

Stress promotes changes in resource allocation to growth and reproduction in a simultaneous hermaphrodite with indeterminate growth

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Received 31 January 2006; accepted for publication 15 September 2006

In iteroparous animals, investment in growth is compromised by investment in reproduction, especially in species with indeterminate growth. Life-history theory predicts that growth should be favoured over reproduction, assuming size-related fecundity or survival. Hence, increase body condition represents an increase in reproductive potential. Simultaneous hermaphrodites should adjust their resource allocation to each sex function in response to current conditions but, recently, it has been suggested that, in hermaphrodites, gender allocation should be considered as a three-way trade-off, including the investment in somatic growth. Due to the higher costs involved, the female function is affected to a greater extent by environmentally stressful conditions rather than the male function. To examine this, we induced stress in the hermaphroditic earthworm *Eisenia fetida* (Savigny, 1826) and looked for changes in resource allocation in nonreproductive and reproductive individuals. Experimental stress was induced by using tweezers to elicit contractile escape movements. We predicted that stressed earthworms would preferentially allocate resources to growth. In nonreproductive individuals, however, stress had a negative effect on growth, although weight recovery was rapid once manipulation ceased, indicating the importance of body condition, as well as the existence of mechanisms of compensatory growth for growth trajectories in this earthworm species. The response of reproductive individuals was consistent with our expectation: (1) stressed worms maintained their growth rate at the expense of current reproduction and (2) stressed earthworms laid 25% fewer cocoons, which were 30% lighter than cocoons laid by control earthworms. The present results suggest that *E. fetida* regulates its reproductive effort and that future reproduction has more impact on its fitness than current reproduction. The trade-off between current and future reproduction should be taken into consideration in models of sex allocation in simultaneous hermaphrodites. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 593–600.

ADDITIONAL KEYWORDS: body condition – compensatory growth – current reproduction – earthworms – iteroparity – life-history trade-off – residual reproductive value.

INTRODUCTION

A constrained relationship between traits (i.e. a trade-off) is the linkage between two traits that affects the relative fitness of genotypes, while avoiding independent evolution of the traits. Allocation of resources to one trait that enhances fitness will thus result in changes in other traits that diminish fitness (Stearns, 1992). A central point in life-history theory is that parental investment in current reproduction should be balanced by the costs in terms of residual reproductive

value (Williams, 1966; Stearns, 1992). Iteroparous animals must decide how to allocate their energy resources obtained between themselves and their offspring, and their current reproductive investment is more likely to be regulated by the effect of reproductive effort on future reproduction (Stearns, 1976; Charlesworth, 1980; Maynard Smith, 1982). In iteroparous invertebrates with indeterminate growth (i.e. growth that continues after maturation), the investment in growth increases the possibility of future reproduction because size is related to fecundity and/or survival (Reznick, 1983; Shine & Schwarzkopf, 1992; Schwarzkopf, 1993).

Simultaneous hermaphrodites, unlike gonochoristic animals, should adjust their resource allocation to

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each sex function in response to current conditions (Charnov, 1979); the division of reproductive resources into male and female functions is therefore an important strategy for optimizing fitness (Charnov, 1982). Although, the trade-off between male and female allocation is the implicit assumption of sex allocation theory (Charnov, 1979, 1982), empirical studies have produced contradictory results (Schärer, Sandner & Michiels, 2005); this may be in part due to the allocation of resources, including other life-history traits. It has been suggested that, in hermaphrodites, gender allocation should be considered as a three- and not a two-way trade-off (Yund, Marcum & Stewart-Savage, 1997; Schärer *et al.*, 2005), including the investment in somatic growth. In this way, colonies of the hermaphroditic bryozoan *Celleporella hyalina* reduce their growth, favouring allocation to female function whereas male function remains constant (Hughes, Manríquez & Bishop, 2002). Due to the higher costs involved, female function is affected to a greater extent by environmentally stressful conditions than is the male function (Lloyd & Bawa, 1984) and, for example, it has been demonstrated that experimentally induced environmental stress causes maleness in hermaphroditic animals (Hughes *et al.*, 2003). Consequently, trade-off between current and future reproduction will be driven to a greater extent by the female rather than by the male function.

In hermaphrodites, there is often a positive correlation between female fecundity and body size (Baur & Raboud, 1988; Baur, 1988; Yusa, 1994; De Witt, 1996; Tomiyama, 1996; Vreys & Michiels, 1997; Wedekind, Stahm & Schärer, 1998; Trouvé *et al.*, 1999; Madec, Desbuquois & Coutellec-Vetro, 2000). As copulation is often costly, due to the time invested and the increased risk of predation, and as many hermaphroditic species occur at high densities, a preference for larger partners may be expected (Ridley, 1983). Thus, as fecundity increases with body size in hermaphrodites with indeterminate growth, we expect that small changes in growth will have a large effect on future reproduction and hence on total fitness.

Earthworms belonging to the genus *Eisenia* are simultaneously hermaphroditic animals with indeterminate growth (for a review of their life-history traits, see Domínguez, 2004). As in many hermaphrodites, 'female' fecundity in *Eisenia fetida* is positively correlated with growth (Domínguez & Edwards, 1997; Domínguez, Briones & Mato, 1997) and females also appear to prefer larger partners (Monroy *et al.*, 2005); thus, it is expected that the female function will be increased in each reproductive event. Because they are iteroparous, with continuous and high reproduction rates (2–3 cocoons per week) and with a maximum life span of approxi-

mately 2 years (Michon, 1957; Venter & Reinecke, 1988), a reduction in growth should have a potentially negative effect on the residual reproductive value. The results of other studies suggest that *Eisenia* spp. is able to allocate resources according to their current and future reproductive value (Tato, Velando & Domínguez, 2006).

In the present study, we tested the effect of experimentally induced stress on the trade-off between growth and reproduction in the earthworm *E. fetida*. First, we studied the effect of the stressful conditions on earthworm growth in nonreproductive individuals (i.e. when the animals do not have to choose between growth and reproduction) by manipulating the energy levels available to earthworms to produce a divergence in growth trajectories of experimental and control individuals (Álvarez & Nicieza, 2005). Although it is assumed that growth patterns in animals are programmed and fixed (Stearns, 1992), there is increasing evidence that some organisms may respond, after a period of food scarcity, by increasing their growth rates compared with well-fed organisms (Álvarez & Nicieza, 2005). We therefore expected that, under stressful conditions, which should lead to a reduction in the energy available for metabolism (Sibly & Calow, 1986), there would be decrease in the growth rate of earthworms but, after the period of stress, earthworm growth should be compensated for by increased growth rates. Second, we studied the effect of stressful conditions in reproductive earthworms to determine whether the cost of the stress is passed to offspring (i.e. reduction in reproduction) or whether they absorb the cost themselves (i.e. by a reduction in growth). We expect that, under unfavourable conditions, earthworms should sacrifice their current reproduction to maximize their residual reproductive value.

MATERIAL AND METHODS

STUDIED SPECIES AND EXPERIMENTAL INDUCTION OF STRESS

Individuals of *E. fetida* (Oligochaeta: Lumbricidae) were obtained from a compost heap (Mos, Galicia, Spain), then maintained in the laboratory at a temperature of 20 ± 2 °C, and supplied with cow manure *ad libitum*. Stress was induced by stimulating the typical contractile movement of the earthworms by squeezing them with laboratory tweezers, but avoiding causing any physical damage. This contractile movement has been described in neuronal experiments and is related to an escape mechanism when earthworms are attacked (Rushton, 1945). The contractile reaction can be graded, and is minimized or maximized according to stimuli received (Roberts, 1962).

NONREPRODUCTIVE EXPERIMENT

For this experiment, 40 earthworms were reared in isolation until no cocoons were laid (approximately 2 months after deposition of the last cocoon) and were then randomly divided into two groups (experimental and control). Experimental earthworms were stressed once a day over a period of 7 days and control earthworms were gently manipulated but not stressed during the same period. We consciously intensified the stress treatment to obtain a rapid response, and to determine the suitability of the treatment chosen. During the experiment, earthworms were maintained in isolation in Petri dishes and fed *ad libitum*; earthworms were placed at random in four groups of ten Petri dishes in a laboratory chamber. The growth of the earthworms, measured as changes in body weight, was recorded at the end of the experimental period and also after a further 7 days without manipulation. Accordingly, we were able to test the reliability of the treatment chosen, and whether earthworms have the capacity for growth compensation after a limiting energy condition, once the stressful situation has ceased (Álvarez & Nicieza, 2005).

Three earthworms in each group died (control and experimental) and were not included into the analyses. There were no differences between control and experimental groups in terms of the initial weight of earthworms ($P = 0.09$), with the earthworms in the control group being slightly heavier than the earthworms in the experimental group (0.58 ± 0.04 g and 0.51 ± 0.3 g, respectively). Uniparental reproduction has been described in this species, although at very low rates (<4%; Domínguez *et al.*, 2003), and no cocoons were found in the present study

REPRODUCTIVE EXPERIMENT

For this experiment, 40 mature earthworms were collected from the natural population in early spring, the period of maximum mating in this population (Monroy *et al.*, 2006), and then randomly divided into two groups (experimental and control). Experimental earthworms were stressed thrice a week over a 20-month period (the laying period), and control earthworms were gently manipulated but not stressed during the same period. In the present study, we aimed to understand how earthworms allocate their resources between growth and reproduction. We therefore deliberately reduced the amount of stress because we wanted to test for any changes in how the earthworms allocated their resources (current reproduction vs. growth); if we intensified the treatment (as we did in the nonreproductive experiment to seven pinches with the tweezers per week), it is quite possible that earthworms could not cope with the stress and therefore a reduction in both traits (reproduction and growth)

would be expected. In the latter case, we would be unable to test allocation decisions.

During the experiment, earthworms were kept in isolation in 100-mL plastic jars and covered with perforated lids and fed *ad libitum*; earthworms in each group were randomly placed in eight groups of five jars in a laboratory chamber. Earthworm weight and the number and biomass of cocoons they produced (determined by hand-sorting) were measured weekly for the duration of the experiment. All cocoons were placed on dampened cotton in microplate wells to enable measurement of incubation time, viability rate, number of hatchlings per cocoon, and hatchling biomass. During the experimental period, eight earthworms died (four in each group) and were not included in the statistical analyses. There were no differences between groups in terms of the initial earthworm weight ($P = 0.12$), with the earthworms in the control group being slightly heavier than those in the experimental groups (0.31 ± 0.02 g and 0.28 ± 0.01 g, respectively).

STATISTICAL ANALYSIS

The effect of experimental stress on earthworm growth (mg day^{-1}) in the nonreproductive experiment was analysed using a repeated measures analysis of variance (ANOVA), where experimental manipulation was the between subject factor, and time (during and after treatment) the within subject factor. The initial weight of earthworms was introduced as a covariate in the model. Post-hoc comparisons were performed by a Tukey's HSD test. This design allowed us to test the existence of compensatory growth in earthworms (Álvarez & Nicieza, 2005).

In the reproductive experiment, the earthworm was used as the unit of analyses; thus, the mean value of the reproductive parameters per earthworm was calculated. The effect of experimental stress on the earthworm growth rate over 2 months (9 weeks) was analysed using a repeated measures ANOVA, where the experimental manipulation was the between subject factor and time (week) the within subject factor. To check for any possible effect of sperm depletion on cocoons produced during the experiment, we tested the interaction between treatment and time, and found that it was not significant ($P = 0.52$); thus, we used the total number of cocoons per earthworm in the analyses. The effect of experimental stress on the reproductive variables in the reproductive experiment was analysed by fitting generalized linear models (GLM) to the data (McCullagh & Nelder, 1989). The error distribution and link function were chosen, according to presumed error in the data, to reduce the deviance in the model (Herrera, 2000). The number of cocoons and hatchlings were analysed using a Poisson

distribution and log link. Earthworm growth rates, the mean weight of cocoons and hatchlings, and the number of hatchlings per cocoon were analysed using a normal distribution and identity link. The initial weight of the earthworms was introduced as a covariate in all models, and had a significant negative effect over all reproductive variables tested ($P < 0.05$ in all cases) except growth rate, hatchling mean weight, and number of hatchlings per cocoon ($P > 0.06$ in all cases).

RESULTS

NONREPRODUCTIVE EXPERIMENT

During the 7 days of manipulation, the stressed earthworms showed negligible growth, whereas control earthworms grew eight-fold faster (Fig. 1). However, 1 week after the end of manipulation, the growth rate of the stressed earthworms was higher than the growth rate of controls (Fig. 1). There was a significant interaction between the treatment and time (repeated measures ANOVA, $F_{1,31} = 21.29$, $P = 0.00006$); post-hoc comparisons revealed significant differences between treatments only during the stressful conditions, but not 1 week after the end of the manipulation (Fig. 1). Growth rate of earthworms was not affected by initial weight (repeated measures ANOVA, $F_{1,31} = 0.01$, $P = 0.9$).

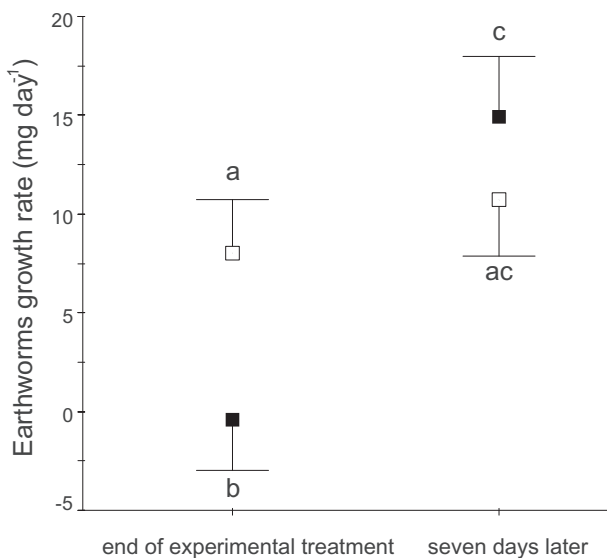


Figure 1. Growth rate (mean \pm standard error) of *Eisenia fetida* in the nonreproductive experiment in the control (open symbols, $N = 17$) and in the experimentally stressed group (closed symbols, $n = 17$) at the end of the manipulation period and 7 days later. Different letters indicate significant differences ($P < 0.05$) among treatments (Tukey's HSD test).

REPRODUCTIVE EXPERIMENT

After 2 months, the growth rate was similar in both groups (control: 2.94 ± 0.70 mg day⁻¹; experimental: 2.38 ± 0.45 mg day⁻¹; GLM, $\chi^2 = 0.44$, d.f. = 1, $P = 0.51$). The growth rate of earthworms during the experiment was similar over time (repeated measures ANOVA, $F_{8,216} = 0.27$, $P = 0.9$), and there was no interaction between treatment and the time (repeated measures ANOVA, $F_{8,216} = 0.73$, $P = 0.6$).

Experimental stress significantly reduced cocoon production (-25%) and cocoon weight (-30%) compared with the control (cocoon production: GLM, $\chi^2 = 12.21$, d.f. = 1, $P = 0.0004$, Fig. 2A; cocoon weight: GLM, $\chi^2 = 4.19$, d.f. = 1, $P = 0.04$, Fig. 2B); but no differences were found in cocoon viability (control: $63 \pm 8\%$ and experimental: $52 \pm 8\%$; GLM, $\chi^2 = 0.44$, d.f. = 1, $P = 0.51$). The total number of hatchlings per earthworm was significantly lower (-37%) in the experimental group than in the control (GLM, $\chi^2 = 36.39$, d.f. = 1, $P < 0.0001$, Fig. 2C), but no differences were found in either hatchling weight (GLM, $\chi^2 = 0.69$, d.f. = 1, $P = 0.41$) or in the number of hatchlings per cocoon (GLM, $\chi^2 = 0.51$, d.f. = 1, $P = 0.47$).

DISCUSSION

The present results show that earthworms responded differentially to experimental stress, depending on their reproductive status. When nonreproductive earthworms were subject to the stress, there was a reduction in their growth rates but, interestingly, once stress manipulation ceased, the growth rate rapidly increased. The significant interaction between treatment and time resulting from this behaviour indicates the existence of mechanisms for a compensatory response for growth trajectories, at least under laboratory conditions (Álvarez & Nicieza, 2005).

In the reproductive experiment, the growth curves of both control and stressed earthworms were very similar, and the absence of any interaction between treatment and time suggests similar growth rates. The difference between reproductive and nonreproductive experiments should be considered carefully because there may have been growth compensation in reproductive earthworms due to the low intensity of treatment compared with the nonreproductive experiment. Nevertheless, the present evidence indicates that, during reproductive events, earthworms appear to allocate resources preferentially to reproduction rather than to growth. In control, nonreproductive earthworms, the growth rate was three-fold higher than in reproductive earthworms, suggesting that there is a high energy demand associated with reproduction, although this effect may also be attributed to initial weight difference in the experiments (the non-

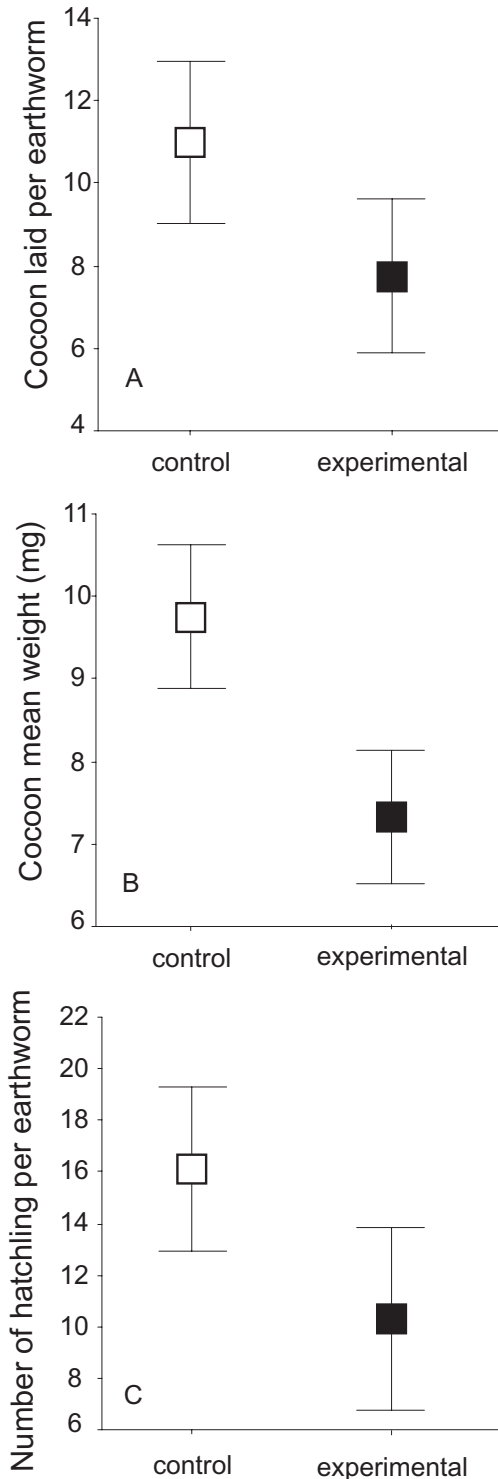


Figure 2. Reproductive parameters of *Eisenia fetida* after 2 months of experimental stress. Data show (A) the mean number \pm standard error of cocoons laid per earthworm, (B) the mean weight of the cocoons and (C) the total number of hatchlings per earthworm in the control (open symbols, $N = 16$) and the experimentally stressed groups (closed symbols, $N = 16$).

reproductive earthworms were heavier than reproductive ones). In this context, Sella & Lorenzi (2003) found that the growth rate of protandrous males of the hermaphroditic polychaete *Ophryotrocha diadema* that were allowed to fertilize hermaphrodites' eggs was lower than that of control males.

The response to stress in the reproductive experiment clearly indicated that earthworms invested preferentially in growth rather than in reproduction. Unlike in many taxa of hermaphrodites in which sperm digestion is widespread (Michiels, 1998), *E. fetida* is unable to digest allosperm that are received (Richards & Fleming, 1982) and therefore the earthworms in the reproductive experiment could not avoid the cost derived from reproduction (i.e. nutritional compensation through digestion of received allosperm). The resources devoted to maintaining growth in stressed reproductive earthworms were probably obtained from those necessary for reproduction and, as a consequence, the reproductive effort was diminished. The induced stress did not affect cocoon viability or the number of hatchlings per cocoon. Nevertheless, stressed earthworms produced less and lighter cocoons than unstressed earthworms, which in turn resulted in a lower number of hatchlings from stressed earthworms. Thus, experimental stress reduced cocoon production, but not the quality (with a similar number of hatchlings per cocoon). Hence, the results of the present study showed that, under unfavourable conditions, earthworms sacrifice their current reproduction, probably to maximize their residual reproductive value.

It is also possible that earthworms were responding as if to an increase in predation pressure because the experimental stress induced may be similar to predation by birds. However, predation pressure cannot explain the different responses to manipulation in reproductive and nonreproductive earthworms. Thus, the present results are more consistent with the hypothesis of a decision in life traits for iteroparous animals with indeterminate growth, in which allocation should be driven to growth when the available energy is not sufficient to support both activities. This is also consistent with the negative correlation between growth and reproduction in organisms with indeterminate growth (Stearns, 1992). Furthermore, because it is expected that an investment in growth leads to an increase in future reproduction due to size-related fecundity, the trade-off between growth and reproduction may be seen as a trade-off between current and future reproduction (Heino & Kaitala, 1999). By maintaining its growth rate (i.e. ensuring a better body condition for future reproductive events), *E. fetida* may maximize its residual reproductive value through its female fecundity function (Domínguez & Edwards, 1997; Domínguez *et al.*, 1997;

Meyer & Bowman, 1997) and future mate choice (Monroy *et al.*, 2005). Moreover, in this earthworm species, body size affects the quality of cocoons; large individuals lay large cocoons that produce a high number of hatchlings (Hartenstein, Neuhauser & Kaplan, 1979). Therefore, the present evidence indicates that *E. fetida* appears to be able to regulate its reproductive decisions according to its physiological conditions, and give priority to future reproduction over current reproduction, probably to maximize fitness.

Similar strategies of resource allocation to growth and reproduction have been observed in experiments where organisms were exposed to suboptimal environments, in which dealing with stress incurred a cost in terms of metabolic resources; thus, the earthworm *E. andrei* reared in artificial soil under environmental stress (i.e. a range of pH, temperature and moisture regimes) preferentially maintained growth, resulting in production of less cocoons (van Gestel, Dirven-van Breemen & Baerselman, 1992). Moreover, West *et al.* (2003) reported that resource allocation in adult individuals of the earthworm *Lumbricus rubellus* could be altered by stress (low Ca²⁺ levels in soil), thereby reducing its reproductive output. As these studies analysed groups of earthworms, they cannot separate the effects on reproductive output from confounding population traits such as differential mortality, changes in mating behaviour, and sperm quality, as can be achieved in individual level studies. Indeed, Kaitala (1987) showed that, in the waterstrider *Gerris thoracicus*, whose lifespan is related to reproductive effort, individual females with limited food supply switched off reproduction to ensure survival.

The result of stress in organisms is a reduction in the scope of allocation decisions, resulting in reduced fitness (Sibly & Calow, 1986) and indeed, in hermaphrodites, this should affect sex allocation to each sex function. In the present study, we show that, in the simultaneous hermaphrodite *E. fetida*, the female function is dramatically affected by growth and stressful conditions, which have important implications for both current and future reproduction. Although the total amount of reproduction via eggs and sperm is probably equal (Fisher, 1930), the costs associated with each sexual function would differ, mainly because reproduction via sperm has a lower cost than egg production due to anisogamy (Bateman, 1948). In hermaphrodites, the sex allocation theory assumes that there is a trade-off between male and female function (Charnov, 1982). However, this trade-off should be considered as three-way (i.e. allocation to male, female and growth) (Yund *et al.*, 1997) and indeed, in the hermaphroditic colonial bryozoan *C. hyalina*, more females developed in response to the presence of allosperm, whereas the number of males remained unaltered, producing a decrease in the somatic growth

of the colony (Hughes *et al.*, 2003). Although we did not measure the male reproductive function in the present study, it would be expected that stressful conditions may bias sex allocation in *E. fetida* towards male rather than female function because of the lower cost involved. We believe that this aspect should be taken into consideration in constructing theoretical models of sex allocation in simultaneous hermaphrodites.

ACKNOWLEDGEMENTS

This research was financially supported by grants from CICYT (AGL2003-01570) and Xunta de Galicia (PGIDIT03P-XIB30102PR). Manuel Aira was financially supported by a postdoctoral grant from the Xunta de Galicia.

REFERENCES

- Álvarez D, Nicieza AG. 2005. Compensatory response 'defends' energy levels but not growth trajectories in brown trout, *Salmo trutta* L. *Proceedings of the Royal Society of London Series B, Biological Sciences* **272**: 601–607.
- Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. *Heredity* **2**: 349–368.
- Baur B. 1988. Repeated mating and female fecundity in the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Invertebrate Reproduction and Development* **14**: 197–204.
- Baur B, Raboud C. 1988. Life history of the land snail *Arianta arbustorum* along an altitudinal gradient. *Journal of Animal Ecology* **57**: 71–87.
- Charlesworth B. 1980. *Evolution in age-structured populations*. Cambridge: Cambridge University Press.
- Charnov EL. 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* **76**: 2480–2484.
- Charnov EL. 1982. *The theory of sex allocation*. Princeton, NJ: Princeton University Press.
- De Witt TJ. 1996. Gender contests in a simultaneous hermaphrodite snail – a size advantage model for behaviour. *Animal Behaviour* **51**: 345–351.
- Domínguez J. 2004. State of the art and new perspectives in vermicomposting research. In: Edwards CA, ed. *Earthworm ecology*. Boca Raton, FL: CRC Press, 401–424.
- Domínguez J, Briones MJI, Mato S. 1997. Effect of the diet on growth and reproduction of *Eisenia andrei*. *Pedobiologia* **41**: 566–576.
- Domínguez J, Edwards CA. 1997. Effects of stocking rate and moisture content on the growth and maturation of *Eisenia andrei* (Oligochaeta) in pig manure. *Soil Biology and Biochemistry* **29**: 743–746.
- Domínguez J, Velando A, Aira M, Monroy F. 2003. Uniparental reproduction of *Eisenia fetida* and *E. andrei* (Oligochaeta: Lumbricidae): evidence of self-insemination. *Pedobiologia* **47**: 530–534.

- Fisher RA. 1930.** *The genetical theory of natural selection*. Oxford: Clarendon Press.
- van Gestel CMA, Dirven-van Breemen EM, Baerselman R. 1992.** Influence of environmental conditions on the growth and reproduction of the earthworm *Eisenia andrei* in artificial soil substrate. *Pedobiologia* **36**: 109–120.
- Hartenstein R, Neuhauser EF, Kaplan DL. 1979.** Reproductive potential of the earthworm *Eisenia foetida*. *Oecologia* **43**: 329–340.
- Heino M, Kaitala V. 1999.** Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. *Journal of Evolutionary Biology* **12**: 423–429.
- Herrera CM. 2000.** Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. *Ecology* **81**: 15–29.
- Hughes RN, Manríquez PH, Bishop JDD. 2002.** Female investment is retarded pending reception of allosperm in a hermaphroditic colonial invertebrate. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 14884–14886.
- Hughes RN, Manríquez PH, Bishop JDD, Burrows MT. 2003.** Stress promotes maleness in hermaphroditic modular animals. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 10326–10330.
- Kaitala A. 1987.** Dynamic life-history strategy of the water-strider *Gerris thoracicus* as an adaptation to food and habitat variation. *Oikos* **48**: 125–131.
- Lloyd DG, Bawa KS. 1984.** Modification of the gender of seed plants in varying conditions. *Evolutionary Biology* **17**: 255–338.
- Madec L, Desbuquois C, Coutellec-Vetro MA. 2000.** Phenotypic plasticity in reproductive traits: importance in the life history of *Helix aspersa* (Mollusca: Helicidae) in a recently colonized habitat. *Biological Journal of the Linnean Society* **69**: 25–39.
- Maynard Smith J. 1982.** *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- McCullagh P, Nelder JA. 1989.** *Generalized linear models*. London: Chapman & Hall.
- Meyer WJ, Bowman H. 1997.** Anisopary in compost earthworm reproductive strategies (Oligochaeta). *Soil Biology and Biochemistry* **29**: 731–735.
- Michiels NK. 1998.** Mating conflicts and sperm competition in simultaneous hermaphrodites. In: Birkhead TR, Møller AP, eds. *Sperm competition and sexual selection*. London: Academic Press, 219–254.
- Michon J. 1957.** Contribution expérimentale à l'étude de la biologie des Lumbricidae. Les variations podérales au cours des différentes modalités du développement postembryonnaire. *Annales de Biologie* **33**: 367–376.
- Monroy F, Aira M, Velando A, Domínguez J. 2005.** Size-assortative mating in the earthworm *Eisenia fetida* (Oligochaeta, Lumbricidae). *Journal of Ethology* **23**: 69–70.
- Monroy F, Aira M, Domínguez J, Velando A. 2006.** Seasonal population dynamics of *Eisenia fetida* (Savigny, 1826) in the field. *Comptes Rendus Biologies* **329**: 912–915.
- Reznick D. 1983.** The structure of guppy life histories: the trade-off between growth and reproduction. *Ecology* **64**: 862–873.
- Richards KS, Fleming TP. 1982.** Spermatozoal phagocytosis by the spermathecae of *Dendrobaena subrubicunda* and other lumbricids (Oligochaeta, Annelida). *International Journal of Invertebrate Reproduction* **5**: 233–241.
- Ridley M. 1983.** *The explanation of organic diversity*. Oxford: Oxford University Press.
- Roberts MBV. 1962.** The giant fibre reflex of the earthworm *Lumbricus terrestris* L. I. The rapid response. *Journal of Experimental Biology* **39**: 219–227.
- Rushton WAH. 1945.** Motor response from giant fibers in the earthworm. *Nature* **156**: 109–110.
- Schärer L, Sandner P, Michiels NK. 2005.** Trade-off between male and female allocation in the simultaneously hermaphroditic flatworm *Macrostomum* sp. *Journal of Evolutionary Biology* **18**: 396–404.
- Schwarzkopf L. 1993.** Cost of reproduction in water skinks. *Ecology* **74**: 1970–1982.
- Sella G, Lorenzi MC. 2003.** Increased sperm allocation delays body growth in a protandrous simultaneous hermaphrodite. *Biological Journal of the Linnean Society* **78**: 149–154.
- Shine R, Schwarzkopf L. 1992.** The evolution of reproductive effort in lizards and snakes. *Evolution* **46**: 62–75.
- Sibly RM, Calow P. 1986.** *Physiological ecology of animals: an evolutionary approach*. Oxford: Blackwell Scientific.
- Stearns SC. 1976.** Life history tactics: a review of the ideas. *Quarterly Review of Biology* **51**: 3–47.
- Stearns SC. 1992.** *The evolution of life histories*. Oxford: Oxford University Press.
- Tato A, Velando A, Domínguez J. 2006.** Influence of size and partner preference on the female function of the earthworm *Eisenia andrei* (Oligochaeta, Lumbricidae). *European Journal of Soil Biology* **42**: S331–S336.
- Tomiyama K. 1996.** Mate-choice criteria in a protandrous simultaneously hermaphroditic land snail *Achatina fulica* (Férussac) (Stylommatophora: Achatinidae). *Journal of Molluscan Studies* **62**: 101–111.
- Trouvé S, Jourdan J, Renaud F, Durand P, Morand S. 1999.** Adaptive sex allocation in a simultaneous hermaphrodite. *Evolution* **53**: 1599–1604.
- Venter JM, Reinecke AJ. 1988.** The life-cycle of the compost worm *Eisenia fetida* (Oligochaeta). *South African Journal of Zoology* **23**: 161–165.
- Vreys C, Michiels NK. 1997.** Flatworms flatten to size up each other. *Proceedings of the Royal Society of London Series B, Biological Sciences* **264**: 1559–1564.
- Wedekind C, Strahm D, Schärer L. 1998.** Evidence for strategic egg production in a hermaphroditic cestode. *Parasitology* **117**: 373–382.
- West HK, Morgan AJ, Bowker DW, Davies MS, Herbert RJ. 2003.** Evidence for interpopulation differences in life history parameters of adult and F1 generation *Lumbricus rubellus*. *Pedobiologia* **47**: 535–541.
- Williams R. 1966.** *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.

Yund PO, Marcum Y, Stewart-Savage J. 1997. Life-history variation in a colonial ascidian: broad-sense heritabilities and tradeoffs in allocation to asexual growth and male and female reproduction. *Biology Bulletin* **192**: 290–299.

Yusa Y. 1994. Size-related egg production in a simultaneous hermaphrodite, the sea hare *Aplysia kurodai* Baba (Mollusca: Opisthobranchia). *Publications of the Seto Marine Biology Laboratory* **36**: 249–254.