

Site Selection and Foraging in the Eresid Spider *Stegodyphus tentoriicola*

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Abstract Habitat selection has profound consequences for survival and reproductive success. We investigated web relocation behaviour in relation to plant structure and body condition as well as the plasticity of foraging behaviour of the spider *Stegodyphus tentoriicola*. Spiders inhabiting thorny vegetation were larger, built larger webs than spiders in thornless plants and relocated their webs less frequently. Web relocation affected reproductive success through a delay of oviposition. Spiders supplemented with extra food improved body condition and built smaller webs than control spiders implying a crucial role of food in limiting fitness of *S. tentoriicola*. Reduced investment in webs suggests a trade-off between the benefit of more food against the cost of web-construction. We propose that *S. tentoriicola* exhibit a “silk and energy saving” strategy when saturated.

Keywords *Stegodyphus tentoriicola* · Eresidae · site selection · web relocation · food supplementation

Introduction

Habitat selection has extensive influence on the survival and reproductive success of an animal (Orians and Wittenberger 1991). In web building spiders, structures and sites for web construction, thermal conditions, food availability, and protection against predators are vital factors in this context (Riechert and Gillespie 1986). The web represents a valuable resource and deserting it is costly for several reasons

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(Vollrath 1985). For example, web relocation is associated with increased predation risk during movement (Lubin et al. 1993), high energetic costs of migration and rebuilding of the web (Pasquet et al. 1999), as well as missed foraging opportunities while moving (Jakob et al. 2001). Furthermore, relocation implies an uncertainty about whether a more suitable site can be found. Nevertheless, spiders do relocate their webs in response to prey availability (Vollrath and Houston 1986; Nakata and Ushimaru 1999), competition (Smallwood 1993), web destruction (Leclerc 1991; Chmiel et al. 2000) or kleptoparasitic load (Rypstra 1981). Large mammals for example may negatively affect web spider densities by simplifying vegetation complexity (and thereby reducing number of web sites) or by direct physical destruction (Takada et al. 2008). Spider webs that are built in tough or spiny plants that are less likely to be destroyed may therefore be protected from larger animals. Thus, spiders could increase their foraging success and thereby their body size and reproductive success (Ward and Lubin 1993) by selecting habitat structures that have high food availability and a low risk of web damage.

Within species, many studies have emphasised the crucial effect of foraging success on patch site residence time (Persons and Uetz 1997; Hengeveld et al. 2009; Corley et al. 2010). According to the “marginal value theorem”, a forager should leave a patch once its net energy gain equals the average rate of energy gain in the habitat (Charnov 1976). A spider as a sit-and-wait predator, however, usually does not deplete food resources significantly in its site because it forages on highly mobile insect prey (Janetos 1986). Moreover, Edwards et al. (2009) proposed that “optimal foraging” is unlikely to be the most relevant mechanism for moving decisions of a sit-and-wait predator, whereas factors such as predation risk, web destruction and environmental change (Edwards et al. 2009) as well as interaction with conspecifics (Smallwood 1993; Salomon 2009) may be more relevant.

In periods of food depression spiders can modify their traps to improve their chances of catching prey (Olive 1982). One mechanism of trap modification is adapting web size to foraging success. For example, several studies have demonstrated that well-fed spiders reduced their effort in foraging by investing less in web construction (i.e. by building smaller webs) while hungry spiders built comparatively larger webs (Higgins and Buskirk 1992; Venner et al. 2000). Alternatively, even food-supplemented spiders may build large webs since spiders regard prey capture as a cue indicating whether a current web site is profitable or not (Nakata 2007). However, depending on the cost of web building, a hungry spider may be incapable to invest in larger webs and thus build smaller webs than a well-fed spider that might still be able to benefit from maintaining a large web (Segoli et al. 2004).

Thus, web relocation and web modification are the two main possibilities for spiders to respond to variation in foraging success which, however, are determined by the quality of the current web site.

We investigated relocation behaviour with regard to plant structure and condition as well as the plasticity of foraging behaviour of the South African eresid spider *Stegodyphus tentoriicola* (Purcell 1904). *S. tentoriicola* builds its silken tube-like nests and capture webs into the low Karoo vegetation, using thorny as well as thornless plants as web attachment structures. The capture web is sheet-like and consists of sticky cribellate silk threads. Like the well-studied species *S. lineatus*, *S.*

tentoriicola does not renew its entire capture web daily but it renews parts of the web frequently (personal observation). The construction of the whole web is comparatively costly in terms of energy expenditure and silk production because old silk will not be recycled and previous energy being spent for silk production is lost (Pasquet et al. 1999).

We ask whether relocation of the nest and web depend on vegetation structure and/or on the condition of the spider. Thorny plants could be nest sites with fewer disturbances compared to thornless vegetation due to the protection that thorns provide against browsing animals. In addition, we test the prediction that spiders in a poor condition should be more likely to desert their web site (Nakata and Ushimaru 1999). Moreover, we ask whether *S. tentoriicola* trades off the investment in foraging (web building) against prey capture rate to reduce foraging costs (predation risk), or whether high costs of web building constrain web size. To evaluate this, we conducted a food supplementation experiment. If predation risk is the deciding factor, supplemented spiders are expected to build smaller webs because then they would be less exposed to predators and consequently would have higher survival rates. If high costs of web building constrain web size, spiders provided with extra prey are expected to build larger webs.

Material & Methods

Study Species

Stegodyphus tentoriicola (Purcell 1904) (Eresidae) is exclusively distributed in South Africa (Kraus and Kraus 1988). It is an annual and semelparous species that mates during February, produces an egg sac approximately 4 weeks after mating and after another 5 weeks spiderlings hatch (personal observation). Female spiders provide care for their egg sac and mothers feed their offspring via regurgitation before being finally consumed (matriphagy). During the period of care, females continue foraging and web renewal (personal observation). After matriphagy and prior to juvenile dispersal, spiderlings have a period of cooperation within the maternal nest (Kraus and Kraus 1988). Spiders leave their maternal nest shortly before maturation and build their own silken retreats (nests) and capture webs. Adult males leave their retreat after maturity to search for females and no longer build capture webs. During daytime *S. tentoriicola* females stay in their nests and only come out to secure insects entangled in the web. Prey in the study area mainly consisted of grasshoppers, dipterans, termites and beetles (personal observation).

Study Site

The research was conducted on two populations of the spider *S. tentoriicola* in the Karoo of South Africa (Eastern Cape) near Cradock from February ('early season') until the end of April ('advanced season') 2008. The first population (Pop 1) was located on a 3.12 ha area near the entrance to the Mountain Zebra National Park (MZNPN) (32°8'20.94"S, 25°30'38.64"E). The second population (Pop 2) was on a 4.5 ha area near Lake Arthur (32°12'23.48"S, 25°47'56.55"E). Both locations were

habitat for grazing game and sheep were driven over the area near Lake Arthur periodically. The vegetation of both sites was rather similar: low perennial microphyllous shrubs (dominated by *Penzia incana*, *Helichrysum rosom*), thorny lower plants (*Asparagus* spec., *Lebeckia spinescens*, *Ruschia intricate*) interspersed with graminaceous annuals and scattered higher thorny shrubs (*Lycium cinereum*, *Zygophyllum* spec.) or trees (*Acacia karoo*).

Web Relocation

All female nests of both study sites (Pop 1 & Pop 2) were marked with numbered waterproof flags and their position was mapped with a GPS (Garmin 12 XL). Prosoma width and opisthosoma length were measured with callipers to the nearest 0.2 mm and each spider was marked with a unique colour code using non-toxic watercolour (Plaka[®], Pelikan). Prosoma width is a fixed measure for each developmental stage (Vollrath 1988; Lubin et al. 1991). Opisthosoma length is flexible and correlated with the amount of food ingested and thus an indicator of the spider's foraging condition (Jakob et al. 1996). There is a positive correlation between prosoma width and opisthosoma length in adult *S. tentoriicola* (Pearson correlation: $r=0.68$, $p=0.001$, $N=169$, Ruch et al. 2009). A body condition index was calculated from the residuals of a regression of opisthosoma length on prosoma width (residual index, Jakob et al. 1996).

During the study, all nests were checked daily for the presence of spiders. For all analyses, only adult females were included. If a nest was found empty we scanned the vicinity (20 m radius) for a newly built nest. The inhabiting spider could be identified easily with its individual marking. The new nest was marked and distances between old and new nests were measured with a measuring tape. Spiders that disappeared and were not found again were presumed dead. For analysis of relocation behaviour we excluded 81 spiders that were observed for a few days only or that were presumed dead. In total, 88 spiders fulfilled the criterion of being observed until oviposition.

All plants that spiders used to attach their nests were specified and classified into two broad categories: thorny and thornless. As thorny plants we classified those with stiff and spiky parts, either of epidermal origin (spike) or due to reorganisation of stem axes and leaves (thorn). The category included plant species (see examples above). In total, 17 plant species were involved in the study. We compared body condition index ($N=168$) and spider relocation frequency ($N=88$ spiders) of adult female spiders inhabiting the two vegetation categories.

Food Supplementation Experiment and Web Size

To evaluate whether high costs of web building or high predation risk constrain web size, we conducted a food supplementation experiment. All spiders were measured and the web size was classified into three categories: 0 = no web, 1 = small web, 2 = large web (see below). Web status (whether a web had been partly or fully renewed) and web size were determined daily. Fresh cribellate capture silk could easily be identified by its bright whitish appearance (Erez et al. 2005). A web was classified as large if the capture sheet bridged an open space

of more than 10 cm distance from the nest entrance while we noted a small web if the sticky capture silk was restricted to an area of 10 cm around the nest entrance and did not extend over the borders of one plant. Spiders were measured before and after the experiment.

38 female spiders were chosen randomly for food supplementation (27 ♀ from Pop 1, 11 ♀ from Pop 2), the other spiders of the population were used as control. Every third or fourth day from February 28th 2008 on, each spider in the supplement group received one extra prey item. The period of supplementation was 34 days on average. We caught the prey animals nearby (small grasshoppers, termites, flies) and made sure that they generally had approximately the same size. We carefully placed the prey into the capture web (or gently pushed it directly into the entrance if there was no capture web). Spiders generally accepted the extra prey, regardless of prey type and web type. We could not feed all spiders in the supplemented group on the same days which caused variance in the time interval between supplementation events. We used the data from the daily control of nests (see “[Web Relocation](#)” section above) to compare survival rates and web sizes between supplemented and the non-supplemented spiders.

Data Analysis

Statistical data analyses were carried out with JMP 7.0. Continuous data were tested for normal distribution (Shapiro-Wilk-Test) as well as for equal variances. Parametric tests were applied when the data fulfilled the criteria otherwise we used non-parametric tests. All statistical tests are 2-tailed ($\alpha=0.05$). Descriptive statistics are given as mean \pm standard deviation (SD). Sample sizes may differ between the particular questions because of disappearance of some individuals within the study period.

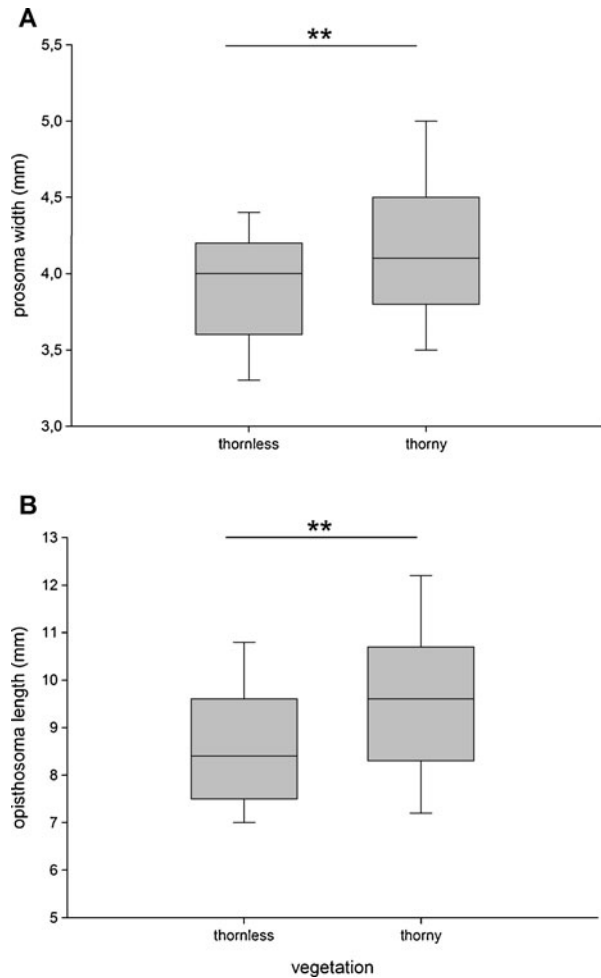
Results

Web Relocation

In total, 169 spiders in two populations were observed, 88 of which were included for web relocation analyses. Relocation occurred before producing an egg sac in the period between February 10th 2008 and March 3rd 2008, none of these spiders were supplemented with food. Nests were found clustered around old maternal nests from the past season (Ruch et al. 2009), however all except two nests were found alone on a given plant. In Pop 1, the mean density was 0.42 females per 100 m² and 0.08 females per 100 m² in Pop 2 (Ruch et al. 2009). 26 female spiders (29.55%) relocated their webs, four of which relocated it twice. The mean relocation distance was 7.56 ± 1.79 m (min: 0.62, max: 31.66, $N=23$).

At the beginning of the study, spiders inhabiting thorny plants built significantly larger webs ($\chi^2=10.68$, $p=0.001$, $N=147$), had a significantly larger prosoma (One-way ANOVA: $F_{1,166}=8.72$, $p=0.0036$, Fig. 1A), a larger opisthosoma (One-way ANOVA: $F_{1,166}=11.13$, $p=0.0011$, Fig. 1B) and consequently a better condition index than spiders in thornless plants (One-way ANOVA: $F_{1,166}=4.32$, $p=0.039$).

Fig. 1 **A** Prosoma width ($\bar{x}\pm SD$) and **B** opisthosoma length ($\bar{x}\pm SD$) of spiders in different vegetation types. ****** = $p < 0.01$



A logistic regression showed that vegetation structure (thorny or thornless) was a significant predictor of relocation probability ($\chi^2=7.29$, $p=0.0069$, whole model: $\chi^2=8.07$, $r^2=0.075$, $p=0.017$, $N=88$) thus, spiders in thornless plants were more likely to relocate, while the body condition index ($\chi^2=0.40$, $p=0.53$) was not significant.

An ANOVA revealed that the timing of oviposition was negatively influenced by relocation but not by vegetation structure (ANOVA: $F_{2,70}=3.95$, $r^2=0.10$, $p=0.024$, web relocation: $F=7.09$, $p=0.0096$, vegetation: $F=0.16$, $p=0.69$, $N=73$). We did not compute the interaction because of too few relocation events out of thorny plants.

Since spiders in thorny plants relocated less often, we tested whether spiders showed a preference for thorny plants after relocation, but we found no preference ($\chi^2=0.022$, $p=0.88$, $N=25$).

54 of the marked 169 females (31.95%) survived until the end of the survey. Survival was neither influenced by vegetation structure ($\chi^2=0.01$, $p=0.98$, $N=168$) nor by web relocation ($\chi^2=0.28$, $p=0.60$, $N=169$).

Food Supplementation Experiment and Web Size

To determine the effect of food supplementation, we compared female opisthosoma length of the first (when marked and measured) and second measurement (after 34 days on average). Both treatment groups significantly increased in opisthosoma length between measurements (paired *t*-test: 10.18 $p < 0.001$, $N = 64$) however the increase in the supplemented group was significantly stronger than in the control group (*t*-test = 6.64, $p < 0.0001$, $N_{\text{supplemented}} = 21$, 3.81 ± 1.23 mm, $N_{\text{control}} = 43$, 1.49 ± 1.46 mm). None of the spiders relocated during the experiment.

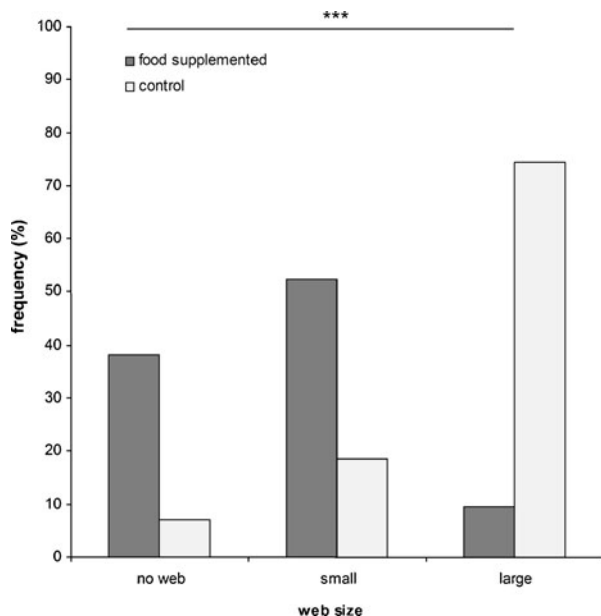
Since the interval between the two measurements was not equal for all spiders, we conducted an ANCOVA to account for the potential influence of time on opisthosoma length increase. The covariate time interval had no influence on the increase in opisthosoma length while food supplementation remained highly significant (ANCOVA: $F_{2,61} = 21.60$, $r^2 = 0.41$, $p < 0.0001$, interval of the two measurements: $F = 2.84$, $p = 0.09$, treatment: $F = 35.96$, $p < 0.0001$, $N = 64$).

To test the hypothesis that foraging effort is a function of condition, we compared web sizes of the two treatment groups at the end of the experiment. A logistic regression revealed that the web size after the experiment was strongly influenced by food supplementation ($\chi^2 = 27.56$, $p < 0.0001$, Fig. 2) but not by plant structure ($\chi^2 = 0.26$, $p = 0.55$; whole model: $\chi^2 = 29.70$, $r^2 = 0.23$, $p < 0.0001$, $N = 64$). Food supplementation had no influence on the timing of oviposition (*t*-test: 0.37, $p = 0.72$, $N = 72$).

Discussion

Habitat selection in animals is a complex behavioural decision which requires context-dependent plasticity. Web relocation and web modification are two possible

Fig. 2 Relative frequencies of capture web sizes of the two treatment groups. The values are based on the following sample sizes: **no web**: supplemented = 8, control = 3; **small web**: supplemented = 11, control = 8; **large web**: supplemented = 2, control = 32. *** = $p < 0.0001$



modes of spiders to respond to variation in foraging success. We examined web relocation behaviour as well as plasticity in foraging in the eresid spider *Stegodyphus tentoriicola*. Web relocation behaviour was mainly affected by the structure of vegetation of the current location, while the hypothesis that body condition is a predictor for web relocation was not supported. Spiders inhabiting thorny plants were larger, built larger webs and were less likely to relocate than spiders in thornless vegetation. Thorny plants may be better protected against browsing animals and hence make web destruction less likely (Lubin et al. 1998). Web destruction could enforce higher relocation frequencies which result in shorter sedentary periods and thus limit foraging success. For example, browsing mammals that more easily damage thornless plants (and thereby destroy attached spider webs) could be the driving force. Lubin et al. (1998) found in *S. lineatus* that spiders preferentially resided in tall, spiny or poisonous plants that were rejected by large herbivores and thus may provide safer nest sites with less disturbance. It is also possible that thorny plants provide better possibilities for web attachment and thereby allow a larger web size. The construction of larger webs may have led to a higher foraging success and thus larger absolute body sizes in *S. tentoriicola*.

For *S. tentoriicola*, thorny plants seem to be beneficial for two reasons: their structure itself facilitates the construction of larger webs and they protect from web destruction. Even though individuals inhabiting thornless plants had higher relocation probabilities, settling decisions did not follow any pattern with regard to plant species and structural features. Thus, we suggest that the decision to settle at a certain plant species might be random while the sedentary period is determined by the quality of the location. The quality of the location is not only determined by prey availability, but also by features that influence the investment in web building. Web building has considerable costs in the genus *Stegodyphus*. *S. lineatus* for example needed approximately 6 h to build a complete web and lost up to 10% body mass per web (Pasquet et al. 1999). Since webs of both species are very similar, *S. tentoriicola* spiders in thorny plants may have saved energy due to a lower requirement of web repair.

Infrequent relocation and reduced web repair effort does not only save energy, it simultaneously increases foraging success (Jakob et al. 2001). Foraging can be seen as a compromise between the energetic needs of an individual for maintenance, growth and reproduction and the costs and risks associated with foraging activity (Lima and Dill 1990). Our results show that food-supplemented spiders had a significantly larger opisthosoma than the control group, which is an important result since opisthosoma length in spiders has a strong effect on a female's fitness: it influences reproductive success because of the positive correlation between female opisthosoma length and clutch size (Ruch, unpublished data). In *S. lineatus* an increase of 1 mg body mass of a juvenile female at dispersal corresponded to ten more eggs (5–10% of total clutch size) when the female reproduced (Schneider 1992). *S. tentoriicola* females showed a two-fold higher investment into clutch mass than *S. lineatus* (Ruch, unpublished data). This higher investment was achieved through a higher number of eggs as well as through a slightly higher weight per egg. In *S. lineatus*, larger females reproduced earlier (Schneider 1997) and early-hatched spiderlings had a higher survival probability (Schneider 1992). If we assume that faster growth and larger opisthosoma has a similar positive impact on fitness of our

study species, we would expect preference for web building in thorny plants. More detailed studies of the relative occurrence of high quality web sites in relation to web site selection are required to reveal such a preference.

We did not detect differential mortality rates in spiders that relocated, but during this study many *S. tentoriicola* females disappeared and were not included for web relocation analyses. Disappearance could either be due to predation during web renewal or to unsuccessful web relocation attempts. The finding that nests were found clustered around old maternal nests (Ruch et al. 2009) suggests short migration distances and could be the result of high predation pressure. Predation risk is difficult to measure and therefore the reason for the disappearance of spiders is unknown. In the desert spider *Latrodectus revivensis*, however, mortality was estimated to be a major cost of web relocation (Lubin et al. 1993).

In the food supplementation experiment, we did not detect earlier reproduction of supplemented spiders. The reason could have been that food supplementation was initiated late in the season when most females were close to oviposition. However, a significant increase in opisthosoma length of food supplemented spiders may indicate food shortage earlier in the season which could limit the reproductive success of *S. tentoriicola* as demonstrated for other spider species (Ward and Lubin 1993). We found delayed oviposition in females that relocated their web, suggesting a cost of web relocation. Similar results were found in the orb-web spider *Zygiella x-notata* (Wherry and Elwood 2009). Rittschof and Ruggles (2010) suggested that spiders that experienced food shortages in the past and thus had a smaller absolute body size may adapt their foraging strategy and relocate their webs more often. This may be a possible scenario for *S. tentoriicola* inhabiting thornless plants. Even though body condition was not significantly different in the two vegetation structures, it is possible that spiders in thornless plants might have suffered from limited foraging success in the past which led to a smaller total body size.

The pattern that larger webs were more common in thorny plants as found early in the season (in February) was no longer detected after the food-supplementation experiment (at the end of April). However, a better foraging success in the early season due to for example larger webs in thorny plants might allow a reduction of web size in the advanced season and thereby a reduced predation risk close to reproduction. The reduction of web size in supplemented spiders can be interpreted as a decreased foraging effort (Higgins and Buskirk 1992; Venner et al. 2000). Thus, in the advanced season *S. tentoriicola* appears to trade-off the benefit of foraging against the costs. A reduction in foraging activity in food-supplemented animals has been demonstrated for other spider species (Lubin and Henschel 1996; Pasquet et al. 1999). This behaviour can be ascribed to saturation due to digestive constraints or large foraging costs (predation, energetic costs), which decrease the marginal benefit of additional food. One part of the foraging costs in spiders is the increased predation risk while building the web and while dragging the prey insect into the retreat. Indeed, during our study we found several empty nests with obviously renewed cribellate silk threads in the capture web, indicating predation during web renewal. However, we never directly observed predation. These risks are equal for individuals in any feeding state, but spiders in a good condition have less to gain than individuals in a poor condition. Thus, *S. tentoriicola* might have reduced

foraging effort to reduce predation risk as suggested for other eresid spiders (Lubin and Henschel 1996; Pasquet et al. 1999).

Further foraging-related costs include the energetic investment of movement and silk production. Since energetic costs for locomotion increase with body mass while the basal metabolic rate is independent of body size, it is less costly for a large spider to remain in the nest without investing in its web than for a small individual (Venner et al. 2003). As mentioned before, silk expenditure for web construction is considerable in the genus *Stegodyphus*. Therefore, we suggest that fed *S. tentoriicola* females reduce their investment in web building to save energy of movement and silk production. In summary, *S. tentoriicola* seems to be food limited and able to adjust its investment in foraging to its individual satiation state.

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