

Mortality risk of rapid growth in the spider *Nephila clavipes*

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Summary

1. Female *Nephila clavipes* from univoltine populations have greatly reduced reproductive success if they grow slowly and reach maturity late in the growing season. Although such fitness costs are expected to select for rapid increases in mass, several authors have presented models and data describing physiological costs of rapidly increasing mass.
2. In order to test the hypothesis that there are inherent costs of rapid growth (increasing mass), laboratory-reared juveniles of the orb-weaving spider *Nephila clavipes* were randomly assigned to receive daily feedings ranging from 2.5% to 23% of their initial mass.
3. Spiders receiving higher amounts of food were more likely to die at or immediately before the next moulting cycle.
4. These results indicate that there may be inherent physiological costs of rapidly increasing mass. In opportunistic feeders such as spiders that tend to gorge when prey are abundant, this could present a real cost to a common foraging strategy.

Key-words: Aranea, fitness costs, growth rates, plasticity, Tetragnathidae

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Introduction

Although variation in growth rate has traditionally been assumed to reflect non-adaptive phenotypic responses to the availability of food (e.g. Roff 1980, 1983; Stearns & Koella 1986), experimental work with some insects has demonstrated adaptive variation in rate of growth (reviewed in Gotthard *et al.* 1994). Low rate of increasing mass in larval arthropods increases the duration of each larval stage, and is associated with both increased risk of prereproductive mortality (Higgins & Rankin 1996) and reproductive costs of delayed maturation (Stearns & Koella 1986; Higgins & Rankin 1996; Higgins 2000). Although very high rates of growth have been often assumed to increase fitness, allowing animals to avoid the above-mentioned costs of slow growth, there is increasing evidence that there are ecological and physiological costs associated with rapidly increasing mass (Stockhoff 1991; Wiklund *et al.* 1991; Gotthard *et al.* 1994; Abrams *et al.* 1996; Arendt 1997).

Ecological costs of rapid growth are primarily assumed to reflect risk of predation and parasitism associated with the increased foraging necessary to increase mass more rapidly (Abrams *et al.* 1996). Such costs are postulated to underlie observed patterns

of declining investment into foraging when prey are abundant (Lubin & Henschel 1996). The best demonstrated physiological cost of rapid growth is decreased resistance to starvation and other environmental stresses (Stockhoff 1991; Gotthard *et al.* 1994). One can postulate other physiological costs of rapidly increasing mass. For example, rapidly increasing mass may decrease resource allocation to other functions, such as development (Arendt 1997). Under these circumstances, high rates of growth alone could increase mortality in the absence of external environmental stresses.

In populations of the orb-weaving spider *Nephila clavipes* (Linnaeus) (Araneae: Tetragnathidae) inhabiting strongly seasonal environments, there are strong fitness costs associated with slow growth and development in females (Higgins 2000). The duration of each juvenile instar is negatively correlated with the rate of increasing mass, and the number of juvenile instars is variable (Higgins 1992, 1993). Size at maturity is determined in large part in this species by the number of juvenile instars (Higgins & Rankin 1996), and rapidly growing females pass through several instars and reach maturity at a large size earlier than slowly growing females. There is a strong reproductive advantage to early maturation: large, early maturing females have disproportionately greater reproductive success, producing multiple large clutches.

Late-maturing females are smaller and have a lower likelihood of copulating and producing even one clutch (Higgins 2000). Various spiders have been shown to have very low metabolic rates and to be capable of ingesting large amounts of prey when prey is available (Anderson 1974). These characteristics are consistent with the assumption that spiders are sit-and-wait predators that gorge when prey are abundant (Riechert & Luczak 1982). Such a strategy would result in periods of very rapid increases in mass.

To test the hypothesis that rapid increases in mass carry physiological costs, laboratory-reared *N. clavipes* juvenile spiders were randomly assigned to one of five diets that varied quantitatively but were qualitatively identical. The rate of increasing mass, duration of the instar, survival through the moult, and change in size at the moult were compared among these individuals.

Methods

Individual *Nephila clavipes* express great plasticity in both growth rate (rate of change in mass) and development rate (time between moults and number of juvenile stages). However, the growth per moult, measured as the change in length of the sclerotized leg segments, is canalized and varies little with diet (Higgins 1992, 1993). The typical juvenile growth pattern in this spider is that an individual increases in mass until it achieves the critical premoult mass, at which time it moults to the next instar.

This experiment was conducted on fourth-instar laboratory-reared juveniles, and lasted one instar (one intermoult period). Offspring of four females from two Mexican populations (one from Los Tuxtlas, Veracruz, three from Tehuacán, Puebla) were reared in groups of ≈ 20 individuals per container (20 cm deep \times 40 cm wide \times 30 cm tall boxes, screened with nylon on the narrow sides, with sliding Plexiglas doors on one or both large faces). They received *ad libitum* food from open vials of *Drosophila melanogaster* refreshed three times a week. Upon moulting to the fourth instar, individuals were moved into separate boxes and randomly assigned each to a food level, calculated as a percentage of the average initial mass at the beginning of the fourth instar (Table 1). All spiders were fed on alternate days, the only regimen permitting the lowest food level, and all spiders were fed 50% *D. melanogaster* and 50% *D. virilis* (average mass: *D. melanogaster* 0.86 mg; *D. virilis* 1.4 mg). There were

Table 1. Treatment groups, sample sizes and feeding regimes

Treatment	N	Food level (% initial mass)	Number of prey offered per foraging bout
I	10	2.5	1
II	10	5.0	2
III	13	11.3	4
IV	11	17.0	6
V	11	23.0	8

no differences among the treatment groups in initial size (first leg tibia + patella length (TPL) mean (SD) = 0.371 cm (0.038); $F_{4,51} = 0.713$, $P = 0.59$) or initial mass (mean (SD) = 20.11 mg (2.371); $F_{4,51} = 0.202$, $P = 0.936$). The experimental treatments ended when each individual moulted or died.

When each spider was fed, the number of prey captured was recorded. Each week, the length and width of the abdomen were measured and from abdomen volume (estimated as a cylinder), mass was estimated from published equations (Higgins 1992). When it appeared that a spider was preparing to moult, by ceasing to capture prey and by having a large, distended abdomen, the length and width of the abdomen were measured nearly daily until the moult occurred. If the spiders successfully moulted, the TPL length of the new exoskeleton was measured. 'Intermoult' for spiders dying rather than moulting was measured as the time to death or moribund state (hanging or fallen from web with no response to contact by the observer).

The rate of increasing mass was calculated as an exponential function:

$$\text{Increase in mass (\%)} = [(m_2/m_1)^{1/t} - 1] \times 100,$$

using either the maximum mass prior to the moult (t = intermoult duration) or, for some comparisons, the mass after one week of the experiment (t = interval between measurements), as the second measure of mass (m_2).

Results

The different feeding regimes significantly altered growth and development in the spiders (Fig. 1). The total mass of prey captured by each spider increased significantly with increasing number offered ($F_{4,51} = 69.152$, $P < 0.001$): most spiders captured most of the prey offered. With such a large difference in prey captured, it is not surprising that the rate of growth increased and the length of the intermoult decreased with increasing food levels (change in mass: considering all spiders $F_{4,51} = 14.81$, $P < 0.001$; intermoult duration: considering only spiders that successfully moulted $F_{4,41} = 7.324$, $P < 0.001$). The change in size (TPL) at the moult was significantly affected by treatment; spiders on the higher diet grew more when they moulted (ANCOVA of TPL_2 with TPL_1 as covariate; no significant TPL_1 -treatment interaction. TPL_1 : $F_{1,41} = 69.34$, $P < 0.001$; treatment: $F_{4,41} = 5.84$, $P = 0.001$).

There was a significant effect of treatment on survival to the next instar (Table 2). Pooling treatments I and II and pooling treatments IV and V (to avoid small cell sizes), spiders in the two highest feeding regimes were significantly more likely either to die or to fail moulting (a failed moult is when ecdysis is initiated but not completed or the spiders emerge seriously deformed; Pearson $\chi^2 = 6.44$, $P = 0.04$). Since most deaths occurred in the two highest food groups,

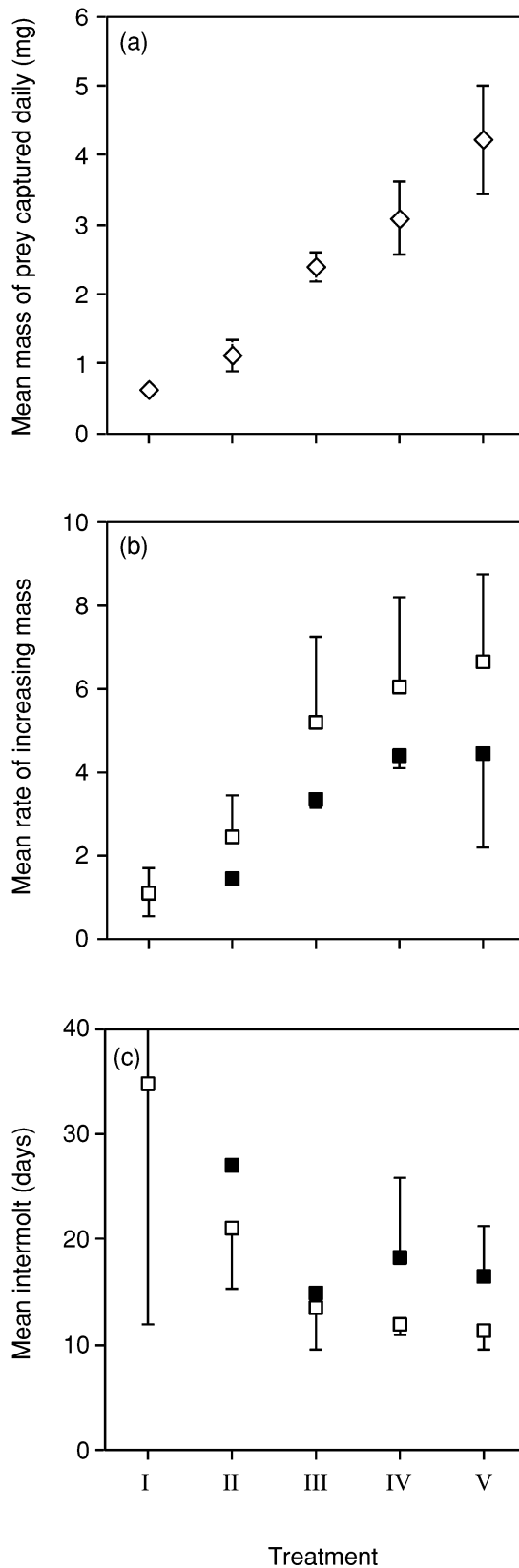


Fig. 1. Response of the spiders to treatment. (a) Mean (\pm s.e.m.) mass of prey captured in each treatment; data from all animals are included. (b) Mean increase in mass (\pm 1 s.d.) in each treatment. (c) Mean intermolt duration (\pm 1 s.d.) in each treatment. \square Animals that successfully moulted; \blacksquare animals that died.

Table 2. Mortality risk as a percentage of individuals dying during each treatment

Treatment	<i>N</i>	% dying
I	10	0
II	10	10
III	13	7.7
IV	11	27
V	11	41

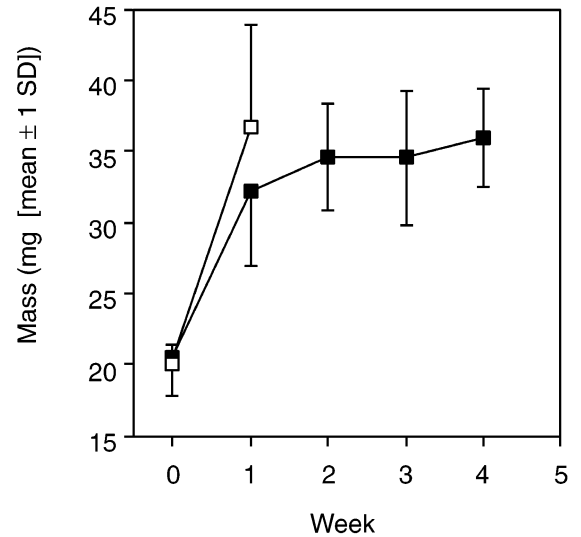


Fig. 2. Mean mass at each week following initiation of treatment (week 0) for spiders in treatments IV and V that moulted successfully (\square) or died (\blacksquare).

and since there was no difference in increase in mass or intermolt duration between these two groups, the data from these spiders were pooled and examined for predictors of death (increase in mass: separate variances Student *t*-test = -0.158 , $df = 20.8$, $P = 0.88$; intermolt (only moulting spiders): pooled variances Student *t*-test = 0.785 , $df = 13$, $P = 0.446$).

The rate of increase in mass over the entire study and the intermolt duration or time to death differed between those animals that died and those that moulted. Spiders that died were the same initial size and mass as spiders that moulted. Successfully moulting spiders in these treatment groups had an intermolt period of 7–10 days. Therefore, to compare the rate of increasing mass between these animals and those that died, the rate of increase in mass over the first 7–10 days was compared. During the first week of treatment, spiders that died grew at the same rate as those that moulted successfully (Fig. 2; moulting spiders: mean rate (SD) = 6.36 (1.98); dying spiders: mean rate (SD) = 5.43 (1.83); pooled variances Student *t*-test = 1.10 , $P = 0.284$). However, the spiders that died continued to eat and build webs for several days after achieving necessary premoult mass (Fig. 2; time to death: mean (SD) = 17.25 (5.45); intermolt: mean

(SD) = 11.73 (1.39); separate variances Student *t*-test = -2.82, *df* = 7.5, *P* = 0.024). Following the first week, these spiders did not continue to increase in mass (Fig. 2). Therefore, when the rate of increasing mass over the entire instar is compared between moulting and dying spiders, the latter had a significantly lower growth rate (Fig. 1b; separate variances Student *t*-test = 2.37 *P* = 0.03).

Discussion

In univoltine populations of *N. clavipes*, there is strong selection in females for rapid growth and early maturation. Within a cohort, late-maturing females had reduced likelihood of mating, and reduced reproductive output if mated. Late maturation is associated with slow rates of growth and development (Higgins & Rankin 1996; Lubin & Henschel 1996). However, the results from this experiment indicate that there may be physiological costs of rapidly increasing mass.

The increasing mortality risk of spiders fed extremely large numbers of prey is a novel, inherent physiological cost of a high rate of growth. Very little is known of the internal digestive processes or of the hormone cycles of spiders, so the proximal physiological causes of this mortality are unknowable at this time. Death occurred either immediately prior to the moult or during ecdysis; owing to the small sample sizes these two types of death were not treated separately. Approximately one-half of the animals that died did so prior to any external sign that ecdysis had been initiated; the remainder died stuck in their exoskeleton or emerged from ecdysis with extremely malformed legs. Commonly, researchers rearing spiders in the laboratory have linked mortality during ecdysis to unbalanced (monotypic) diets (e.g. Uetz *et al.* 1992). This cannot be the case in this experiment as there was no qualitative difference in diet among the treatment groups.

The prey capture rates used in this experiment are within the range of naturally occurring prey capture rates, but variation in time and space perhaps reduces the likelihood that any individual would capture such large numbers of prey each day during an instar. However, failed moults are seen in the field in both *N. clavipes* and the old-world congener *N. maculata*. One particular case appears linked to rapidly increasing mass: a juvenile female spun her orb directly in front of a stingless bee colony (*Trigona* sp.) on Barro Colorado Island (Panama) and captured large numbers of bees each day. This spider increased in mass very rapidly and died at the next moult cycle (L. E. Higgins, personal observation). In the orb-weaving spider *Metapiera incrassata* F. O. Pickard-Cambridge, a more dramatic death due to overeating has been observed: well-fed mature females may split open or even explode (E. Jakob, personal communication).

Possible physiological mechanisms of the death of well-fed *N. clavipes* juveniles include, but are not

limited to, gut failure following overeating, failure of proper regulation of moulting hormones, or nutritional imbalance. Blood-feeding insects are known, in the laboratory, occasionally to die following overeating (J. Stoffolano, personal communication). In these cases, death appears to be due to sepsis following failure of the gut lining with the stress of too large a meal. In *N. clavipes*, the temporal link between the moulting cycle and death suggests that exceedingly rapid increases in mass may interfere with the moulting process. In adult insects that require a protein meal to initiate female reproduction, a hormone cascade initiated by a hormone released in the mid-gut ends with release of juvenile hormone from the brain (M. Tu, personal communication). It is imaginable that similar hormone cascades initiate juvenile moulting in insects where moulting follows closely upon achievement of a critical mass (Nijhout 1979). Although a hormonal response to increasing mass has not been documented in other arthropods, *N. clavipes* juveniles do need to achieve a critical premoult mass prior to moulting and exceedingly rapid increases in mass may disrupt the complex moulting process. Lastly, nutritional imbalance is a possibility because, during external digestion, different compounds are liquefied and ingested before others (Cohen 1995); in particular proteins and glycogen are extracted prior to lipids. If spiders abandoned each prey without completely feeding (Sebrier *et al.* 1994), an imbalanced diet low in lipids could result.

Recent discussions of the possible costs of rapid growth (rapid increases in mass) have emphasized ecological costs such as increased risk of predation and physiological costs such as reduced resistance to stress (Abrams *et al.* 1996; Gotthard *et al.* 1994). Although the direct cause of mortality is unknown, for these spiders the physiological risk of rapidly increasing mass is real.

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