Fertility tables of two populations of the parthenogenetic species *Poratia salvator* (Diplopoda, Polydesmida, Pyrgodesmidae)

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(With 4 figures)

Abstract

Diplopods are very susceptible to various degrees of environmental disturbance, particularly climate, altitude and diet. In order to increase our understanding of millipede ecological plasticity, we used fertility tables to access and to compare the fertility and survival of two populations of the parthenogenetic species *Poratia salvator* from two areas with distinct characteristics. Collecting was conducted in two localities within the state of Mato Grosso, in the Pantanal of Mato Grosso, municipality of Nossa Senhora do Livramento, and in the municipality of Várzea Grande. The specimens were maintained at room temperature. In the first generation, individuals from the Pantanal of Mato Grosso population reproduced early and also died earlier when compared with individuals from the Várzea Grande population. Furthermore, the population from the Pantanal had a lower net reproduction rate and a higher intrinsic growth rate than the population from the Várzea Grande. The generation time was lower for the Pantanal population than for the Várzea Grande population. In the second generation, the net reproduction rate observed for both populations was higher than that observed in the first generation, suggesting an increase in the reproductive potential of the females throughout their lives. The intrinsic growth rate of both populations decreased as a function of an increase in generation time observed in the second generation. As a result, the population growth rate in the second generation was slower when compared with the first generation, probably a result of the longer life expectancy of the second generation, which may have become adapted to the artificial conditions of the experiment.

Keywords: life-cycle, population growth, reproduction, intrinsic growth rate, generation time.

Tabela de fertilidade de duas populações da espécie partenogenética *P. salvator* (Diplopoda, Polydesmida, Pyrgodesmidae)

Resumo

Os Diplopoda demonstram forte sensibilidade às mudanças ambientais em diferentes escalas, sendo que fatores como clima, altitude e disponibilidade de alimento são os que mais influenciam o seu desenvolvimento biológico. Dessa maneira, este estudo objetivou estimar as taxas de sobrevivência e fertilidade da espécie partenogenética *Poratia salvator* através da elaboração de tabelas de fertilidade, a fim de caracterizar o crescimento populacional desta espécie, oriunda de diferentes ambientes. As coletas foram realizadas em duas localidades, uma no Pantanal de Mato Grosso, município de Nossa Senhora do Livramento, e outra no município de Várzea Grande-MT. Os indivíduos foram mantidos sob temperatura ambiente. Como resultado observou-se que a população proveniente do Pantanal apresentou aceleração da reprodução, na primeira geração, com mortalidade prematura das progenitoras. Para a população oriunda de Várzea Grande, a reprodução ocorreu em idades mais avançadas do período reprodutivo, e as fêmeas viveram por um maior período. Na primeira geração, a população do Pantanal teve menor taxa líquida de reprodução e maior taxa intrínseca de crescimento que a população de Várzea Grande. O tempo de geração da população do Pantanal foi menor que a de Várzea Grande. Na segunda geração, observou-se que a taxa líquida de reprodução das duas populações foi maior que a observada na primeira geração, evidenciando um incremento no potencial reprodutivo de cada uma das fêmeas ao longo da vida. A taxa intrínseca de crescimento diminuiu devido ao aumento no tempo de geração da segunda geração estudada. Com isso, a taxa de crescimento das populações, na segunda geração, foi mais lenta que a primeira, visto que houve um prolongamento na vida das progenitoras, aparentemente, devido à adaptação dos animais às condições artificiais.

Palavras-chave: ciclo de vida, crescimento populacional, reprodução, taxa intrínseca de crescimento, tempo de geração.

1. Introduction

Millipedes require environments with high levels of humidity. As a consequence of their dependence on moisture, these organisms are more abundant and diverse in tropical and sub-tropical climates, being rare or absent in extremely dry environments such as deserts and tundras (Hoffman et al., 1996). In addition to their relative intolerance to low humidity, diplopods are very susceptible to various degrees of environmental changes, particularly climate, altitude and diet (Hopkin and Read, 1992).

In humid ecosystems of the Pantanal and the Amazon, periodical inundations may pose an additional problem to millipedes. In response to this particular factor, these organisms have developed an array of ethological, physiological, morphological and phenological adaptations (Adis, 1997) that allow them higher ecological plasticity (Hoffman et al., 2002). Furthermore, millipedes have different life-cycle strategies which, associated with variations in the timing of reproductive maturity, enable these organisms to better cope with alterations in their habitats (Hopkin and Read, 1992).

Among millipedes, the predominantly tropical order Polydesmida is the largest. Most species of this order have with short life-cycles that can be completed within a year (Hoffman et al., 1996, 2002). One interesting characteristic of some members of the Polydesmida, including most species of the genus *Poratia* (Cook & Collins, 1895), is their ability to reproduce parthenogenetically.

Poratia salvator Golovatch & Sierwald, 2000, the object of this study, is a good example of milliped ecological and reproductive plasticity. This species, originally described from El Salvador (Golovatch et al., 2005) and recently found in Brazil, is characterised by small size (3.5 mm length and 0.5 mm width) and 19 body segments that are brownish-yellow in colouration (Golovatch and Sierwald, 2000). *Poratia salvator* is a species that reproduces parthenogenetically, although the birth of males in a very small number was registered (Pinheiro et al., 2009). This species shows high adaptability to different environmental conditions, inhabiting both strictly terrestrial as well as partly inundated areas (Battirola et al., 2009).

In order to further study the latter aspect of the ecological flexibility of *P. salvator*, thus increasing our understanding of millipede ecological plasticity in general, we used fertility tables to estimate the fertility and the survival rates and to compare the population growth of two populations of *P. salvator* inhabiting two areas with distinct characteristics: a strictly terrestrial area, and a periodically inundated floodplain.

2. Material and Methods

2.1. Study area

Individuals of *P. salvator* were manually collected in two different localities. The first one, located in the Pantanal of Mato Grosso (16° 15' 12'' S and 56º 22' 12'' W), municipality of Nossa Senhora do Livramento, state of Mato Grosso,

is a floodplain with well-defined seasons and periodical, annual flooding. The second sampling area, located at the experimental field of the Centro Universitário de Várzea Grande - UNIVAG (15° 38' 41'' S and 56° 5' 53'' W), municipality of Várzea Grande, Mato Grosso, is characterised by a homogenous Cerrado vegetation not subjected to periodical floods.

2.2. Life cycle monitoring

Following the methodology proposed by Adis et al. (2000), the life cycle of *P. salvator* was monitored in the following manner: individuals were accommodated into plastic containers covered with lids and containing a mixture of plaster and coal (8:2) on the bottom, covered with a thin layer of soil. The plaster-coal mixture has the role of keeping humidity constant inside the container, since these two materials have high capacity to absorb water. In the laboratory, the animals were reared on organic gardening soil containing pieces of wood, leaves, roots and chips. This substrate was kept in the freezer for at least 24 hours before setting up the experiment, to control the proliferation of fungi and remaining arthropods.

Individuals were fed flaked dried food for carnivorous fish. This type of food is recommended for containing high levels of animal protein (tetramine), which is an important component of the exoskeleton (Adis et al., 2000). The food was placed onto a piece of filter paper to avoid direct contact with the soil, thus facilitating the removal of leftovers and constant food replacement to avoid contamination by fungi. Additionally, the filter paper provided better visualisation of the young, thus facilitating the visualisation and separation of the offspring, particularly during their first developmental stage.

The millipedes were monitored three times a week for observation of births and determination of the development stages the young. In order to ensure that the females used in the subsequent experiment had not reproduced before, individuals were separated as soon as they reached the adult phase.

The experiment to study of the life-cycle of *P. salvator* had a total of 18 females (parental generation), nine from the Pantanal of Mato Grosso and nine from the Várzea Grande. These starter females were individualised and kept at room temperature. With the help of a stereoscopic microscope, both populations were monitored three times a week, when births were recorded.

When juveniles were found, their developmental stage was determined. Next, individuals were counted, transferred to a new container, and labelled with two numbers: the number of their progenitor, and a number of their own. All young individuals in the same developmental stage were grouped together in one same container. Thus, the number of young individuals differed between the various rearing containers.

Offspring development was monitored under a stereoscopic microscope three times a week. The developmental stage of each individual was determined based on the number of body segments with leg pairs.

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The duration of each stage was ascertained as follows: the duration of stage I was counted from the first day individuals in stage I were found until the first day these individuals were observed in stage II (Adis et al., 2000), including the ecdysis period. This procedure was repeated for the subsequent stadia until individuals reached the seventh stage, which corresponds to the adult phase. The duration of the latter stage was counted from the first day of the adult phase until the birth of the first young.

In order to study the life-cycle of the second generation, three adult daughters of each starter female were randomly selected and distributed into nine replicates, totalling 27 individuals.

The complete life-cycle of *P. salvator* was followed for the first and second generations, but the third generation was maintained only to enable the calculations of fecundity and longevity of the second generation females. In a manner similar to the one described above, three adult females from each second generation mother were randomly selected (n = 27) and observed throughout their reproductive period until they died. The juveniles were counted and separated from their mothers, but their development was not monitored.

The life-history of each population of *P. salvator* was constructed based on fertility tables that allowed for the quantification of population growth.

3. Results

The analysis of the fertility tables corresponding to the first generation showed that females of both populations laid their eggs for the first time within 10 days after reaching reproductive maturity (Tables 1 and 2), a pattern that was maintained in the second generation (Tables 3 and 4). Despite this similarity, the two first generation populations differed in the time when they were most prolific: while the population from the Pantanal generated the highest number of juveniles (156 individuals) at age zero, the Várzea Grande population produced the highest number of juveniles at the age intervals 10 and 20 (109 individuals for each age interval) (Figure 1a).

An overall increase in offspring production was observed in the second generation, for both populations. Regardless of this, the period when they were most prolific followed the pattern that characterised the first generation: while the population from the Pantanal generated the highest number of juveniles (906 individuals) at age zero, the Várzea Grande population produced the greatest majority of juveniles at the ages of 10 (1,238) and 20 days (1,040), respectively (Figure 1b).

The first generation of females from the Pantanal stopped reproducing in the 50th day of their reproductive period, and lived a maximum of 70 days, whereas females from Várzea Grande reproduced until they were 60 days of age. Females of the latter also lived longer, ca. 30 days after they stopped reproducing, with the oldest females reaching 100 days (Tables 1 and 2; Figure 1a).

Second generation females had a longer reproductive phase with respect to females from the first generation: 60 additional days for the Pantanal population, and 50 additional days for the Várzea Grande population (Tables 3 and 4; Figure 1b). In contrast with first generation females, which stopped reproducing in their last age intervals, second generation females kept reproducing until their very end. This conclusion was drawn based on the numerous births that happened after the death of the progenitors of both populations, which indicates that females laid eggs in the substrate shortly before expiring.

Specific survival rates per age interval of first generation females of *P. salvator* showed a decline with increased reproductive investment. That is, female survival decreased as more individuals were born (Figure 2). This pattern was repeated in the second generation (Figure 3). Despite the increased fertility and the longer reproductive phase that characterised the latter, the survival rate per age group also followed the variations in reproductive rate that characterised the first generation. These variations, however, were less abrupt in the second generation than in the first (Figure 3).

The analysis of the reproductive potential of the first generation of *P. salvator* revealed that the reproductive peak of the Pantanal population happened between zero and 10 days, whereas the reproductive peak of the Várzea Grande population happened between 10 and 20 days (Tables 1 and 2). In both populations, reproductive peaks were followed by a significant decline in reproduction at older ages (Figure 4a). This pattern changed in the second generation (Tables 3 and 4) when a second reproductive peak was observed for both populations: at the ages of 50 and 60 days for the Pantanal population and 70 days for the Várzea Grande population, respectively. The age interval of this second reproductive peak coincided with the age when first generation females stopped reproducing (Figure 4b).

With respect to the growth parameters analysis, the first generation from the Pantanal population had a lower net reproductive rate and a higher growth rate ($R_0 = 37$; $r = 0.46$) when compared with the first generation from the Várzea Grande ($R_0 = 40.33$; $r = 0.20$). However, the generation time for the Várzea Grande population ($G = 18.37$) was longer than the generation time obtained for the Pantanal population ($G = 7.93$). In the second generation, the net reproduction rate was also higher for the Várzea Grande population ($R_0 = 300.25$) when compared with the population from the Pantanal ($R_0 = 226.33$). However, only a small difference in the rate of intrinsic growth was observed between the two populations: $r = 0.17$ for the Pantanal and $r = 0.16$ for the Várzea Grande. The generation time, on the other hand, was longer for the Várzea Grande population ($G = 34.89$) when compared with the Pantanal population ($G = 31.65$).

Table 1. Fecundity table for the first generation adults of *P. salvator* from the Pantanal of Mato Grosso, maintained under laboratory conditions. R_0 = net reproductive rate; G = generation time; r = rate of intrinsic growth.

Time interval (days)	Age X	Total of females N	Specific survival per age l(x)	Probability of survival g(x)	Total offspring produced per time interval F(x)	Mean number of descendents produced per female b(x)	Reproductive expectancy l(x)b(x)	l(x)b(x)x
0-9	0	9	1	0.89	156	17.33	17.33	0
10-19	10	8	0.89	0.75	126	15.75	14.00	140.00
20-29	20	6	0.67	0.83	26	4.33	2.89	57.78
30-39	30	5	0.56	0.6	15	3.00	1.67	50.00
40-49	40	3	0.33	0.67	9	3.00	1.00	40.00
50-59	50	2	0.22	0.5	1	0.50	0.11	5.56
60-69	60	1	0.11	0	0	0	0	0
70-79	70	0	0	0	0	0	0	0
				Total	333	43.92	37.00	293.33

$R_0 = 37$; G = 7.93; r = 0.46

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Table 2. Fecundity table for the first generation adults of *P. salvator* from the Várzea Grande, Mato Grosso, maintained under laboratory conditions. R_0 = net reproductive rate; G = generation time; r = rate of intrinsic growth.

Time interval (days)	Age	Total of females	Specific survival per age	Probability of survival	Total offspring produced per time interval	Mean number of descendents produced per female	Reproductive expectancy	
	X	N	l(x)	g(x)	F(x)	b(x)	l(x)b(x)	l(x)b(x)x
0-9	0	9	1	0.78	49	5.44	5.44	0
10-19	10	7	0.78	0.86	109	15.57	12.11	121.11
20-29	20	6	0.67	0.83	109	18.17	12.11	242.22
30-39	30	5	0.56	0.8	59	11.80	6.56	196.67
40-49	40	4	0.44	0.75	23	5.75	2.56	102.22
50-59	50	3	0.33	0.67	13	4.33	1.44	72.22
60-69	60	2	0.22	1	1	0.50	0.11	6.67
70-79	70	2	0.22	1	0	0	0	0
80-89	80	2	0.22	1	0	0	0	0
90-99	90	2	0.22	0	0	0	0	0
100-110	100	0	0	0	0	0	0	0
				Total	363	61.57	40.33	741.11

R_0 = 40.33; G = 18.37; r = 0.20

Table 3. Fecundity table for the second generation adults of *P. salvator* from the Pantanal population, maintained under laboratory conditions. R_0 = net reproductive rate; G = generation time; r = rate of intrinsic growth.

Time interval (days)	Age x	Total of females N	Specific survival per age l(x)	Probability of survival g(x)	Total offspring produced per time interval F(x)	Mean number of descendents produced per female b(x)	Reproductive expectancy	
							l(x)b(x)	l(x)b(x)x
0-9	0	21	1	1.00	906	43.14	43.14	0
10-19	10	21	1.00	1.00	692	32.95	32.95	329.52
20-29	20	21	1.00	1.00	703	33.48	33.48	669.52
30-39	30	21	1.00	1.00	514	24.48	24.48	734.29
40-49	40	21	1.00	1.00	439	20.90	20.90	836.19
50-59	50	21	1.00	0.90	506	24.10	24.10	1204.76
60-69	60	19	0.90	1.00	463	24.37	22.05	1322.86
70-79	70	19	0.90	0.79	224	11.79	10.67	746.67
80-89	80	15	0.71	0.73	111	7.40	5.29	422.86
90-99	90	11	0.52	0.82	116	10.55	5.52	497.14
100-109	100	9	0.43	0.56	36	4.00	1.71	171.43
110-119	110	5	0.24	0.40	38	7.60	1.81	199.05
120-129	120	2	0.10	0	5	2.50	0.24	28.57
130-139	130	0	0	0	1	0	0	0
140-149	140	0	0	0	1	0	0	0
				Total	4,755	247.25	226.33	7,162.86

R_0 = 226,33; G = 31,65; r = 0,17

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Table 4. Fecundity table for the second generation adults of *P. salvator* from the Várzea Grande, Mato Grosso, maintained under laboratory conditions. R_0 = net reproductive rate; G = generation time; r = rate of intrinsic growth.

| Time interval (days)	Age	Total of females	Specific survival per age	Probability of survival	Total offspring produced per time interval	Mean number of descendents produced per female	Reproductive expectancy	
	x	N	l(x)	g (x)	F(x)	b(x)	l(x)b(x)	l(x)b(x)x
0-9	0	24	1	1.00	958	39.92	39.92	0
10-19	10	24	1.00	0.96	1238	51.58	51.58	515.83
20-29	20	23	0.96	1.00	1040	45.22	43.33	866.67
30-39	30	23	0.96	0.96	933	40.57	38.88	1166.25
40-49	40	22	0.92	0.91	612	27.82	25.50	1020.00
50-59	50	20	0.83	0.95	619	30.95	25.79	1289.58
60-69	60	19	0.79	0.95	477	25.11	19.88	1192.50
70-79	70	18	0.75	0.94	602	33.44	25.08	1755.83
80-89	80	17	0.71	0.94	355	20.88	14.79	1183.33
90-99	90	16	0.67	0.81	189	11.81	7.88	708.75
100-109	100	13	0.54	0.85	151	11.62	6.29	629.17
110-119	110	11	0.46	0.09	28	2.55	1.17	128.33
120-129	120	1	0.04	0	4	4.00	0.17	20.00
130-139	130	0	0	0	3	0	0	0
				Total	7,209	345.46	300.25	10,476.25

R_0 = 300.25; G = 34.89; r = 0.16
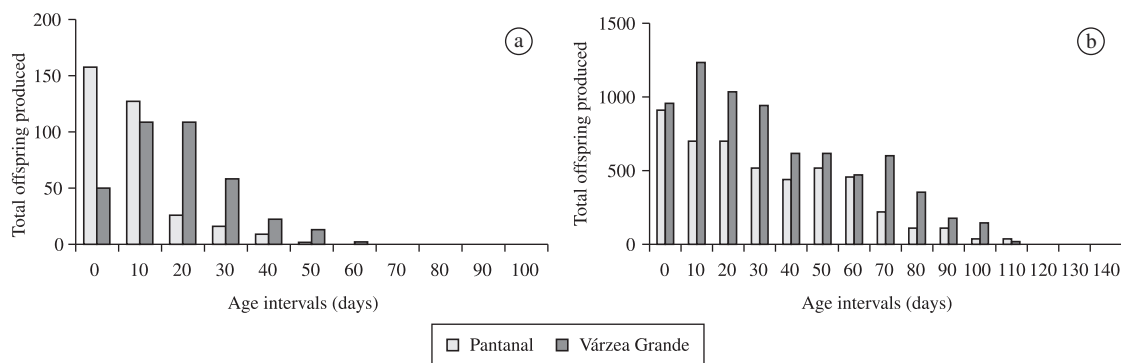
Figure 1. Offsprings produced in a) first generation and b) second generation of *P. salvator* from the Pantanal and Várzea Grande populations, per age interval (days), maintained under laboratory conditions.
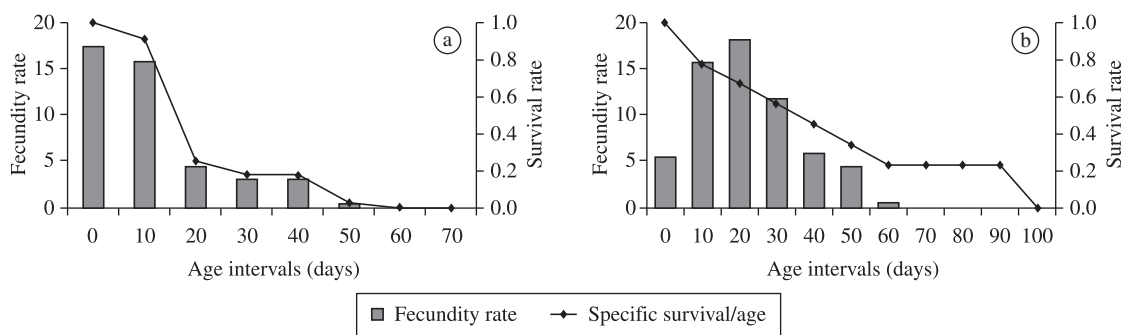

Figure 2. Survival and fecundity rates obtained for the first generation females of *P. salvator* from a) the Pantanal and b) Várzea Grande of Mato Grosso, maintained under laboratory conditions.
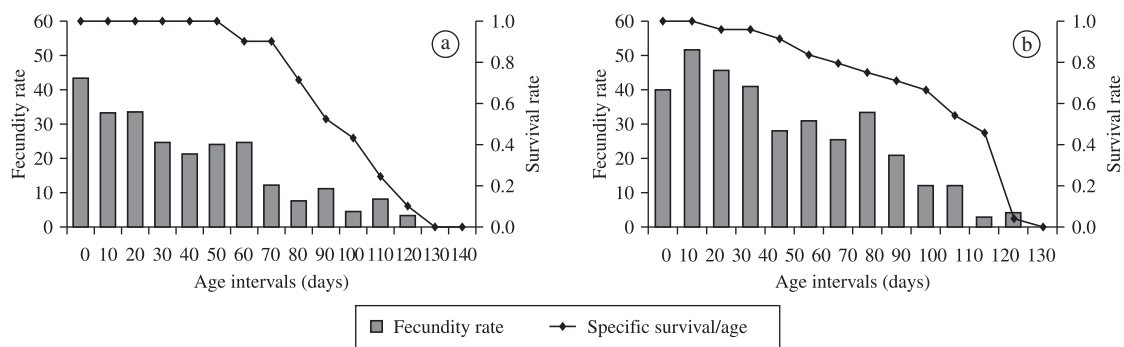

Figure 3. Survival and fecundity rates obtained for the second generation females of *P. salvator* from a) the Pantanal and b) Várzea Grande of Mato Grosso, maintained under laboratory conditions.

4. Discussion

Despite the fact that females of *P. salvator* displayed similar reproductive patterns for the two generations studied, the overall increase in mean fecundity observed in the second generation may be a reflex of the abundance and quality of the food available. The extra energy accumulated by the females may have been invested in the production of more offspring. A similar result had been found by David and Céléries (1997), who reported increased fecundity for individuals of *Polydesmus angustus* (Latzel, 1884) (Polydesmidae) following improved diet regimens.

The accelerated start of the reproductive period of the Pantanal population when compared with the Várzea Grande
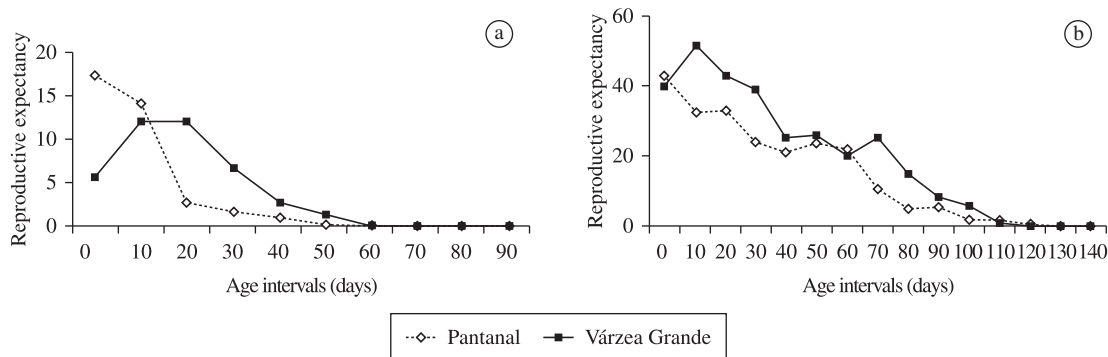
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Figure 4. Reproductive expectancy for the a) first and b) second generation populations from the Pantanal and Várzea Grande, Mato Grosso, maintained under laboratory conditions.

population may be a reflex of the extreme and variable conditions of the Pantanal of Mato Grosso, particularly with respect to humidity and temperature, a result of the strong seasonality and periodical (annual) inundations (Junk et al., 1989) that characterise that ecosystem. Such conditions may have resulted in adaptive survival strategies (Adis, 1997; Adis et al., 2001; Battirola et al., 2009) to cope with higher mortality rates, such as the development of accelerated reproduction before the death of the progenitors.

The hypothesis that organisms may reproduce earlier and faster when mortality rates are high had been previously proposed by Krebs (1986) and Roff (1992). According to the authors, the high energy investment involved in reproduction compromises the survival of the progenitors, a phenomenon also observed for *P. salvator* in the present study: as mentioned in the results section, high reproductive investment in this species was accompanied by lower specific survival rates per age category.

The relatively lower range between survival rate and increased reproduction found in the second generation is an indication of the ecological plasticity of *P. salvator*. Faced with optimal humidity conditions and better diet, the progenitors of the second generation had a lower mortality rate. The plasticity of *P. salvator* females is also indicated by the appearance of a second reproductive peak in the second generation, what means increased reproduction with improved conditions. The decreased offspring production as a function of an increase in reproductive age is in agreement with the pattern previously proposed by Krebs (1986), in which female survival is inversely correlated with fecundity, a result of the high energy investment involved in the production of juveniles.

The results obtained for the growth paramenters of *P. salvator* indicate that the net reproduction rate was higher in the second generation populations, a reflex of the increased reproductive potential of the females of both populations. However, the intrinsic growth rate of the species decreased as a result of an increase in generation time observed in the second generation. Consequently, the growth rate of both populations was slower in the second generation when compared with the first generation, given

that the progenitors lived longer as a function of improved living conditions. Most likely, the population from the Várzea Grande had an advantage over the population from the Pantanal from the start, because it already inhabited a more stable and favourable environment.

Strong differences in the life history like increase mortality of individuals, decrease in generation time, variation in fertility can occur when comparing the life cycle of parthenogenetic and bisexual co-specifics lineages (Vrijenhoek, 1998). The results of this study do not provide an indication of advantages or disadvantages of parthenogenetic reproduction in *P. salvator*. For this, it is more appropriate to test the participation of males in reproduction and its influence in population growth.

In conclusion, it is safe to assume that the natural differences in the life-history of each wild population were observed only in the first generation, which seems to have retained the reproductive characteristics brought from their natural environments: the first a periodically inundated, constantly changing environment, the Pantanal, and the second an ecologically more stable area, with homogenous conditions and most likely more suitable for the development of the species.

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