

Effects of rearing history and geographical origin on reproduction and body size of the predator *Podisus nigrispinus* (Heteroptera: Pentatomidae)

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Abstract. The relationship between body size and reproduction was investigated for two laboratory strains of *Podisus nigrispinus* (Dallas). A strain originating from Surinam and maintained for about 15 years under laboratory conditions, did not demonstrate any significant relationship between body length and fecundity. A second strain originated from Brazil where it had been reared in the laboratory for several generations but under different conditions of climate, food and housing. In the first generation of the Brazilian strain, a significant positive relationship was found between body length and total number of eggs. Results suggest that colonization might act initially in favour of a positive body size/fecundity relationship. In contrast, females of the fifth and tenth generations, like those of the Surinamese strain, showed no significant relationship between body length and reproduction. Fecundity of the tenth generation of the Brazilian strain, with an average of 317 eggs per female, was significantly greater than that of the first and fifth generation, with 220 and 243 eggs per female, respectively. The strain from Surinam, with 545 eggs per female, had a markedly higher reproductive capacity than any generation of the Brazilian strain. Adult body weights of different generations of the Brazilian strain increased consistently from the first to the tenth generation, indicating an adaptation to the new environment. Females and males of the Surinamese strain lived longer than those of the Brazilian one. Besides differences related to the geographical origin of the strains, greater fecundity and longevity in long-term laboratory strains of *P. nigrispinus* may reflect selective adaptation to food and climatic conditions in the laboratory environment.

INTRODUCTION

Reproduction appears to be related to a variety of internal and external cues in insects (Jervis & Copland, 1996). Among environmental factors, nutrition is considered as the most important parameter influencing egg production. In other words, oogenesis in insects is typically a nutrient-limited process, triggered only if sufficient nourishment is available (Wheeler, 1996). On the other hand, body size of insects is also affected by quality and quantity of food supplied. The relationship between body size and reproduction in insects has been the subject of many studies and was mainly revealed to have a positive correlation, although with some exceptions (reviewed by Honěk, 1993).

In *Podisus* bugs, fecundity and body weight are negatively affected by unfavourable environmental conditions, in particular by the quantity and quality of food consumed, during the nymphal stages and/or adult lifetime (e.g., Mukerji & LeRoux, 1969; O'Neil & Wiedenmann, 1990; Wiedenmann & O'Neil, 1990; De Clercq & Degheele, 1992; Legaspi & O'Neil, 1993). In *Podisus maculiventris* (Say), a positive relationship between body size and fecundity was established for individuals receiving varying amounts of prey during the nymphal stage (Evans, 1982). In contrast, Mohaghegh-Neyshabouri et al. (1996) stated that fecundity was not correlated with body weight in laboratory-reared *P. maculiventris* and *Podisus nigrispinus* (Dallas) supplied an excess of prey.

P. nigrispinus has been reported to suppress numerous economically important agricultural pests (Saini, 1994; De Clercq et al., 1998). Mass release of the predator has been shown to control *eucalyptus* defoliator caterpillars (Zanuncio et al., 1994). A better understanding of the reproductive biology of the insect may help mass producers to improve propagation procedures. In this paper, the relationship between body size and fecundity is evaluated in two strains of *P. nigrispinus* differing in geographical origin and rearing history, provided with an excess of food.

Fecundity, body length and weight were compared between strains and generations, indicating the role of adaptation in the traits studied.

MATERIAL AND METHODS

One colony of *P. nigrispinus* was obtained from the Department of Entomology of the Agricultural University of Wageningen, The Netherlands, in 1982. The insects originated from Surinam and were reared following the methods described in De Clercq & Degheele (1993). The predators were kept in plastic containers furnished with absorbent paper towelling, providing hiding places and oviposition sites. Nymphs were reared in 1.5 liter containers. About 30 egg batches (≈ 800 eggs) were placed in each container; from the second instar onwards, the number of insects per container was halved at each moult. At emergence, adults were transferred to 5.5 l containers, containing 25 pairs each. The predators were supplied ad libitum with late instars of the greater wax moth, *Galleria mellonella* L., and at times with noctuid caterpillars. Water was provided by a moist paper plug fitted into a plastic dish. The stock culture was kept in a growth chamber at $23 \pm 1^\circ\text{C}$, $75 \pm 5\%$ RH, and a photoperiod of 16L : 8D.

The second strain of *P. nigrispinus* was introduced in 1997 and originated from a laboratory colony maintained at the Federal University of Viçosa, Minas Gerais State, Brazil. Rearing conditions in the original colony were: $25 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH, and a photoperiod of 12L : 12D. Larvae of *Musca domestica* L. were the main food. In Brazil, groups of 10 insects were kept in 0.5 l plastic containers without paper towelling. The colony was frequently renewed with individuals collected in plantations of *Eucalyptus* (Saavedra et al., 1995). Upon introduction at the Laboratory of Agrozoology, the colony was maintained under the conditions mentioned for the Surinamese strain. Experiments were carried out on the first, fifth and tenth generations of

the Brazilian strain following introduction to the new laboratory conditions.

For each strain and generation, 15–20 pairs of adults were collected at first copulation from stock cultures, and placed in individual petri dishes (14 cm in diameter) furnished with absorbent paper. Each pair was supplied with one seventh instar of *G. mellonella* (cca 200 mg) daily, which is sufficient for maximal fecundity (De Clercq & Degheele, 1992). A water-saturated plug fitted into a small dish (2.5 cm diameter) provided water. Every day, oviposition and survival were monitored, and water and prey were replenished. Reproductive characters were: preoviposition period, total number of eggs laid, number of eggs per batch, and oviposition rate (total number of eggs of each female divided by its oviposition period). Upon death, females were measured using an ocular micrometer, and dissected to count the number of remaining eggs (egg load). Body length was determined by measuring the distance between the tip of the tylus and the hind margin of the last sternite.

At least 200 newly moulted adults (≤ 12 h) from stock colonies of different strains and generations were weighed on a Sartorius B 120 S digital balance (± 0.1 mg precision) (Sartorius AG, Goettingen, Germany). The sex ratio of stock colonies was also determined.

In the Brazilian strain, 40 egg clutches (1,000–1,500 eggs) were randomly collected from 2- to 4-week-old stock cultures of each generation and incubated to determine hatching percentage.

ANOVA tests, followed by Tukey-HSD tests, were performed to compare reproductive parameters, female body length and adult body weights among different strains and generations. In case of abnormal distribution, data were log-, square root- or arcsine-transformed before analysis. The relationship between body length and total number of eggs was evaluated using reduced major axis regression (Sokal & Rohlf, 1995). All data analyses were conducted using the SPSS statistical package (Norusis, 1993).

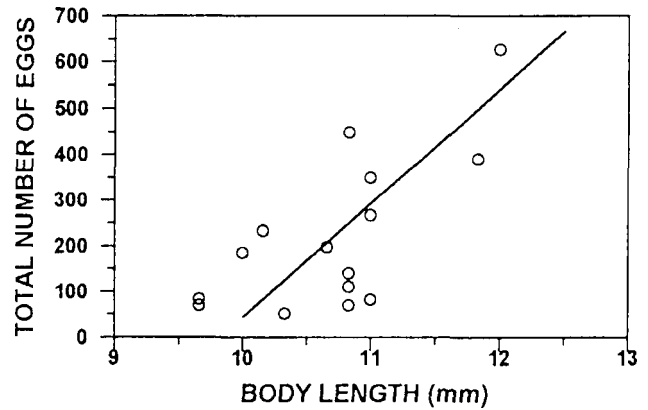


Fig. 1. Relationship between total number of eggs and body length in the first generation of the Brazilian strain of *P. nigrispinus*. Regression equation is: $y = 249.26x - 2449.62$, and $r = 0.70$.

RESULTS

The relationship between body length and reproduction differed among strains and generations. No significant relationships were found between body length and total fecundity for either the Surinamese strain or the fifth and tenth generations of the Brazilian strain. In contrast, the first generation of the Brazilian strain demonstrated a significant relationship between fecundity and body length (ANOVA, $F = 14.28$; $df = 1, 13$; $P < 0.01$) (Fig. 1).

Body weight, body length, reproduction and longevity of the predators are shown in Table 1. Adult body weights of the Brazilian strain increased with generation; females of the tenth generation were also heavier than those of the Surinamese strain, but male body weights of the two populations were similar (ANOVA, $F = 291.3$, $df = 3, 576$; $P < 0.0001$ for females, and $F = 228.3$; $df = 3, 524$; $P < 0.0001$ for males). Similarly, body length of females was significantly higher in the tenth generation of the Brazilian strain than in any other population

TABLE 1. Body weight, body length, reproduction and longevity of two strains of *P. nigrispinus* with a different rearing history and geographical origin^a.

Character	Brazil G1 ^b	Brazil G5 ^b	Brazil G10 ^b	Surinam
Female body weight (mg)	48.0 \pm 0.5d	64.9 \pm 0.7c	74.4 \pm 0.6a	69.6 \pm 0.8b
Male body weight (mg)	35.3 \pm 0.5c	47.2 \pm 0.6b	52.0 \pm 0.4a	51.5 \pm 0.4a
Female body length (mm)	10.7 \pm 0.2c	10.9 \pm 0.2bc	11.5 \pm 0.1a	11.3 \pm 0.1ab
Preoviposition times (days)				
moult-mating	2.2 \pm 0.2a	2.1 \pm 0.1a	2.3 \pm 0.1a	5.2 \pm 0.3b
mating-oviposition	8.6 \pm 0.6b	7.7 \pm 0.9a	5.4 \pm 0.5a	7.6 \pm 0.7a
Total no. eggs	219.5 \pm 43.5c	242.9 \pm 43.4bc	316.7 \pm 34.5b	544.5 \pm 58.1a
No. eggs per batch	22.9 \pm 1.9c	23.2 \pm 1.6c	35.6 \pm 1.5a	29.4 \pm 1.1b
Oviposition rate (eggs/female/day)	9.8 \pm 1.0b	7.9 \pm 0.9b	13.3 \pm 1.1a	7.5 \pm 0.4b
Egg load	5.2 \pm 1.7b	3.2 \pm 1.4b	4.9 \pm 2.1b	22.5 \pm 2.9a
Female longevity (days)	36.8 \pm 3.6b	48.4 \pm 5.1b	39.3 \pm 2.9b	87.1 \pm 7.3a
Male longevity (days)	39.0 \pm 4.1b	39.1 \pm 4.8b	38.8 \pm 5.3b	63.4 \pm 10.2a

^a Mean \pm S.E.; means within rows followed by the same letter are not significantly different (Tukey test, $P > 0.05$).

^b First (G1), fifth (G5), and tenth generations (G10) of a Brazilian strain after switching to new rearing conditions.

$n = 15, 18, 19$, and 20 for body length and reproductive parameters of females of strains Brazil G1, Brazil G5, Brazil G10 and Surinam, respectively; $n = 116, 126, 196$ and 142 for body weight of females, and $n = 73, 93, 193$, and 169 for body weight of males of the respective strains.

(ANOVA, $F = 7.5$; $df = 3, 68$; $P = 0.0002$). The longer preoviposition period in the Surinamese strain, compared to that in the three generations of the Brazilian strain, was due to the longer period between emergence and first mating (ANOVA, $F = 59.7$; $df = 3, 68$; $P < 0.0001$). The Surinamese strain, with an average of 544.5 eggs per female, had a markedly higher fecundity than any generation of the Brazilian strain (ANOVA, $F = 11.9$; $df = 3, 68$; $P < 0.0001$). Fecundity of the tenth generation of the Brazilian strain, with 316.7 eggs per female, was significantly higher than that of the first and fifth generation, with 219.5 and 242.9 eggs per female, respectively. The tenth generation of the Brazilian strain had a higher oviposition rate and number of eggs per batch, compared with the other populations (ANOVA, $F = 9.3$; $df = 3, 68$; $P < 0.0001$, and $F = 15.8$; $df = 3, 68$; $P < 0.0001$ for the respective characters). Egg load at the time of death was markedly higher in the Surinamese strain than in the three generations of the Brazilian one (ANOVA, $F = 19.9$; $df = 3, 68$; $P < 0.0001$). Adults of the Surinamese strain lived longer than those of the Brazilian populations (ANOVA, $F = 20.9$; $df = 3, 68$; $P < 0.0001$ for females, and $F = 3.3$; $df = 3, 67$; $P = 0.025$ for males).

In the Brazilian strain, egg hatch improved with generation, averaging 74, 82 and 88% for the first, fifth and tenth generation, respectively (ANOVA, $F = 3.9$; $df = 2, 117$; $P = 0.02$).

Sex ratio was initially female-biased in the Brazilian strain, but the proportion of females and males became similar when reaching the tenth generation: female : male ratio was 1.6 (116 : 73), 1.4 (126 : 93) and 1.0 (196 : 193) for the first, fifth, and tenth generation of the Brazilian strain, respectively. The ratio was 0.8 (153 : 183) for the tested generation of the Surinamese strain; however, sex ratio of this strain tended to vary among generations (e.g., De Clercq & Degheele, 1993).

DISCUSSION

The relationship between body size and fecundity in insects depends on a complex of genetic and non-genetic features. In terms of non-genetic cues, both parameters are affected by a number of factors such as quantity and quality of food consumed, temperature and crowding (Danks, 1994).

Differential relationship between body length and fecundity in different generations of the Brazilian strain may also be interpreted as a colonization effect. Insects are often encountered with population bottlenecks in the first generation of colonization (Boller, 1972). Leppla et al. (1983) stated that switching a colony of Mediterranean fruit flies from one rearing regime to another caused potentially deleterious readaptation at a rate and magnitude similar to original colonization. Significant relationship between body length and fecundity parameters in the first generation of the Brazilian strain may be the result of selective adaptation. Rearing conditions in the new laboratory environment (Gent) differed considerably from those of the original colony (Viçosa): temperature, relative humidity, photoperiod, density, and prey differed between rearing sites.

On the other hand, in the Surinamese strain and later generations of the Brazilian strain no significant relationship between body length and fecundity was observed. This corroborates the findings of an earlier study (Mohaghegh-Neyshabouri et al., 1996), which could not establish a significant relationship between fecundity and body weight of laboratory-reared *P. nigrispinus* and *P. maculiventris* receiving prey in excess. However, a positive correlation between body size and fecundity was reported for *P. maculiventris* reared in the fifth stadium on different amounts of prey (Evans, 1982). In laboratory-adapted insects, body size differences may primarily be attributed to

inherent genetic variability of the predator, and may not necessarily be linked with fecundity.

Lower adult weights in the first generation of the Brazilian strain, compared with the fifth and tenth generation, may be the result of difficulties in adapting to the new environment and diet. Over ten generations of the Brazilian strain, fecundity increased concomitantly with body size, suggesting a good adaptability to new conditions and a positive relationship between body size and reproduction capacity. However, no such relationship could be established for individual predators in the fifth and tenth generation. Higher fecundity of the Surinamese strain compared with that of the tenth generation of the Brazilian one, appears to be related to greater longevity of the former strain, providing females with more opportunities to produce eggs. Higher egg load at the time of death in the Surinamese strain implies that there is no real postoviposition period for females which are well-adapted to laboratory conditions.

In long-term laboratory colonies deleterious effects of both temporary adaptations and permanent genetic changes may occur (Mackauer, 1976). Reproductive quality of the Surinamese strain decreased over time; i.e., total fecundity of the population in the current investigation (545 eggs) is half of that in an earlier study (910 eggs, De Clercq & Degheele, 1993), despite similar climatic conditions and strain maintenance. The shorter period between adult emergence and first mating in the Brazilian strain than in the Surinamese one, indicates that adaptation to laboratory conditions may interfere with mate finding ability. Moore et al. (1985) stated that the close association of large numbers of both sexes in the rearing environment reduces the need for traits used to find and select mates.

In summary, our findings indicate that adaptation to laboratory conditions may change the relationship between body size and fecundity. Further, differences between the two populations studied could reflect normal geographical variation within *P. nigrispinus*, the effect of rearing conditions, or both. Searching for better-performing geographical strains may be rewarding. Well-adapted laboratory strains of *Podisus* may demonstrate higher fecundity and greater body size.

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