BODY SIZE AND SURVIVORSHIP IN OVERWINTERING POPULATIONS OF *PORCELLIO LAEVIS* (ISOPODA: ONISCIDEA)[1]

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ABSTRACT: Because female *Porcellio laevis* (Isopoda: Oniscidea) carry eggs and young manca in a ventral marsupium, fecundity and body size are positively correlated. We examined female body size in November and February, a period in which breeding does not occur and changes in body size are unlikely to be attributed to growth. Our results from two consecutive years revealed several general patterns. First, the sex-ratio of individuals collected with baited traps was extremely female-biased. Second, body size was significantly larger (as indicated by length of antennae and appendages) in samples collected during November than in those collected during February. Third, no same-month differences in body size were found between years, suggesting that differential mortality during the non-breeding season does not result in natural selection on body size. These results suggest that older (presumably senescent) females suffer increased mortality risk over the winter.

Terrestrial isopods (Crustacea: Oniscidea) of several genera are widely distributed throughout North America (Schultz 1982; Jass & Klausmeier 1996). Nearctic Oniscidea appear to be recent European introductions (Vandel 1962), which may account for the relative paucity of recent studies on the natural history of North American populations (but see Miller & Cameron 1983; Jass & Klausmeier 1996) in comparison to populations in Europe (Grundy & Sutton, 1989; Souty-Grosset et al. 1994; Zimmer & Kautz 1997; Jones & Hopkins, 1998) and Africa (Aljetlawi & Nair 1994; Dangerfield & Hassall 1994; Dangerfield & Telford 1995). The present study addresses this gap by investigating aspects of the natural history of *Porcellio laevis* (Latreille) in the northeastern United States.

Reproduction of terrestrial isopods is seasonal in temperate climates (Souty-Grosset et al, 1998), and variation in the onset and waning of reproduction, as well as the number of reproductive episodes, is associated with photoperiod (Juchault et al. 1981; Souty-Grosset et al. 1994) and latitude/temperature (Mocquard et al.1980; Souty-Grosset et al. 1988,1998). For example, long-day photoperiods stimulate the onset of reproduction and extend the length of the reproductive period in *Armadillidium vulgare* (Souty-Grosset et al. 1994), but high ambient temperature only marginally accelerates reproductive onset and does not appear to influence its duration (Mocquard et al. 1980). However, *A. vulgare* females from southern (presumably warmer) latitudes undergo three parturial molts in a season, whereas those from northern latitudes were observed to undergo only a single parturial molt (Souty-Grosset et al. 1998).

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Thus, reproductive strategies appear to be plastic (Dangerfield & Hassall 1992), and variation in reproductive phenology may depend on subtle differences in habitat.

Seasonal variation is also evident in fecundity and egg-mass (e.g. *Ligia oceanica,* Willows 1987). Variation in these factors, as well as quality/quantity of progeny, is also associated with other factors, such as diet and condition. For example, *A. vulgare* reared on dicotyledonous food sources exhibit higher growth rates and fecundity in comparison to those reared on monocotyledonous food (Rushton & Hassall 1983). In addition, competition among individuals for limited resources can result in diminished growth and fecundity (Hassall & Dangerfield 1997). Feminizing *Wolbachia* infections also appear to diminish fecundity (e.g. *Oniscus asellus*, Rigaud et al. 1999). Such factors are therefore predicted to directly impact female reproductive success.

Because female terrestrial isopods retain eggs and young mancas in the marsupium (a fluid-filled brood pouch formed by specialized oostegites on the ventral pereon), body size also places an important constraint on female reproductive success — fecundity is positively correlated with size of the marsupium (Dangerfield & Telford 1995) and body size in general (Tomescu et al. 1992). Although it might be predicted that selection would favor correlations between maternal and egg/manca size, such associations have not been observed (Telford & Dangerfield 1995). Hence, offspring quantity, but not necessarily quality, is governed by maternal body size.

It is unclear, however, how body size and survivorship are associated. Grundy and Sutton (1989) found that adult *Philoscia muscorum* had higher survivorship than smaller-bodied juveniles. Dangerfield (1997), however, found no substantial relationships between birth mass and offspring fitness in *Porcellionides pruinosus* and *Aphiloscia vilis.* In a recent study by Hassall (1996), the relationships between growth and survivorship varied widely depending on habitat structure. Given the importance of body size in reproductive success, there is a need for additional investigation into the role body size plays throughout the life cycle of terrestrial isopods.

In the present study, we examine population-level changes in body size of the terrestrial isopod, *Porcellio laevis* (Latreille) during the non-breeding season. Winter growth rates are expected to be low in temperate climates (Pavese 1987), and we may therefore attribute any differences in average body size primarily to differences in mortality. Because body size and fecundity are associated, selection on body size during the non-breeding season should influence the evolution of terrestrial isopod life histories.

MATERIALS AND METHODS

Porcellio laevis (Latreille) were collected over a two year period (1998-2000) in Essex County, New Jersey, USA using an array of ten 'potato traps' during each of four one-week sampling periods. Traps were constructed by bisecting small garden potatoes, carving a cavity of approximately 5 cm^2 into the exposed parenchyma, and placing each potato hollow-side down near a deposit of decaying wood. All traps were spaced approximately 1 m apart and all *P. laevis* in contact with each trap were removed and immediately preserved each day.

One-week sampling periods were conducted on four occasions: twice during winter 1998-99 (11/15/98-11/22/98 and 02/15/99-02/22/99) and twice during winter 1999-2000 (11/15/99-11/22/99 and 02/15/00-02/22/00). Sex of each specimen was determined by visual inspection of the pleon (males possess elongated 1st and 2nd pleopods) and all females were subsequently examined. The following measurements were recorded for each specimen to the nearest 0.1 mm: leng th of left antenna (LA), length of right 7th cephalothoracic appendage (RCTA7), and width of 1st cephalothoracic segment (CTS1). These measurements served as indices of the physical dimensions of female exoskeletons — the factor expected to place absolute limits on marsupium egg capacity during the reproductive season.

Data were statistically analyzed with *Minitab©* v.8.0 following Sokal & Rohlf (1981) with $\alpha = 0.05$.

RESULTS

Sample sizes for each collection period were as follows: 11/98, N = 74; 02/99, N = 38; 11/99, N = 80; 02/00, N = 100. With few exceptions (< 10 males), specimens were phenotypically female. Data collected during winter 1998-99 (Fig. 1) revealed a significant decrease in length of right 7th cephalothoracic appendage between November and February (Two-Sample T-test, T = 1.93, P = 0.05) but no significant differences in length of left antenna or width of 1st cephalothoracic segment (Two-Sample T-test, T = 0.82, P = 0.41 and T = 0.38, P = 0.71, respectively).

Data collected during winter 1999-2000 (Fig. 2) revealed significant decreases in lengths of both the right 7th cephalothoracic appendage and left antenna (Two-Sample T-test, T = 5.88, P<0.01 and T = 2.14, P = 0.03, res pectively) but no significant difference in width of 1st cephalothoracic segment (Two-Sample T-test, T = 0.50, P = 0.62).

The measured characters did not significantly differ between November specimens collected in different years (LA, Two-Sample T-test, T = 0.67, P = 0.51; RCTA7, Two-Sample T-test, T = -1.23, P = 0.22; CTS1, Two-Sample T-test, T = -0.89, P = 0.38), nor were there significant differences between February specimens in different years (LA, Two-Sample T-test, T = 1.20, P = 0.23; RCTA7, Two-Sample T-test, T = 0.09, P = 0.93; CTS1, Two-Sample T-test, T = -1.49, P = 0.14). The detection of within-year but not between-year differences suggests that the phenomenon is a natural component of the annual life history of *P. laevis*.

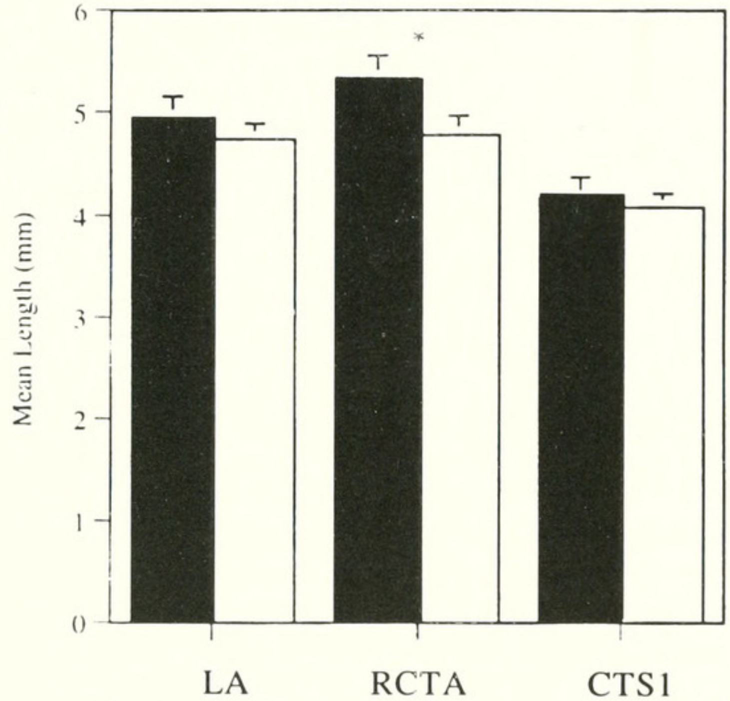

Figure 1. Average length (mm) of left antenna (LA), right 7th cephalothoracic appendage (RCTA7), and width of 1st cephalothoracic segment (CTS1) in November 1998 (black bars) and February 1999 (white bars). Error bars represent standard error on the mean. Asterisk indicates significant difference ($P < 0.05$).

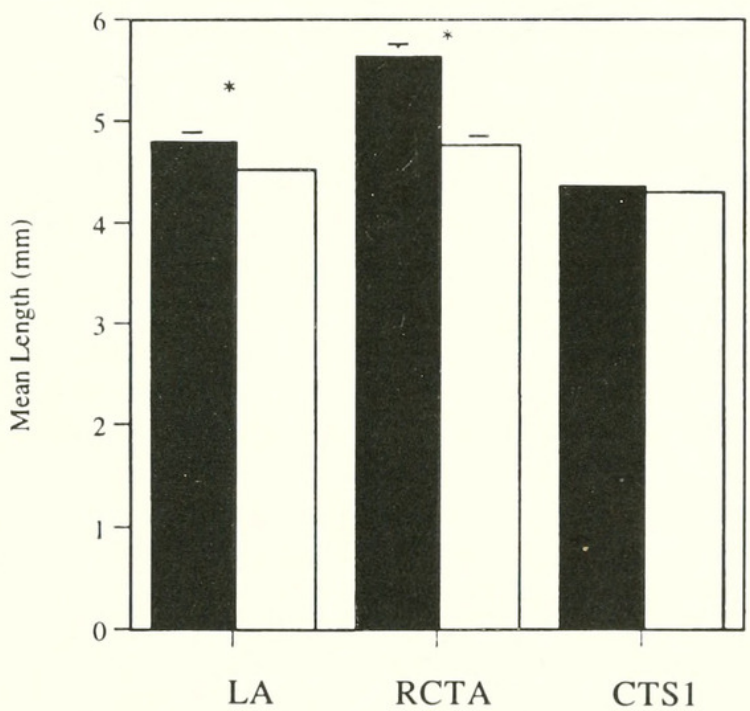

Figure 2. Average length (mm) of left antenna (LA), right 7th cephalothoracic appendage (RCTA7), and width of 1st cephalothoracic segment (CTS1) in November 1999 (black bars) and February 2000 (white bars). Error bars represent standard error on the mean. Asterisk indicates significant difference ($P < 0.05$).

DISCUSSION

The results of the present study revealed two fundamental life history patterns of *P. laevis* during the non-breeding season in temperate North America. First, the sex-ratio of individuals collected with baited traps was extremely female-biased. Second, body size was significantly larger (as indicated by length of antennae and appendages) in samples collected during the early winter than those collected in the late winter.

In the present study, almost all sampled individuals were phenotypically female. These results are not surprising in light of numerous studies that have addressed female-biased sex ratios in terrestrial isopods (Williams & Franks 1988; Farkas 1998). Recent studies indicate that this phenomenon is associated with microbes of the genus *Wolbachia* (Grandjean et al. 1993; Rigaud, et al. 1999), which drive populations to a female bias through cytoplasmic incompatibility mechanisms and feminization of males. Ambient temperature also appears to influence the direction of this bias in some species (Rigaud et al. 1997). It remains possible, however, that females in the present study were differentially attracted to baited traps, and we are therefore reluctant to speculate further on the actual sex-ratio of the population.

It is also possible that larger females were more attracted to the traps during early winter than in late winter. Large females may have thereby fed more heavily in the early winter and stored fat reserves sufficient to forego late-winter foraging. While we cannot conclusively reject this explanation, it seems unlikely. Winter feeding presumably functions more in maintenance than growth. Larger individuals should have greater maintenance requirements, and we might therefore expect them to be over-represented in late winter feeding activity. Even if winter females undergo vitellogenesis, as suggested by studies in less temperate climates (e.g. Mediterranean populations of *P. ficulneus,* Hornung & Warburg 1993), the metabolic demand on larger females, with corresponding higher fecundities, would be greater.

Alternatively, females in larger size-classes may have suffered differential mortality over the winter months. This interpretation is not consistent with general relationships between organism body size, surface-area:volume ratios and resistance to flux in extreme climates. However, it is consistent with the relationship between body size and age in continuously growing arthropods — larger females are older (and presumably more senescent) organisms. In this case, the largest females in the November samples would have already reproduced through one or more breeding seasons. Such females would be under-represented in February samples if there were a senescence-mediated increase in mortality risk under extreme winter environmental conditions. We are aware of no experimental investigations of Oniscidean senescence and suggest that such studies would yield important insight into the life history of terrestrial isopods. If, as our data suggest, there is differential mortality among larger females during the non-breeding season, it does not necessarily follow that natural selection is acting upon body size per se. Senescent females are expected to have large realized:residual reproductive success ratios – i.e. any natural selection has already acted upon them in previous breeding seasons. This hypothesis is consistent with the results of the present study, in which there was no response to selection between years in female body size. Selection may act indirectly, however, by favoring terminal-investment strategies (Scott & Gladstein 1993; Kight et al. 2000) in aging females unlikely to survive the coming winter. Terminal investment theory pre dicts that older (larger) females should reproductively invest more heavily than younger (smaller) females late in the breeding season. A careful study of body size and late-season reproductive allocation is therefore needed to better understand the life history of *P. laevis* in temperate North America.

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LITERATURE CITED

Aljetlawi, A.A. & Nair, G. A. 1994. Breeding and population biology of *Armadillo officinalis* (Isopoda: Oniscidea) in Benghazi, Libya. J. Arid. Env. 27, p. 241-255.

Dangerfield, J.M. 1997. Growth and survivorship in juvenile woodlice: Is birth mass important? Ecography. 20, p. 132-136.

Dangerfield, J.M. & Hassall, M. 1992. Phenotypic variation in the breeding phenology of the woodlouse *Armadillidium vulgare*. Oecologia. 89, p. 140-146.

Dangerfield, J.M. & Hassall, M. 1994. Shelter site use and secondary sex ratios in the woodlice *Armadillidium vulgare* and *Porcellio scaber* (Crustacea: Isopoda). J. Zool. Lond. 233, p. 1-7.

Dangerfield, J.M. & Telford, S.R. 1995. Tactics of reproduction and reproductive allocation in four species of woodlice from southern Africa. J. Trop. Eco. 11, p. 641-649.

Farkas, S. 1998. Population dynamics, spatial distribution, and sex ratio of *Trachelipus rathkei* Brandt (Isopoda: Oniscidea) in a wetland forest by the Drava River. Israel J. Zool. 44, p. 323-331.

Grandjean, F., Rigaud, T., Raimond, R., Juchault, P. & Souty-Grosset, C. 1993. Mitochondrial DNA polymorphism and feminizing sex factors dynamics in a natural population of *Armadillidium vulgare* (Crustacea, Isopoda). Gen. Dord. 92, p. 55-60.

Grundy, A.J. & Sutton, S.L. 1989. Year class splitting in the woodlouse *Philoscia muscorum* explained through studies of growth and survivorship. Hol. Eco. 12, p. 112-119.

Hassall, M. 1996. Spatial variation in favourability of a grass heath as a habitat for woodlice (Isopoda: Onisci dea). Pedobiologia. 40, p. 514-528.

Hassall, M. & Dangerfield, J.M. 1997. The population dynamics of a woodlouse, *Armadillidium vulgare:* An example of biotic compensatory mechanisms amongst terrestrial macrodecomposers? Pedobiologia. 41, p. 342-360.

Hornung, E. & Warburg, M.R. 1993. Breeding patterns in the oniscid isopod, *Porcellio ficulneus* Verh., at high temperature and under different photophases. Inv. Repr. Dev. 23:151-158.

Jass, J. & Klausmeier, B. 1996. Terrestrial isopods (Isopoda: Oniscidea) of Wisconsin. Great Lakes Entomol. 29, p. 11-20.

Jones, D.T. & Hopkin, S.P. 1998. Reduced survival and body size in the terrestrial isopod *Porcellio scaber* from a metal-polluted environment. Env. Poll. 99, p. 215-223.

Juchault, P., Mocquard, J.P. & Legrand, J.J. 1981. Seasonal reproduction determinism of the *Armadillidium vulgare* females (Crustacea, Isopoda, Oniscoidea): 3. Suppression or lengthening of the seasonal sexual rest period obtained by photoperiodic programs. Ann. Sci. Nat. Zool. Biol. Anim. 3, p. 141-145.

Kight, S.L., Batino, M. & Zhang, Z. 2000. Temperature-dependent parental investment in the giant waterbug, *Belostoma flumineum* (Heteroptera: Belostomatidae). Ann. Entomol. Soc. Am. 93, p. 340-342.

Miller, R.H. & Cameron, G.N. 1983. Intraspecific variation of life history parameters in the terrestrial isopod, *Armadillidium vulgare*. Oecologia. 57, p. 216-226.

Mocquard, J.P., Pavese, A. & Juchault, P. 1980. Seasonal reproduction determinism of *Armadillidium vulgare* females (Crustacea, Isopoda, Oniscoidea): 1. Action of temperature and photoperiod. Ann. Sci. Nat. Zool. Biol. Anim. 2, p. 91-98.

Pavese, A. 1987. Study of a natural population of the Oniscoid Isopod crustacean *Armadillidium vulgare* under the climatic conditions of Marrakech (Morocco): Populations dynamics and reproductive cycle. Vie et Milieu. 37, p. 139-147.

Rigaud, T., Antoine, D., Marcade, I. & Juchault, P. 1997. The effect of temperature on sex ratio in the isopod *Porcellionides pruinosus:* Environmental sex determination or a by-product of cytoplasmic sex determination? Evo. Eco. 11, p. 205-215.

Rigaud, T., Moreau, J. & Juchault, P. 1999. *Wolbachia* infection in the terrestrial isopod *Oniscus asellus:* Sex ratio d istortion and effect on fecundity. Heredity. 83, p. 469-475.

Rushton, S.P. & Hassall, M. 1983. The effects of food quality on the life history parameters of the terrestrial isopod (*Armadillidium vulgare*). Oecologia. 57, p. 257-261.

Schultz, G.A. 1982. Terrestrial isopods (Crustacea: Isopoda: Oniscoidea) from North Carolina (USA). Brimleyana 0(8), p. 1-26.

Scott, M.P. & Gladstein, D.S. 1993. Calculating males? An empirical and theoretical examination of the duration of paternal care in burying beetles. Evo. Eco. 7, p. 362-378.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. San Francisco: W.H. Freeman.

Souty-Grosset, C., Chentoufi, A., Mocquard, J.P. & Juchault, P. 1988. Seasonal reproduction in the terrestrial isopod *Armadillidium vulgare* (Latr beille): Geographical variability and genetic control of the response to photoperiod and temperature. Int. J. Inv. Repr. Dev. 14, p. 131-152.

Souty-Grosset, C., Bouchon, D., Mocquard, J.P. & Juchault, P. 1994. Interpopulation variability of the seasonal reproduction in the terrestrial isopod *Armadillidium vulgare* Latr. (Crustacea, Oniscidea): A review. Act. Oeco. 15, p. 79-91.

Souty-Grosset, C., Nasri, K., Mocquard, J.P. & Juchault, P. 1998. Individual variation in the seasonal reproduction of the terrestrial isopod *Armadillidium vulgare* Latr. (Crustacea, Oniscidea). Act. Oeco. 19, p. 367-375.

Telford, S.R. & Dangerfield, J.M. 1995. Offspring size variation in some southern African woodlice. Afr. J. Eco. 33, p. 236-241.

Tomescu, N., Accola, S. & Berciu, C. 1992. Reproduction of terrestrial isopods of Cheile Turzii natural reservation (Romania). Stud. Univ. Babes Bolyai. 37, p. 39-45.

Vandel, A. 1962. Isopodes Terrestres II. Faune de France. 66, p. 417-931.

Williams, T. & Franks, N.R. 1988. Population size and growth rate, sex ratio and behavior in the ant isopod, *Platyarthrus hoffmannseggi*. J. Zool. Lond. 215, p. 703-718.

Willows, R.K. 1987. Intrapopulation variation in the reproductive characteristics of two populations of *Ligia oceanica* (Crustacea: Oniscidea). J. Anim. Eco. 56, p. 331-340.

Zimmer, M. & Kautz, G. 1997. Breeding phenological strategies of the common woodlouse, *Porcellio scaber* (Isopoda: Oniscidea). Euro. J. Soil Bio. 33, p. 67-73.