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RESEARCH ARTICLE

Life history trade-offs imposed by dragline use in two money spiders

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ABSTRACT

Trade-offs among life history traits are central to understanding the limits of adaptations to stress. In animals, virtually all decisions taken during life are expected to have downstream consequences. To what degree rare, but energy-demanding, decisions carry over to individual performance is rarely studied in arthropods. We used spiders as a model system to test how single investments in silk use – for dispersal or predator escape – affect individual performance. Silk produced for safe lines and as threads for ballooning is of the strongest kind and is energetically costly, especially when resources are limited. We induced dragline spinning in two species of money spider at similar quantities to that under natural conditions and tested trade-offs with lifespan and egg sac production under unlimited prey availability and a dietary restriction treatment. We demonstrate strong trade-offs between dragline spinning and survival and fecundity. Survival trade-offs were additive to those imposed by the dietary treatment, but a reduction in eggs produced after silk use was only prevalent under conditions where food was restricted during the spider's life. Because draglines are not recycled after their use for dispersal or predator escape, their spinning incurs substantial fitness costs in dispersal, especially in environments with prey limitation. Rare but energetically costly decisions related to dispersal or predator escape may thus carry over to adult performance and explain phenotypic heterogeneity in natural populations.

KEY WORDS: Silk, Costs, *Erigone*, Stress, Dietary restriction, Dispersal, Carry-over

INTRODUCTION

Any variation in access to resources and their allocation to individual development or specific behaviours will impact fitness (Stearns, 1989). These trade-offs form a cornerstone of evolutionary biology because they impose constraints to adaptive developments or behaviours under stressful conditions. While there is ample evidence that adaptations towards environmental stress during early-life conditions trade-off with adult fitness (Stearns, 1989; van Noordwijk and De Jong, 1986), the importance of single, rare behaviours on future fitness prospects remains largely untested. Carry-over effects of short-term extreme environmental conditions affect performance of vertebrates over several seasons (Harrison et al., 2011) and are anticipated to explain a large amount of the variation in performance among individuals. Invertebrates have generally much shorter life spans than vertebrates. Rare events that

necessitate the use of substantial energetic reserves are therefore equally likely to impose fitness trade-offs, especially under suboptimal conditions. Dispersal or predator escape are examples of such occasional but energetically costly behaviours (Bonte et al., 2012; Ydenberg and Dill, 1986).

Spiders use silk for a variety of ecological functions throughout their lives. Its use for egg protection, burrow stabilisation or prey capture is well known (Blackledge, 2013). At more rare occasions during life, draglines are produced to enable escape from predators or dispersal (Blackledge, 2013; Bonte, 2013; Bonte et al., 2012). Silk use is energetically costly because it needs to be synthesised from constituent amino acids (Craig et al., 1999; Guehrs et al., 2008) and then spun and drawn from the spinnerets (Vollrath et al., 1998). Based on conservative assumptions (Prestwich, 1977), 18% of all costs are related to spinning activity, the remainder to physiological silk production costs. Variation in protein (Blamires et al., 2012a) and carbohydrate (Blamires et al., 2015) intake determines the amino acid composition of silk and the architectural plasticity of the produced webs. Both silk production and silk spinning are therefore highly dependent on nutritional intake. Many web-building species levy these costs of silk use by recycling webs (Opell, 1998) and allocate resources for web building to other activities (Sherman, 1994) under dietary restrictions.

Draglines are made up of silk produced in the major ampullate glands (Blackledge, 2013). In contrast to silk used for the spiral capture threads in orb webs, they do not contain aggregate glue (Bell et al., 2005). The spider's efficient silk-producing system allows the production of stiff silks at low metabolic cost as long as amino acids are available via prey ingestion (Craig, 2003). Because draglines are never recycled, their production is expected to impose an important energetic cost under dietary restriction (Craig et al., 1999), eventually paid in the currency of fitness through life history trade-offs (Stearns, 1989). We can therefore expect that any investments in dragline due to activities related to predator avoidance or dispersal will be individually optimised according to the expected cost–benefit balances (van Noordwijk and de Jong, 1986). While the use of draglines to drop from elevated structures is an immediate response to the presence of predators, silk use for dispersal has been shown to be more systematically integrated into spider life history. High costs during the different dispersal phases (emigration, transfer and immigration) are known to select for condition- and context-dependent dispersal strategies (Bonte et al., 2012; Clobert et al., 2009). Silk-related dispersal is therefore adjusted according to the spider's physiological and environmental condition (Bonte et al., 2008a; De Meester and Bonte, 2010). Recent evidence on the negative impact of dietary restriction and inbreeding on silk-related dispersal in spiders (Bonte, 2009; Bonte et al., 2008a) does suggest that individuals in poor body condition are not engaging in dispersal.

Based on (1) insights from silk production physiology and (2) earlier reported constraints on silk production under dietary

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restriction, we experimentally tested to what degree induced dragline production is traded off with fecundity and survival in two *Erigone* species. The two species are closely related and ecological similar, and co-exist in a highly disturbed habitat (Downie et al., 2000). Different cost–benefit balances related to dispersal may therefore underlie co-existence strategies (Amarasekare, 2003; Jeltsch et al., 2013). The reported trade-offs represent fitness-related costs of drag line production under typical environmental stress associated with single predator escape or dispersal events rather than pure physiological costs associated with silk production and spinning per se.

MATERIALS AND METHODS
Model species and breeding design
We collected in total 27 mature females of *Erigone atra* Blackwall 1833 and *Erigone dentipalpis* (Wider 1834) in a dune slack of the nature reserve the Westhoek (De Panne, Belgium). These *Erigone* spiders are small (2–3 mm) and have a short generation time. Spiders were collected over a large area to minimise their potential relatedness (see Bonte, 2009). Females were individually maintained in breeding cabinets (16 h:8 h light:dark regime, 90% relative humidity and temperature of 22°C) in small vessels with plaster of Paris, and fed *ad libitum* with springtails *Sinella curviseta*. Offspring were in the first instance raised in batches of five (first two small instars) and fed with small *S. curviseta* springtails. From the sub-adult instar onwards, spider sex could be identified. Offspring from a single mother were raised in isolation and subjected to an *ad libitum* feeding treatment (*S. curviseta* and fruit flies *Drosophila melanogaster*) or a dietary restriction treatment in which we provided one fruit fly every 3 days and no springtails. Under dietary restriction, spiders on average lived 2 days without prey consumption. In order to balance our experimental design according to sex and species, we equally distributed the sons and daughters of a mother among the two feeding treatments. One or two days after final moult, spiders were randomly subjected to the silk induction treatment (see below), thus resulting in full factorial feeding treatment×silk induction treatment controlled for common ancestry. A total 61 female and 105 male *E. atra*, and 43 female and 67 male *E. dentipalpis* were used for the experiments.

Silk induction treatment
We prompted the spinning of dragline silk by inducing a dropping reflex of the spiders from a small stick. When spiders fall from this stick, they rely on the dragline as a safety line to break their fall. By gently shaking the stick, we induced spiders to continue to spin a dragline in order to reach the ground surface. This allowed us to directly measure the length of the produced silk thread. We aimed to vary the induced silk thread length between 0.5 m (minimum length for ballooning; Bonte et al., 2008a) and 100 m (estimated maximal investment in ballooning after multiple trials and take-offs during 1 day; Thomas et al., 2003). The maximum length of one bout was 130 cm, so to generate a greater amount of silk spinning, we wound the threads gently till the spider was brought back to the stick, after which another bout of dropping was induced. Individuals that generated 13 m of silk consequently experienced a sequence of 10 dropping bouts. The silk induction treatment thus combined the drop response induced by the experimenter (initiation of the flight) and the production of silk (length of the thread); all other manipulations were kept identical among the treatments and control. The control group was thus treated in exactly the same manner as the silk induction treatment with the exception of the induced dropping and dragline spinning. Spiders were subjected only once (early adult) to the silk use treatments, thereby approximately mimicking a single day's dispersal event under natural conditions.

Longevity and egg production
Females produce egg sacs even when they are not fertilised and do not consume eggs once they are laid (Bonte et al., 2008b). After experimental treatments, we counted the number of egg sacs produced by females and the number of eggs per egg sac. All egg sacs were conserved in alcohol to prevent dissection.

In order to test the impact of the treatments on lifespan, we quantified the time of birth, and time of reaching the sub-adult instar, maturity and death. The feeding treatment remained identical till death.

Data analysis
The number of egg sacs, number of eggs per egg sac and the total number of eggs produced by a single female were analysed by means of a generalised linear mixed model (SAS 9.4, Proc Glimmix). Independent categorical variables were in the first instance the factors species (*E. atra* or *E. dentipalpis*), feeding treatment (*ad libitum* or dietary restriction) and silk use treatment (drag line induction or not). For the spiders in which silk threads were induced, we additionally used the same independent variables except treatment and added the length of the induced silk thread as a continuous factor. Mother ID (N=27) was always included as a random effect to control for potential genetic dependence among offspring from a single female. All counts were analysed using a log-link and modelling a Poisson error structure (no under- or over-dispersion of the data was observed). Effective degrees of freedom were estimated by the Satterthwaite procedure. Survival was modelled by survival analysis (Proc Phreg) using Kaplan–Meier statistics. Because females and males differ in longevity (e.g. Bonte et al., 2008b), sex was added as an independent variable in addition to those outlined above. Mother ID was again included as a random factor. We used two-sided statistics and backward model selection procedures to eliminate non-significant ($P<0.1$) factors from the full models.

RESULTS
Longevity
Longevity of *Erigone* marginally differed among the two species (χ^2=0.5885, P=0.062) and tended to be 36% lower in males than in females (χ^2=47.33, P=0.062; hazard ratio=2.78). Longevity (Fig. 1) was overall impacted by both the feeding treatment (χ^2=5.65, P=0.017; hazard ratio=0.72) and the silk induction treatment (χ^2=8.82, P=0.003; hazard ratio=0.663). Interactions were non-significant (all χ^2<0.77, all P>0.38) and variation among kin was high (σ=0.8766, s.e.=0.2931).

A greater longevity under dietary restriction was especially clear in males, increasing from 74.71±2.50 days to 81.56±3.30 days. Despite the absence of a statistical interaction between sex and the dietary treatment, no such increase was observed in females (Fig. 1A). Silk production reduced longevity in males from 79.38±3.03 days to 77.28±2.76 days, and in females from 90.55±4.02 days to 81.16± 4.30 days (Fig. 1B). A difference in longevity according to the imposed silk spinning treatments occurred from day 45 onwards, which corresponds to 20 days after reaching the adult stage. The length of the thread did not affect survival in spiders subjected to the treatment (χ^2=1.89, P=0.129)

Egg sac production
Erigone atra produced on average twice the amount of egg sacs as *E. dentipalpis* (4.65 versus 2.30; $F_{1,20.57}$=6.78, P=0.016). Egg sac production was significantly lower in the silk induction treatment under dietary restriction ($F_{1,97.96}$=7.16, P=0.0088; t_{66}=4.14, P=0.0004). On average, the number of egg sacs was highest in the treatments with unlimited food availability ($F_{1,97.31}$=12.32, P=0.0007) and those without silk induction ($F_{1,24.45}$=4.83, P=0.037; Fig. 2A). The number of egg sacs produced was not affected by the three-way interactions ($F_{2,68.94}$=0.92, P=0.405), or by the interaction between species and treatment ($F_{1,27.25}$=1.06, P=0.312) or between species and feeding condition ($F_{1,96.58}$=1.03, P=0.313). Variation in egg sac production was high among kin (σ=0.2555, s.e.=0.1921), and among their interactions with the induced treatment (σ=0.2383, s.e.=0.1210). Among-kin variation in feeding treatment reaction norms was low (σ=0.1311, s.e.=0.1921).

Fig. 1. Impact of dietary treatment and silk spinning on the survival of the tested *Erigone* species. (A) Dietary treatment (χ^2=5.65, P=0.017). (B) Silk spinning (χ^2=8.82, P=0.003). *Erigone atra*: N=61 males, N=105 females; *E. dentipalpis*: N=67 males, N=43 females. The graphs show the proportion of individuals alive according to age (counting from the day of birth).

Within the individuals that were forced to produce a silk thread, the number of egg sacs strongly depended on the feeding treatment (see above; $F_{1,12.19}$=12.75, P=0038). With increased silk spinning, a marginally lower egg sac production was recorded (thread length×species: $F_{1,51}$=3.57, P=0.064) in *E. dentipalpis* (β=−0.02, s.e.=0.011) but not in *E. atra* (β=−0.008, s.e.=0.006). Other interactions (3-way interaction: $F_{1,31.05}$=0.36, P=0.555; feeding treatment×species interaction: $F_{1,10.53}$=0.50, P=0.495; length×feeding treatment interaction; $F_{1,47.22}$=0.45, P=0.466) and main factors were not significant (length: $F_{1,48.12}$=0.69, P=0.411; species: $F_{1,33.92}$=0.01, P=0.998).

Fecundity

The mean number of eggs per egg sac was only affected by the feeding treatment ($F_{1,107}$=11.12, P<0.0001). Therefore, total fecundity followed patterns of egg sac production. *Erigone atra* produced on average twice the amount of eggs relative to *E. dentipalpis* (48.89 versus 23.90; $F_{1,23.33}$=6.28, P=0.019). The

impact of silk induction depended on the feeding treatment (interaction: $F_{1,107}$=8.02, P=0.005; feeding treatment: $F_{1,106.1}$=19.79, P<0.0001; treatment: $F_{1,113.2}$=1.68, P=0.197). While the silk induction treatment did not affect total fecundity under well-fed conditions, a 53% drop in fecundity was observed after silk spinning under dietary restriction (t_{66}=2.67, P=0.043; see Fig. 2B). The two species reacted similarly to the silk induction treatment ($F_{1,110.5}$=1.45, P=0.232) and the feeding treatment ($F_{1,104.6}$=0.97, P=0.327), and the 3-way interaction was not significant ($F_{1,104}$=0.77, P=0.389). There was high within-kin variation in egg sac production (σ=0.1998, s.e.=0.1346).

The length of the induced thread length was negatively related to fecundity in *E. dentipalpis* (β=−0.03, s.e.=0.015), but not in *E. atra* (β=−0.005, s.e.=0.003) (species effect: $F_{1,33.84}$=0.00, P=0.954; length effect: $F_{1,52.79}$=1.81, P=0.184; species×thread length: $F_{1,52.76}$=4.32, P=0.042). The fecundity loss observed in *E. dentipalpis* coincides with a fecundity cost of 2% (∼1.2 eggs) per metre of silk thread produced. Overall, dietary restriction
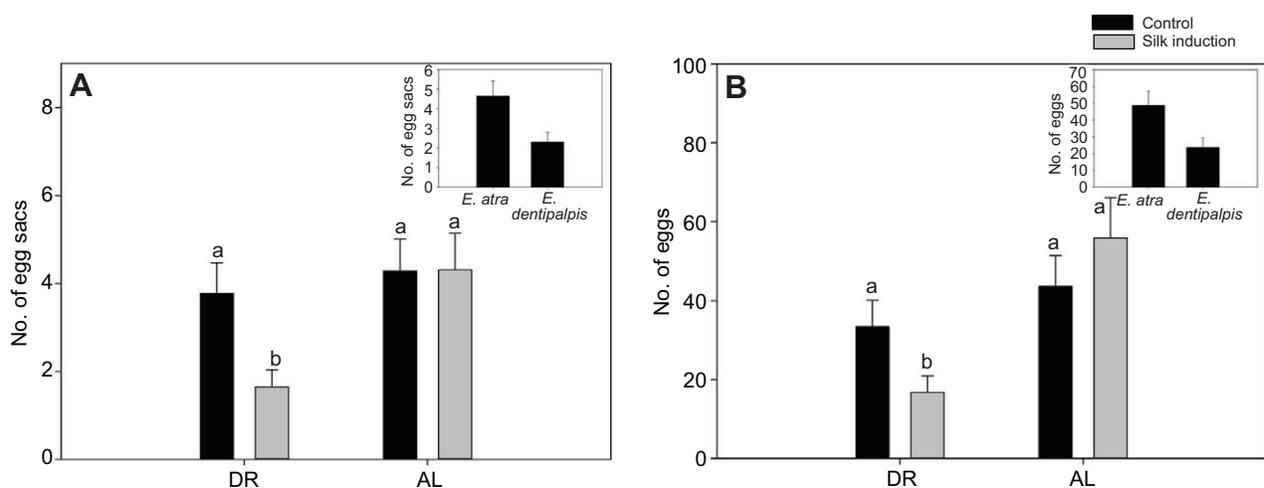

Fig. 2. Average impact of dietary treatment and silk spinning on the number of egg sacs and total number of eggs produced in *E. dentipalpis*. Dietary conditions: DR, dietary restriction; AL, *ad libitum*. (A) Number of egg sacs (interaction $F_{1,97.96}$=7.16, P=0.0088). (B) Total number of eggs produced (interaction $F_{1,107}$=8.02, P=0.005). The same magnitude of effect was found in *E. atra* (inset: relative differences in fecundity). *Erigone atra*: N=105; *E. dentipalpis*: N=43. Different letters indicate statistically significant pair-wise differences corrected for multiple comparisons (LSD test) of the dependent variable according to the treatment after GLMM with Poisson error structure and log-link. Error bars are s.e.m. as calculated for the effective sample sizes (Satterthwaite procedure to account for among-kin variation – see Results for variance estimates).

decreased fecundity ($F_{1,38.48}$=54.38, P<0.001). All of the possible interactions between the species, feeding and silk induction treatments (3-way interaction: $F_{1,36.05}$=0.24, P=0.6263, feeding treatment×species interaction: $F_{1,38.75}$=0.25, P=0.61; length×feeding treatment; $F_{1,37.05}$=1.21, P=0.279) and other single factors were not significant (length: $F_{1,52.79}$=1.81, P=0.185; species: $F_{1,33.84}$=0.01, P=0.954).

DISCUSSION

Spiders use draglines for web building, but also as safety lines to escape potential enemies and as sails for aerial dispersal. Such dispersal or predator escape behaviours are typically rare, and often single events during an individual's life. The production and use of these silk lines is expected to induce severe energetic costs under food shortage (Craig, 2003). When metabolic costs are incurred, trade-offs with various life history traits are expected (Bonte, 2013). Such trade-offs are known to feed back on demography and population dynamics (Cameron et al., 2013). By experimentally controlling the spinning of draglines in two species of money spiders, we were able to demonstrate direct trade-offs with fecundity and survival. The observed patterns were consistent among the two species and therefore suggest their general relevance in spider life histories. Differences in cost–benefit balances of silk-related behaviours consequently do not explain the co-existence of the two studied species in a large array of disturbed habitats (Downie et al., 2000).

We experimentally induced dragline spinning at rates comparable to single dispersal events under natural conditions (Bonte et al., 2008b; Thomas et al., 2003). Survival costs of silk spinning were independent and additive to those imposed by dietary restriction. In contrast, trade-offs with fecundity were only prevalent under conditions of dietary restriction. Single dragline spinning events during early maturity can thus strongly carry over to later life, dependent on (e.g. fecundity) or independent of (e.g. survival) the dietary conditions experienced. Therefore, not only environmental circumstances during development but also rare behaviours during early adulthood may strongly carry over to future individual performance (O'Connor et al., 2014). The additive effects of dietary restriction on survival even demonstrate fitness costs that cannot be compensated for by alternative foraging behaviours.

Life history trade-offs were found when comparing spiders that were subjected to experimental dragline production and those that were not, independent of the amount of thread that was spun. Under the assumption that energetic costs associated with silk spinning are related to the length of the produced silk threads (Prestwich, 1977; Vollrath, 1999), we expected more quantitative effects related to the length of the induced threads. This hypothesis could not, with exception of a small borderline significant effect on fecundity in *E. dentipalis*, be verified. Fecundity and survival were shown to be under maternal control (variance components of random effects were >0), but variation within maternal lineages remained high. We therefore attribute the absence of a correlation between silk thread length and the components of life history measured to individual variation in physiological and behavioural mechanisms that mitigate potential costs of silk use. Spiders may, for instance, change the thickness and amino acid composition of the produced threads during the spinning process, or adjust the rate of silk production according to the experimental conditions experienced (Blamires et al., 2012a,b).

Because draglines are used during dispersal, as anchoring or as ballooning lines, energetic costs imposed by the production of these silk threads are expected to levy a strong selection pressure on the dispersal behaviour of spiders (Bonte et al., 2009). The energetic cost of the production of silk threads can thus be compared with investment in wing formation in insects. Both silk production and wing formation require energetic investment before the dispersal event (Bonte et al., 2012). Silk-related costs do differ from those imposed by wing development by the short time window necessary to invest in these dispersal attributes and the ability to mediate this production behaviourally. In *Erigone*, individuals that produced silk threads eventually had reduced fecundity by 53% under dietary restriction. A recent meta-analysis (Guerra, 2011) found that long-winged insects had a later onset of reproduction, a lower fecundity, and a decreased investment into gonads relative to non-dispersive ones. Overall, short-winged insects increased fecundity by 18–31% (Guerra, 2011; Roff and Bradford, 1996). In contrast, while silk spinning reduced longevity substantially in *Erigone*, only weak differences in survival were found between winged and unwinged morphs of several species of insects.

We found an enhanced longevity combined with a decreased fecundity under dietary restriction. The reduced fecundity under dietary restriction was expected (Chen et al., 2013; Metaxakis and Partridge, 2013). Lifespan extension by dietary restriction is also a widely observed phenomenon (Masoro, 2005) and is the result of differential gene expression where genes involved in anabolism and fecundity are actively repressed while genes that regulate stress resistance and somatic maintenance are upregulated (Fontana and Partridge, 2015). Food composition (protein: carbohydrate ratio), sex and fasting pattern are important determinants of the longevity phenotype (Fontana and Partridge, 2015; Jensen et al., 2015). The decrease in fecundity under food deprivation that we found thus represents an energetic trade-off between maintenance and reproduction (Stearns, 1989; Roff and Fairbairn, 2012).

The fact that only trade-offs between silk spinning and fecundity were found under dietary restriction agrees with the literature (e.g. Bodasing et al., 2002). In nature, such trade-offs will be manifested when individuals inhabit marginal or over-populated groups. Earlier research by us demonstrated either a constraining (Bonte et al., 2008a) or facilitating (Mestre and Bonte, 2012) impact of starvation on dispersal behaviour. Dispersal by ballooning can only occur by means of silk production and is considered to be a form of aerial lottery with high immigration costs when habitat is scarce, i.e. when the chances of reaching suitable habitat are low (Bonte et al., 2006). Costs incurred during different dispersal stages (initiation, transfer and settlement) eventually determine dispersal strategies and feed back among each other (Bonte et al., 2012; Delgado et al., 2014; Travis et al., 2012). We demonstrated here trade-offs between silk spinning and fitness-related life history components, with an overall effect under dietary restriction. Costs related to the production and use of silk may thus impact the decision to disperse by silk. Depending on the environmental conditions that spiders experience, different optimal dispersal strategies may exist. Starved *Erigone* spiders from unproductive dune slacks (Bonte et al., 2008a) showed reduced dispersal, while opposite patterns of dispersal stimulation were recorded in *Erigone* collected from highly productive arable fields (Mestre and Bonte, 2012). As the latter may compensate for the costs of silk use more easily relative to the former, simple cost–benefit balances can explain this variation in silk-mediated dispersal strategies.

In conclusion, the spinning of dragline silk imposes severe trade-offs with fitness-related components of spider life history. These trade-offs are especially prevalent under conditions of food restriction and are suggested to explain variation in dispersal

strategies. A single peak production of draglines is related to dispersal or predatory avoidance in spiders. These occasional spinning events impose strong carry-over effects in the life histories of the studied *Erigone* spiders. Our results thus demonstrate that occasional, energy-demanding behaviours during life have the potential to affect adult performance and fitness. This finding opens avenues for further research to explore the impact of such carry-over effects on higher level ecological processes like population and community dynamics.

Competing interests
The authors declare no competing or financial interests.

Author contributions
D.B. conceived the idea for the experiment; L.V. executed the experiment for her MSc thesis; and all authors designed and interpreted the experiment, and drafted and revised the manuscript.

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