

Reproductive ecology of terrestrial isopods (Crustacea: Oniscidea)

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Summary

Terrestrial isopods (Crustacea: Oniscidea) are important detritivores in many ecosystems. Because reproductive success and population dynamics of the Oniscidea depend on diverse biotic and abiotic environmental factors, the effects of global climate change on their biology may be significant. Although few studies have examined the relationship between climate change and population ecology in terrestrial isopods, much is known about their environment, genetics, physiology, behavior, life history, population biology, and evolutionary patterns. This review addresses the influence of biotic and abiotic environmental factors on terrestrial isopod reproduction. Significant biotic factors include microorganism-mediated sex determination, mate choice, sperm competition, maternal effects, food availability, and predation. Significant abiotic factors include temperature and moisture regimes, photoperiod, altitude, latitude, and microhabitat diversity. Studies of these factors reveal general patterns, as well as informative exceptions, in the ways different oniscid species, as well as different populations within a species, respond to environmental variation.

Keywords

Terrestrial Isopod; Oniscidea; reproduction; ecology; life history; *Wolbachia*; environment; detritivore

Introduction

Terrestrial isopods (Crustacea: Oniscidea) are widely distributed across the globe with more than 3600 named species in five major taxonomic groups: Diplocheta, Tylida, Microcheta, Synocheta, and Crinocheta (Schmalfuss, 2003). Their ubiquity, ecological significance, and adaptations to terrestrial existence make them ideal subjects for study, as seen in an extensive literature on their biology (reviewed by Sutton, 1972; Warburg, 1994; see also proceedings of international symposia on the biology of terrestrial isopods, i.e. Sfenthourakis et al., 2003; Hassall et al., 2005b) (Figure 1).

Terrestrial isopods are important detritivores in many terrestrial ecosystems (Zimmer et al., 2002), and global climate change could affect the relationships between the environment, reproductive behavior, recruitment, population dynamics and the



Figure 1. *Armadillidium vulgare*, a terrestrial isopod (Crustacea: Oniscidea).

evolution of life histories in oniscids. These impacts on oniscid communities are in turn expected to affect microbial decomposition and nutrient cycling (Zimmer, 2004). Studies of climate change on detritivore communities are therefore needed, but presently rare. One of the first studies was conducted by Zimmer (2004) over a five-year period on relationships between climate change and oniscid population dynamics in Germany, where climate models predict warmer future winters with less precipitation in summers (IPCC 2001). Several species (*Porcellio scaber*, *Philoscia muscorum*, and *Oniscus asellus*) had low population densities under these conditions, but another species (*Hyloniscus riparius*) underwent population growth. This may have been due in part to changes in breeding phenology of some species, with *P. scaber* and *O. asellus* breeding earlier.

The Oniscidea are relatively unique among terrestrial arthropods because females provide substantial maternal care to eggs and young (Sutton, 1972; Surbida and Wright, 2001; Kight and Nevo, 2004; Lardies et al., 2004b). Females carry eggs and early-instar young (mancae) in a ventral marsupium (a fluid-filled pouch formed by oostegites on the ventral pereon), and further invest in mancae by providing them with nutrients and supplying them an aqueous environment in the marsupium (Warburg, 1987; Warburg and Rosenberg, 1996). This mode of reproduction appears to be an adaptation for reproduction on land (Warburg, 1993) but it places constraints on female reproductive potential: fecundity is physically limited by the size of the marsupium (Schmalfuss, 1984). Hence maternal care is a limiting factor on higher-level phenomena such as recruitment and population growth.

The present review will address ways in which terrestrial isopod reproduction is shaped by (and to some degree shapes) the biotic and abiotic environments. I will first discuss the evolution of chromosomal versus microorganism-mediated sex determination in terrestrial isopods and the resulting effects on individual reproductive effort and population biology. The discussion will then turn to male and female reproductive behavior and mating strategies. Female reproduction in particular has received much attention in the context of life history tradeoffs. Female reproductive patterns vary within and between species and environments in ecologically meaningful ways.

Genetic and environmental sex determination in terrestrial isopods

Chromosomal sex determination in terrestrial isopods is ancestrally heterogametic (ZW) in females and homogametic (ZZ) in males (Rigaud, 1997; Charlat et al., 2003). Homogametic ZZ embryos produce androgenic hormone, which induces the development of the androgenic gland and subsequently the male phenotype. However, in some populations, bacteria of the genus *Wolbachia* interfere with chromosomal sex determination by feminizing infected homogametic ZZ embryos (*Armadillidium vulgare*, Juchault et al., 1993; Bouchon et al., 1998; Rigaud and Moreau, 2004). These individuals do not develop the androgenic gland and therefore express the female phenotype.

The bacterium is an obligate intracellular parasite and is transmitted vertically from mother to offspring in egg cytoplasm. Hence the evolutionary significance of host feminization: *Wolbachia* can only be transmitted through females. One consequence for host populations is a strong drive toward female biased sex ratios. Infected individuals produce more daughters than sons, which in turn produce female biased broods (Juchault et al., 1993; Moreau and Rigaud, 2000, 2003). An even more profound evolutionary consequence is that some host populations have lost the W chromosome entirely, with sex entirely determined by whether an individual is infected with *Wolbachia* (Charlat et al., 2003).

Because sons enjoy a reproductive advantage when males are rare, *Wolbachia*-induced female bias in populations is expected to generate selection pressure for the production of sons. For example, a shortage of males could reduce female reproductive success if males are not encountered for fertilization, or if males produce less sperm after repeated mating. Indeed Rigaud and Moreau (2004) demonstrated sperm depletion in males that mated multiple times. Interestingly, this only seemed to reduce the fertility of *Wolbachia*-infected females. The authors suggest that infected females do not use sperm as efficiently as uninfected females.

A shortage of males could also produce a condition of sex-role-reversal in which males become the choosy sex. It appears that *Wolbachia*-infected females receive fewer matings due to male preference for uninfected females, perhaps because the missing W chromosome affects sexual behavior in infected females (Moreau et al., 2001). Males also appear to deliver less sperm when mating with infected females (Moreau

et al., 2001). Male mate choice could therefore influence the transmission dynamics of *Wolbachia* in isopod populations (Hatcher, 2000). Rigaud and Moreau (2004) have suggested that frequency-dependent selection, in which male choice reduces fitness of infected females when the latter are common, could explain why *Wolbachia* infections are generally polymorphic (not all females are infected) in oniscid populations that host the bacterium.

Male reproductive behavior

A great deal of attention has been given to female oniscid reproduction (reviewed below), but fewer studies have examined male mating behavior in detail. In fact, males have been studied for their role in stimulating female reproduction (Jassem et al., 1991). Female *A. vulgare* undergo vitellogenesis when placed in direct contact with a conspecific male, and a single male is sufficient to bring several females into reproductive condition. Interestingly, females with implanted androgenic glands also induced vitellogenesis in other females (Jassem et al., 1991).

Male mating behavior has received more attention in aquatic isopods (Ridley, 1983; Jormalainen et al., 1994), perhaps because males of aquatic species generally exhibit mate-guarding tactics through attachment to females (“amplexus”) for periods ranging from hours to weeks (Jormalainen, 1998). Precopulatory mate guarding in male terrestrial isopods, however, is rare, although males may adopt a posture resembling amplexus during internal fertilization of females. Zimmer (2001) notes that aquatic isopod females generally do not store sperm between matings (Jormalainen et al., 1999), whereas terrestrial isopod females can store sperm for several months (*P. scaber*, Longo et al., 1998) and over several broods (*A. vulgare*, Lueken, 1962; *Venezillo evergladensis*, Johnson, 1982). Hence male mate-guarding behavior in terrestrial isopods would be an ineffective strategy if a female has already mated with a previous male. In addition, the terrestrial environment would make locomotion difficult for amplexed pairs, which could reduce foraging efficiency and increase risks of predation and desiccation. A rare oniscid exception is the genus *Ligia*, in which males exhibit precopulatory mate guarding (Schmalfuss, 1989; Carefoot and Taylor, 1995). The Ligiidae are supralittoral and appear to be prototypal oniscids, suggesting that precopulatory mate guarding was lost early as the Oniscidea evolved in terrestrial environments (Zimmer, 2001).

Mead (1973) described the courtship behavior of *A. vulgare*, in which a courting male assesses a female with his antennae and thereafter attempts to mount her dorsal surface. If the female is receptive she rolls into a balled posture but leaves an opening by which the male copulates. If unreceptive, she may roll completely or attempt to escape. Johnson (1985) provided a descriptive study of courtship and mating behavior in the armadillidid *V. evergladensis*. A male locates a receptive female through chemoreception and solicits matings by tapping his antennae on her cephalon. Female oniscids have two gonopores, and successful males must inseminate each separately, with courtship behavior occurring prior to each bout of copulation. Sperm transfer in

oniscids is accomplished using the modified first two pairs of male abdominal pleopods (Sutton, 1972), with older and larger males more successful at obtaining matings (Gonçalves et al., 2005). Males (Moreau and Rigaud, 2000) and females (Sassaman, 1978; Johnson, 1982; Moreau et al., 2002) of many species mate promiscuously, but a notable exception are species of *Hemilepistus*, in which males and females mate monogamously and males provide parental care behavior to young juveniles (Linsenmair, 1979, 1984, 1989). In some species, females are known to cannibalize young males after mating with them (*Schizidium tiberianum*, Warburg and Cohen, 1991; Warburg et al., 1993).

Sexual dimorphism in many oniscid species (i.e. length of antennae, Vandel, 1960; Lefebvre et al., 2000) suggests that sexual selection has acted on males (Darwin, 1871). In some species, males use the antennae as weapons in aggression against other males (Mead, 1973; Farr, 1978; Linsenmair, 1984; Johnson, 1985). However, in a comparative behavioral study of seven species, Lefebvre et al. (2000) found a negative correlation between the magnitude of sexual dimorphism and the use of antennae during contests between males. In fact, some species of *Armadillidium* were sexually dimorphic but males did not use antennae in contests with other males. The authors further note that some sexually dimorphic species (i.e. *Porcellionides pruinosus*, *O. asellus*) do not use the antennae to stimulate or clasp females during mating. They conclude that a more likely explanation for antennal sexual dimorphism is a scramble contest for females, in which males with larger antennae are more chemosensitive and thereby more successful at locating receptive females.

Some oniscid species exhibit the interesting phenomenon of cohort splitting, in which some individuals in a cohort are slow growing and others are fast-growing (*P. muscorum*, Grundy and Sutton, 1989; *P. scaber*, Zimmer and Kautz, 1997, *Tylos europaeus*, Gonçalves et al., 2005). Gonçalves et al. (2005) studied a population of *T. europaeus* unusual in two regards: there was a strong male bias in the sex ratio, and cohort splitting occurred only in males. Slower growing males lived longer and enjoyed a size-related mating advantage in later seasons when competing against smaller and younger males (Gonçalves et al., 2005).

Sperm competition

Because female oniscids often mate with multiple males, sperm competition may be an important factor in male reproductive success (Parker, 1970). A number of studies have demonstrated that oniscid sperm remains viable across multiple broods when stored by a female (*Armadillidium* sp., Lueken, 1963; Adamkewicz, 1969; *V. evergladensis*, Johnson, 1976). Patterns of sperm competition in terrestrial isopods, however, may be complicated by a number of factors. For example, whether mixed sperm in the spermatheca are from multiple males within the same breeding season or from different seasons could be important in fertilization patterns (Sassaman, 1978). Also, sperm competition could be influenced by the degree to which the operational sex ratio is skewed towards males, as might be expected under ancestral chromosomal

sex determination, or towards females, as might be expected under *Wolbachia*-driven sex ratio distortion (Moreau and Rigaud, 2000). When females significantly outnumber males, sperm competition should be minimal due to diminished female remating opportunities. Finally, it is possible that sperm precedence influences fertilization success (Moreau et al., 2002).

Moreau et al. (2002) addressed some of these factors by using a genetic marker (albinism) to study patterns of paternity in *A. vulgare* when females were virgin, when they mated more than once prior to brooding, and when they mated more than once between broods. Females were significantly less likely to mate again immediately following the first mating than to remate between broods. This pattern was based on female reluctance to mate, as males showed courtship behavior regardless of whether females had already mated. The authors concluded that sperm mixing is most likely to occur between broods and seasons. Interestingly, competing males had similar success in fertilization whether first or second to copulate, and whether the remating was immediate or between broods: the second male could fertilize up to half the brood (Moreau et al., 2002, but see Verne et al., 2007). The authors speculate that female reluctance to immediately remate could be somehow induced by males as a mating tactic, since the first male to mate does not seem to have a precedence advantage in sperm competition.

Despite a lack of last-male precedence, males might still benefit by mating with second season females with stored sperm, because larger females in subsequent seasons have higher fecundities. However, a study by Verne et al. (2007) used a shorter delay between first and second interbrood matings than used by Moreau et al. (2002) (one month instead of four months) and found evidence of first-male precedence, even though sperm seemed less viable the longer it was stored. They concluded that sperm position might be important in fertilization success, because stored sperm from the more successful first males were found in lower numbers (Verne et al., 2007).

Female reproductive behavior

Reproductive behavior in terrestrial isopods is tied closely to the molting cycles of females (Steel, 1980). Reproduction is seasonal in many species, and within the season, females pass through periods of sexual activity and sexual rest (Mocquard et al., 1989; Warburg, 1993). Females exhibit a peak period of sexual receptivity that is correlated with oocyte maturation (Moreau and Rigaud, 2002). Fertilization is internal, and males must transfer sperm through both female genital apertures, each leading to an oviduct and ovary. Sperm are not motile and initially remain in the oviduct, where eggs are fertilized as they pass (Hollande and Fain-Maurel, 1965). Sperm are thereafter stored in spermathecae, and they may be used to fertilize subsequent broods (Warburg, 1993).

During intermolt periods before normal growth molts, Vitellogenesis-Inhibiting Hormone prevents oogenesis (Gohar et al., 1984). Prior to oviposition, females undergo a reproductive molt (the “parturial molt”) in which lamellar structures on the first five

pereon segments differentiate into oostegites and form a marsupium. Females carry the eggs, embryos and mancae in the marsupium for approximately one month and appear to invest substantial energy as evidenced by the depletion of fat reserves over the brooding period (Wright and Surbida, 2001). Females provide nutrition to the developing mancae, likely through the cotyledons (Hoese and Janssen, 1989; Warburg and Rosenberg, 1996). Females can also regulate pH and osmolality of the marsupial fluid (Surbida and Wright, 2001). Young mancae are also coprophagous, gaining significant nutrition from maternal feces after hatching (Wieser, 1978; Hassall and Rushton, 1982; Carefoot, 1993).

After the brooding period ends, females generally undergo a normal molt, after which they may copulate again. Prior to this molt, the marsupium interferes with sperm transfer (Moreau and Rigaud, 2000) and females in most species do not mate (but see Lefebvre and Caubet, 1999; Moreau and Rigaud, 2000; Verne et al., 2007 for exceptions in *Armadillidium* sp). It is also possible for females to undergo another parturial molt (instead of a normal growth molt) after the brooding period ends, in which the next brood is fertilized only by stored sperm (Mocquard et al., 1989; but see Moreau and Rigaud, 2000; Verne et al., 2007).

Many oniscid populations studied to date have been from temperate regions, and reproduce in the spring and summer (Warburg, 1994), whereas Neotropical species can be reproductive throughout the year (*Atlantoscia floridana*, Quadros and Araujo, 2007). Some widely distributed species, such as *P. pruinosus*, reproduce seasonally (Achouri and Charfi-Cheikhroua, 2001) or continuously (Juchault et al., 1985) in different regions. Most species appear to be iteroparous (Warburg, 1992, 1995; Warburg and Cohen, 1992; Hornung and Warburg, 1993) but some are known to be semelparous (i.e. *S. tiberianum*, Warburg, 1992; Warburg and Cohen, 1991; Warburg et al., 1993), and this may vary within a species depending on geographic region and climate.

Several abiotic environmental factors, such as temperature and photoperiod, are associated with the onset and duration of mating and brooding in females. For example, warm ambient temperatures stimulate breeding (*A. vulgare*, Madhavan and Shribbs, 1981; Mocquard et al., 1989; *Porcellio ficulneus*, Hornung and Warburg, 1993), shorten the brooding period (*Trachelipus rathkei*, Snider and Shaddy, 1980), and speed growth of immatures (*A. vulgare*, Helden and Hassall, 1998). Reproduction may also be stimulated by long-day photoperiods, particularly for terrestrial isopod populations in seasonal environments (*A. vulgare*, Mocquard et al., 1989; *P. ficulneus*, Hornung and Warburg, 1993).

The biotic environment also influences reproduction. The presence of male *Armadillidium pelagicum* is associated with a reduction in the number of female growth molts prior to the parturial molt, as well as a shorter intermolt period between the last growth molt and the first parturial molt (Hamaied et al., 2004). Females kept on restricted diets delayed the onset of reproduction (*A. vulgare*, Kight and Hashemi, 2003). The presence of predators can also influence brooding behavior. Female *A. vulgare* had shorter brooding periods when exposed to predatory ants (Castillo and Kight, 2005). However, the brooding period of ant-exposed female *Porcellio laevis* did

not differ from those of females not exposed to ants, suggesting that differences in antipredator behavior between species are associated with reproduction. Female *A. vulgare* roll into defensive ball postures in the presence of predators, whereas female *P. laevis* attempt to flee. Female *A. vulgare* are unable to roll completely in the late brooding period due to the size of the marsupium and may therefore terminate care early when predators are present. Excessive locomotion (in response to chronic disturbance), however, reduces the brooding period in *P. laevis* (Kight and Nevo, 2004).

Terrestrial isopod life history

As ancestral oniscids made the transition from an aquatic to a terrestrial existence, they retained several developmental and reproductive traits, including indeterminate growth (Hubbell, 1971) and iteroparity (Warburg, 1991), setting the stage for intense selection on tradeoffs between maternal growth, reproduction (Lawlor, 1976), and survivorship (Hassall, 1996). Egg brooding is also energetically expensive: brooding females maintain a positive energy balance, but have difficulty storing additional energy, whereas non-brooding conspecific females can generate reserves (*P. laevis*, Lardies et al., 2004b).

Much attention has been given to the life history evolution of terrestrial isopods (Sutton et al., 1984; Warburg et al., 1993; Hassall et al., 2003; Lardies and Carter, 2004). There are three general areas in which females can potentially allocate resources: survivorship, somatic growth, and current reproductive effort (Stearns, 1992, 2000), and the balance between them is predicted to be under selection (Jokela and Haukioja, 2000). Because oniscideans have indeterminate growth, investment in growing a large body contributes to residual reproductive value if larger males have higher mating success and larger females have higher fecundity. The size of the marsupium, however, constrains fecundity (Schmalzfuss, 1984), especially if somatic growth is allometric, with overall body size increasing faster than marsupium size (Hassall et al., 2003).

Current reproductive effort is in turn subject to trade offs between offspring size and offspring number: larger broods generally are comprised of smaller offspring (*A. vulgare*, Lawlor, 1976; *Ligia oceanica*, Willows, 1987). Terrestrial isopods tend to have high juvenile mortality (i.e. *A. vulgare*, Paris, 1963; Sunderland and Sutton, 1980; Hassall and Dangerfield, 1997), which might result in selection for increases in offspring number. Zimmer (2002) suggests that body size for particular developmental stages within a species may be fixed, and that environmental factors determine the amount of time required to grow to that size. Body size of offspring when they leave the marsupium is an important life history variable: even small differences in the weight of manca may result in large differences in the size of adults. Indeed the largest females can be up to ten times heavier than the smallest sexually mature females (Warburg, 1987).

While these predictions are often supported in field and laboratory studies, there are exceptions illustrating the complexity of life history evolution. For example, female

A. vulgare collected from sites with high food quality invested more in reproduction and produced both larger broods and larger offspring (Hassall et al., 2005a). In stable environments with access to resources for growth, however, selection should favor larger broods with smaller offspring that will grow quickly after release from the marsupium (Sibley and Calow, 1986). Hassall et al. (2005a) suggest that temperature fluctuations in the ancestral environment of their study population could have favored the production of large offspring.

Interspecific life history variation

Multiple species of terrestrial isopods often inhabit the same area, but have different adaptations and strategies for reproduction (Sutton et al., 1984; Quadros and Araujo, 2007). Such differences may result from phylogenetic constraints (Glazier et al., 2003). Morphological differences, such as variation in cotyledon number and morphology of the marsupium (Lewis, 1990) and differences in cuticle and respiratory physiology (Wright and Machin, 1993) can affect reproductive success. Behavioral differences, i.e. “running” vs. “rolling” (Schmalfuss, 1984) in response to predators (*A. vulgare* v. *P. laevis*, respectively, Castillo and Kight, 2005) may also be associated with the length of the brooding period.

Different species may inhabit different microhabitats within the same geographic location, from surface-active species to endogean species that remain primarily underground, where they burrow in response to moisture gradients (Warburg, 1987). Different microhabitat use is further correlated with morphological variations such as lack of pigmentation (Quadros and Araujo, 2007) and life history variations, such as slower growth and later maturation in soil-active species (Sutton et al., 1984). Glazier et al. (2003) note that soil-dwelling species tend to more resemble aquatic isopod species than surface dwelling species in that they have larger broods with smaller individual offspring. They suggest this may be due to higher desiccation stress at the soil surface, an argument supported by a tendency for surface-dwelling isopods to have lower surface area to volume ratios (Glazier et al., 2003).

Dias et al. (2005) examined life history traits of four oniscid species (*Tylos ponticus*, *Porcellio lamellatus*, *Halophiloscia couchii*, *Armadillidium album*) inhabiting a salt marsh: a challenging habitat for terrestrial isopods due to osmotic and thermal stresses. Of the four species, *T. ponticus* had unusually high abundance, which the authors report as the highest abundance recorded for a terrestrial isopod. The key life history difference seems to be a delayed age of first reproduction in *T. ponticus* (24 months rather than 12 months in the other three species) that is associated with a larger body size at first reproduction (despite a slower growth rate), and smaller broods that are up to ten times heavier than those of the other species. This appears to reduce juvenile mortality in *T. ponticus* and increases survival through the first year (Dias et al., 2005).

Intraspecific life history variation

Some oniscid species are widely distributed and found in habitats with markedly different biotic and abiotic parameters. Selection within populations may therefore drive the evolution of divergent life history strategies (Hassall et al., 2005a). Brody and Lawlor (1984) found variation in brood and offspring size between populations in *A. vulgare*. In one study, *A. vulgare* females were collected from habitats differing in the quality of available food resources (Hassall et al., 2003). On a laboratory-controlled diet, females collected from habitats with poor food quality, as well as their first generation offspring, grew more slowly, had lower reproductive allocation, and higher survivorship than those collected from areas with good food quality. Different populations of *A. vulgare* can even vary in whether females are semelparous or iteroparous (Hassall et al., 2003).

Lardies et al. (2004a) compared life history traits in populations of *P. laevis* at different altitudes. Females at low altitudes had smaller bodies in general, were smaller at first reproduction, and produced more but smaller eggs. High altitude females produced fewer, but larger, mancae. The authors suggest that offspring at high altitudes require more initial resources to withstand environmental fluctuations and short growing seasons. A similar trade-off can be found across latitudes. *Porcellio laevis* exhibits a gradient from low latitudes with smaller bodies, faster growth, earlier first reproduction, larger broods, and smaller offspring to higher latitude populations with larger, slow growing bodies, smaller broods with larger offspring (Lardies and Bozinovic, 2006). Reproductive output is also greatest at high latitudes, with females at low latitudes investing 5% of body mass in egg production and those at high latitudes investing 18% (Lardies and Bozinovic, 2006).

Unpredictable environmental conditions may shape population reaction norms in life history traits (Caswell, 1983; Via et al., 1995). Hassall et al. (2005a) compared phenotypic plasticity in life history traits of two naturally occurring populations of *A. vulgare*: one with consistent high quality food but fluctuating temperature regimes and a second population with less access to high quality food but more stable ambient temperatures. The former exhibited faster growth rates, whereas the latter had higher survivorship. Under laboratory conditions in which food quality was increased, females from the low food quality ancestral population showed a much stronger response, with substantial increases in reproductive allocation and fecundity. When temperature was increased, however, the females from the ancestral population with unstable temperatures showed the strongest response in life history traits (Hassall et al., 2005a). These populations hence appear to have evolved plasticity in response to the environmental conditions that are most unstable in the ancestral environment.

Maternal effects on oniscid life history

Because oniscid females provide nutrition and shelter to developing young (Warburg, 1993; Helden and Hassall, 1998), phenotypic variation between broods could result from differences among mothers (i.e. maternal behavior or diet) rather than, or in addition to, genetic differences between broods (van Noordwijk and de Jong, 1986;

Mousseau and Fox, 1998; Lardies and Carter, 2004). For example, space limitations in the marsupium might produce trade-offs between offspring number, offspring size and length of incubation period: larger broods should be comprised of smaller individuals with shorter incubations (Mousseau and Fox, 1998). Hence two genetically identical females reared in different growth conditions could have different adult body sizes and produce offspring of different size and fitness because of differing spatial constraints in the marsupium.

Lardies and Carter (2004) found that the direction of these trade-offs is influenced by differences in maternal diet. Female *P. laevis* kept on high protein/low carbohydrate diets exhibited the predicted negative correlation between offspring number and incubation period, whereas those fed a low protein/high carbohydrate diet showed the opposite: broods with larger numbers of offspring were incubated longer before release. The authors attribute this outcome to impaired energy efficiency in crustaceans on low protein diets (see Cuzon et al., 2000). A high protein/low carbohydrate maternal diet also produced more but smaller offspring that had faster growth rates after release from the marsupium (Lardies and Carter, 2004).

A high protein diet may also expose additive genetic variance to selection. Carter et al. (2004) found high narrow-sense heritabilities in *P. laevis* kept on high protein/low carbohydrate diets, but not high carbohydrate/low protein diets. They suggest that the former maternal diet may be stressful to offspring because carbohydrates are required for construction of the exoskeleton (see Harrison, 1990), which could have the effect of minimizing the contribution of the environment to phenotypic variance (see Hoffmann and Merila, 1999).

Conclusions

Recent studies of the Oniscidea demonstrate general patterns, but also meaningful exceptions, in the way the environment interacts with genetics, physiology, behavior, life history, population biology, and evolutionary patterns. It is clear that mechanisms at each of these levels are integrated with those at other levels. Factors such as food availability, precipitation, ambient temperature, and seasonal duration can affect body growth, age and body size at first reproduction, fecundity, and the number of broods terrestrial isopod females produce. As global climate change proceeds, we might therefore expect impacts on the reproductive ecology of oniscid populations, although the magnitude and direction of these impacts may vary between species, as well as between populations of the same species in different geographic regions. Better understanding of reproduction and population dynamics in terrestrial isopods will not only clarify the response of these detritivores in changing ecosystems, but may also provide insight into potentially general effects of climate change on soil arthropods.

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