* and *P. buddelundi* well adapted to arid environment differ considerably in their life history traits. These life history traits are summarized in **Table 3**.

To shelter from the extreme heat and dryness in arid environments, *P. albinus* digs burrows, while *P. buddelundi* performs a vertical migration. Both species are iteroparous and started their breeding activity in March with two breeding seasons. The length of the reproductive activity of *P. albinus* longer than 1 month in spring and less than 1 month in autumn than that of *P. buddelundi*. *P. albinus* has a longer development time, and sexual maturity is reached late, at 9 months old, which represents more than a third (37.5%) of its lifetime. *P. buddelundi* grows faster and reaches sexual maturity at 3–3.5 months old which corresponds to almost 20% of its lifetime. In *P. albinus*, there was no difference between ages of oldest female (largest female) and the largest reproductive females. This indicates that in this species, females were able to reproduce until their death, while in *P. buddelundi*, there is a difference between largest female (18 months) and largest reproductive female (12 months) because largest females in this species were not reproductive. *P. albinus* and *P. buddelundi* have a similar length of breeding period at the first brood: 28–35 and 28–33 days, respectively (**Table 3**). Although females of *P. albinus* were larger than those of *P. buddelundi*, they have a lower fecundity range (36.3 ± 13.8 egg) and fertility (19 ± 9 mancae). *P. albinus* also showed the lower mean reproductive allocation (9.94 ± 6.04) but the higher newborn body mass (1.44 ± 0.75 mg). Only *P. albinus* which has few offspring during each reproductive event often gives extensive parental care. This species with this type of high investment strategy uses much of its energy budget to care for its offspring.

Life history traits	***P. buddelundi***	***P. albinus***
Burrow digging	No	Yes
Body size and newborns mass		
Newborns body-mass (spring)	0.44 ± 0.21mg	1.44 ± 0.75 mg
Size of largest female	1.6 cm	2.4 cm
Body-mass of largest female	210 mg	–
Life span (estimated age)		
Largest female	18 months	24 months
Age at last reproduction	12 months	24 months
Itero/Semelparous	Iteroparous	Iteroparous
Breeding activity	March-May	March-June
	September-October	September
First reproduction		
Female size	0.65 cm	1.4 cm
Female body-mass	41.1 mg	129 mg
Female estimated age	3-3.5 months	9 months
Length of breeding period (first brood)	28-33 days	28-35 days
Fecundity (spring)	60.9 ± 3.5 eggs	36.3 ± 13.8 eggs
Fertility	53.13 ± 3.2 mancae	19 ± 9 mancae
Reproductive allocation (%)	29.06 ± 12.58	9.94 ± 6.04
Care of offspring	No	Yes
Offspring age estimated at the end of parental care	–	2 months

Table 3. Life history traits of the studied xeric species *Porcellio buddelundi* and *Porcellio albinus*.

All these results showed that *P. buddelundi* exhibited a set of characteristics corresponding to those of the r-strategists. In comparison, *P. albinus* displayed opposite trends that fit well with the expected characteristics of a k-strategist.

4. Behavioral strategies

The general objectives of our research are oriented, in this second part, toward understanding the behavioral mechanisms involved in the adaptation of terrestrial isopods to harsh desert conditions. The study model is *P. albinus*; It is found in habitats ranging from coastal sand nebkhas and up to desert ones, hundreds of kilometers away from the sea littoral. The choice of this model is justified by its unique burrowing behavior in the genus *Porcellio* in Tunisia. Based on the knowledge acquired in the terrestrial species model *H. reaumurii,* we propose to analyze the burrowing behavior and to identify the rhythm of activity of *P. albinus*, in order to understand the behavioral mechanisms of adaptations of this species to xeric conditions.

4.1. Spatial distribution of burrows

Among the desert-dwelling *Porcellio* species, widespread in southern Tunisia, only *Porcellio albinus* exhibits a burrowing behavior. *Porcellio albinus* shelters from the extreme heat and dryness of its desert habitat in a burrow. One wonders how this species "chooses" the location of its burrows in this type of habitat. What are the abiotic factors that influence this choice?

To answer these questions, several sampling campaigns were carried out in the Zarat station during 2013. The density of burrows, their spatial distribution, and their orientation were studied (see [23] for further details on material and methods). The species was also observed in the field. The analysis of the data collected showed that the distribution of the burrows depends on several factors. *Porcellio albinus* prefers to dig burrows at sandy nebkhas (the mean density of burrows per nebkha was 1.27 ± 1.64 burrows m^{-2}). This preference is justified by the nature of the soil that is easy to dig and the isopod's low ability to do work on harder soils [23, 44]. It is also explained by the sand which has a low water retention capacity associated with a lack of capillarity between the dry surface and the moisture layers which further reduces the evaporation.

In each nebkha, the *P. albinus* burrows are located in a circular belt. In this belt, a preferred sector in which the burrows were grouped is oriented toward the southern direction, to avoid the prevailing wind direction E-NE at Zarat: *P. albinus*, leaving its burrow for forage stacks the sand torn from the burrow in front of the opening [44]. This sand, marked with the owner's individual-specific chemical signature, is then used as a landmark to find the burrow after excursion [44]. Thus, to regain infallibly its burrow, *P. albinus* chooses, as the location of its burrows, a place sheltered from the prevailing wind.

In addition, *P. albinus* prefers to dig its burrow in nebkhas covered by a mixture of plants. Relating to this last factor, the high densities of burrows determined in nebkhas with a mixture of *Astragalus armatus* and *Stipagrostis pungens* indicate that these nebkhas could be considered as a high-quality micro-ecosystem for *P. albinus* [23].

4.2. Burrow morphology

For this study, five burrows located in nebkhas were randomly selected every month, from July 2012 to June 2013 in the sandy coastal area of Zarat, Gabès (in the southeast of Tunisia). For each burrow, three parameters were always determined: sand depth, angle between descending the neck of burrow and horizontal, and burrow length (**Figure 11**). To study the burrow morphology of *P. albinus*, the use of paraffin casting created an in situ, internal mold of the burrow structure. The cast is then excavated for analysis.

The results of this study showed that *P. albinus* is able to dig a burrow, in the habitat of Zarat, at any time of the year. All the burrows of *P. albinus* are dug toward the center of the nebkha; they were generally inclined and make an angle between descending neck of burrow and the horizontal ranging between 2 and 45°; the mean angle was about 22.2 ± 12.87°. Their depth ranged between 1 and 28 cm with a mean depth of 13.89 ± 9.43 cm. The total burrow length

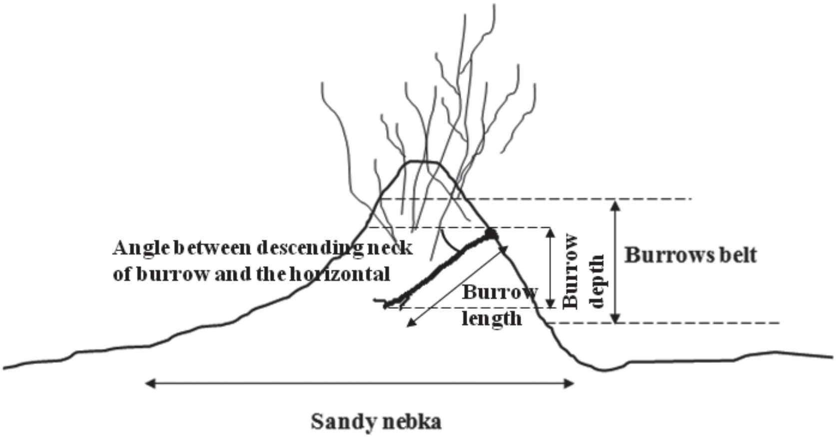

Figure 11. Parameters used to assess the morphology of the burrows.

Figure 12. Burrow with a single nesting chamber.

varied between 8 and 62 cm with an average burrow length of 24.04 ± 10.41 cm. The longest length of the burrow was reached in September, considered the hottest month of the year in Zarat area.

A total of 60 resin casts of the burrows of *P. albinus* were made in the coastal nebkha area of Zarat. The study of these casts showed that the burrows are either of simple form, a tunnel

Figure 13. Burrow with two nesting chamber.

containing only one nesting chamber in its deep part (**Figure 12**), or of complex form, a tunnel containing two or more nesting chambers in its deep part (**Figure 13**); generally, in all casts studied, animals trapped in the cast were confined in the terminal part of the burrow.

4.3. Daily locomotor activity of *P. albinus*

Locomotor activity of *P. albinus*, deducted from monthly field observation data on the first and the last specimens in activity outside their burrows, was studied in synchrony con with light-dark cycle. During all the sampling period from November 2012 to October 2013, *P. albinus* showed a strict nocturnal activity: only individuals whose size is equal to or exceeds 8 mm began to emerge from their burrows after dusk and return to their shelters before dawn. This circadian rhythm of *P. albinus* is regulated by the rhythmic and natural variations of the duration of the dark period; a positive correlation is observed between the circadian period of the locomotor activity of the species and the duration of the scotophase ($r = 0.874$, $p \leq 0.05$).

5. Discussion

According to our results, among terrestrial isopods dwelling in xeric, semiarid, and arid habitats [75], the genus *Porcellio* with five species in Tunisia [76] ranks second after the genus *Hemilepistus* with nine species [50]. The *Porcellio* species discussed in this chapter showed a geographical distribution which depends on many ecological factors mainly climatic and orographic and of less importance edaphic. All of them were distributed south of the Tunisian Dorsal; the distribution of both xeric species *P. simulator* and *P. buddelundi* was limited, in the North, by the 500 mm isohyets. The distribution of *P. olivieri* was restricted to arid environments, while the rare species *P. albicornis* and *P. albinus* tolerate remarkably high temperatures and were able to reach the Sahara. Woodlice showing comparably effective adaptations to desert environments are *H. reaumurii* [26] and *Venezillo arizonicus* [77]. The latter two species possess protection against water loss through the cuticle which corresponds to a thicker and more calcified cuticle, thus reducing water evaporation in arid environments [53] and indicating that permeability to water has been reduced during adaptation to habitats with periodically or permanently low water availability. These physiological adaptations were, however, insufficient for coping with the harsh conditions of desert environments.

To survive in the harsh conditions of the desert and escape the danger of desiccation, the *Porcellio* survive the high temperature during the day in summer and autumn, either by vertically migrating (*P. buddelundi*, *P. simulator*, *P. olivieri*, and *P. albicornis*) or in a burrow which *P. albinus* dig in loose soil at any time of the year unlike *H. reaumurii* [26] who dig new burrows only in early spring. The maximum density of burrows, in nebkhas, was recorded in the southern sector to avoid the main wind direction [23]. *P. albinus* showed no daily activity; all year long it is a strictly nocturnal species. Individuals whose size is more than 8 mm started their activity after dusk to forage and return to their shelter before dawn. This nycthemeral rhythm of *P. albinus* is regulated by the rhythmic and natural variations of the duration of the scotophase. The circadian rhythm in *P. albinus* is probably generated by an internal clock that is synchronized to light-dark cycles and other cues in an organism's environment; this intrinsic timer was apparent in *Tylos europaeus* [78] and *H. reaumurii* [79, 80]. Nocturnal activity of *P. albinus* was correlated to a lower evaporation rate. In burrows, *P. albinus* breed and take care of their offspring for about 2 months [22]. Given the importance of a burrow for this species, the sand, scraped from the burrow and piled outside, when the member of a family started their activity, was used to close the burrow during the day probably as an antipredatory strategy. In addition, *P. albinus* used mechanisms similar to those found in *H. reaumurii* [55, 81], using combination of celestial mechanisms and the sand scraped from the burrow to relocate the burrows after foraging [44]. Burrows of *P. albinus*, in nebkhas of Zarat area, showed a simple or complex tunnel with one nesting chamber in its deep part for the first and with two nesting chamber for the second. *P. albinus'* burrow length reached its maximum in September.

In addition to behavioral adaptations, the pre-desert and desert species of *Porcellio* have developed reproductive strategies that allow them to better succeed in the colonization of arid environments. The study of the reproductive phenology of the populations of the two *Porcellio* species from pre-desert ecosystems in Tunisia allowed to bring new fundamental knowledge on the dynamics of these populations as well as on the reproductive traits of the xeric *Porcellio* species *P. albinus* and *P. buddelundi*. The reproduction of these two iteroparous *Porcellio* was characterized by two breeding seasons: the most important one in spring and the other in autumn distinctly separated by a sexual rest phase [22, 24]. This reproductive phenology differs from that of (1) mesic species such as *P. variabilis* [33, 82], which generally shows a breeding period spread over several months followed by a sexual rest and (2)

H. reaumurii and other desert species from the Middle East characterized by a single spring or autumn breeding season [45, 72, 83]. Our results about reproductive traits of both species showed that *P. buddelundi* exhibited a set of characteristics corresponding to those of the r-strategists: a shorter life span, a smaller size, early sexual maturity, higher fertility, and a reproductive allocation to maximize brood size. In comparison, *P. albinus* displayed opposite trends to which parental care was added which corresponds well to expected characteristics of a k-strategist. These results reinforce the Sutton et al. [25] observations and those of Quadros et al. [74] by showing that *P. buddelundi* and *P. albinus* have opposite life history traits that correspond to their degree of habitat specialization: the steneodynamic species corresponds to a K-selected habitat specialist and the eurydynamic species to an r-selected habitat generalist. According to the study of life history traits of the two species, *P. albinus* with its capacity to dig burrows displays a fairly developed social behavior compared to other species of the genus which allowed him to be the most advanced of the *Porcellio* genus but remain less evolved than *H. reaumurii*.

The quite diverse *Porcellio* genus in arid regions is an integral part of pre-desert macro-arthropod communities. In a single square meter of soil of desert ecosystems, as many as four species of *Porcellio* may be collected [76]. Under comparable conditions where earthworms are absent, ant communities may comprise up to 28 species [84]. All of these *Porcellio* species as many other terrestrial isopods [7, 13–15, 17], termites, and ants contribute to the consumption and mineralization of a significant part of litter (litter transformers) in arid areas [1, 16, 85]; they build holorganic structures (their fecal pellets) that serve as incubators for microbial activities [Lavelle, 1996]. The burrowing and digging activity of *P. albinus* as well as the vertical migration of the other pre-desert species of the genus *Porcellio* may influence the infiltration properties of the soil and, thus, on the whole process of water movement within the soil profile and on the subsurface flow process. This was studied in the genus *Hemilepistus* from arid region of southeastern Russia, at an estimated population density of 1.4 million individuals ha^{-1}; the animals were deemed capable of transporting, from a depth of up to 1 m to the surface, 5–6 tonnes of soil, of a different granulometrical and chemical composition, annually [86]. Macroporosity related to the activity of other arthropod groups such as ants and termites demonstrated prodigious earth-moving abilities, which may contribute importantly to soil formation. For example, in the Chihuahuan desert, four species of ants which have relatively short-lived colonies transported between 21 and 86 kg ha^{-1} yr.$^{-1}$ of subsurface soil to the surface, and some species of termites produce erodible surface galleries different in composition from the surface soil [16]. As result of "ecosystem engineers'" work, topsoil was improved and was able to support a more diverse and dense vegetation.

6. Future prospects

Future prospects, which could be considered from our research and have led to the following questions, are as follows:

- The reproductive phenology of desert *Porcellio* species other than *P. buddelundi* and *P. albinus*, such as *P. olivieri* and *P. simulator*, and their reproductive strategies.

- The behavioral aspect of reproduction in pre-desert and desert species from arid environments: the choice of the sexual partner, sexual conflicts, polygamy, parental care, etc.
- Physiological and genetic mechanisms that facilitate the survival and therefore the reproduction of these species in these desert habitats.
- Social behavior of *P. albinus* (recognition systems of offspring, different members of the same family, volatile or nonvolatile discriminators) is one of the priorities of our future research to better understand the physiological mechanism that allowed its adaptation and prosperity in the difficult conditions that prevail for several months of the year in its range.

The susceptibility of *P. albinus* to temperature rise and moisture decline makes this terrestrial isopod an appropriate biological model for examining its potential responses to climate change. This line of research could be considered in the context of global climate change such as the study in microcosms of the effects of changes in temperature and relative humidity on the activity, aggregation, and survival of *P. albinus*.

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