Web building flexibility of an orb-web spider in a heterogeneous agricultural landscape

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Abstract:

Intensification of land-use in agricultural landscapes is responsible for a decline of biodiversity which provide important ecosystem services like pest-control. Changes in landscape composition may also induce behavioural changes of predators in response to variation in the biotic or abiotic environment. By controlling for environmentally confounding factors, we here demonstrate that the orb web spider *Araneus diadematus* alters its web building behaviour in response to changes in the composition of agricultural landscapes. Thereby, the species increases its foraging efficiency (i.e., investments in silk and web asymmetry) with an increase of agricultural land-use at intermediate spatial scales. This intensification is also related to a decrease in the abundance of larger prey. A negative effect of landscape properties at similar spatial scales on spider fitness was recorded when controlling for relative investments in capture thread length. This study consequently documents the web building flexibility in response to changes in landscape composition, possibly due to changes in prey availability.

Key-words: *Araneus diadematus,* Araneidae, behavioural flexibility, orb web geometry, landscape, model selection, semi-natural habitats

Introduction

In agricultural landscapes, post-war transformation of traditional to modern, high-intensity land-use systems in simplified landscapes involves the conversion of perennial habitats to ephemeral arable fields, the destruction of biologically valuable edge habitats, an increasing input of mineral fertilizers and increased use of pesticides. Both land-use (e.g. organic versus intensive farming) and the accompanying scale of landscape conversion (e.g. diversity and landscape configuration of natural habitats) affect biodiversity and the structure of biological communities associated with crops in a mutually non-exclusive way (Tscharntke et al. 2005). In general, arthropod diversity is higher in heterogeneous landscapes (e.g. Östman et al 2001; Rundlof & Smith 2006; Clough et al. 2007), especially if it is dominated by generalist species (Batáry et al. 2007). These patterns are mechanistically maintained by enhanced colonization of species that refuge in non-crop habitats (Kremen et al. 2007). Because of strong interspecific variation in dispersal capacity (e.g. Bonte et al. 2003, 2004, Dauber et al. 2005) and subsequent altered colonization probabilities under various scales of landscape heterogeneity (Steffan-Dewenter et al. 2002, Schmidt & Tscharntke 2005, Schmidt et al. 2008), a higher arthropod diversity and density is maintained in crops situated in small-scale heterogeneous agricultural landscapes. This is especially true for large, flying arthropods (Beintema et al. 1991; Hendrickx et al. 2007), which are essential prey for orb-web spiders (Venner & Casas 2005).

The design of the orb-web is extremely plastic in response to environmental and physiological variables (Uetz 1992, Sherman 1994, Vollrath et al. 1997), with documented increases in capture area in response to a shortage of prey (Witt 1963, Herberstein et al. 2000) or changes in prey size (Sandoval 1994; Schneider & Vollrath 1998). More-over, asymmetrical webs with a significant up/down asymmetry confer to a relatively higher foraging value to sections below the resting place of the spider, central in the web (the hub), because spiders run down faster than up (Rhisiart & Vollrath, 1994). Similarly, prey in the lower half of the web is more quickly detected (Landolfa & Barth 1996), thereby increasing prey-handling efficiency. Consequently, web building in orb-web spiders provides a unique tool to study behavioural flexibility because it allows the quantification of foraging by measuring the investments in web building (Uetz 1992). Changes in web area, number, density of spirals and capture thread length comprise functional responses towards higher prey capture; changes in web asymmetry a response towards prey handling efficiency (Heiling & Herberstein 2000).

Because (i) previous empirical work has provided evidence of functional behavioural responses in relation to prey limitation and (ii) because changes in land-use are known to induce changes in prey availability, we hypothesised higher investments in web-building through increased asymmetry in intensively used (homogeneous) crop landscapes where essential prey are limited. We additionally inferred the spatial scale at which changes in behaviour are prevalent and questioned whether changes in behaviour are accompanied by changes in fitness costs.

Material and Methods

Model species

Araneus diadematus is a native species from the Palaearctic and Nearctic region. The species mostly lives in shrub or tree dominated habitats (Dahl 1931; Hänggi et al. 1995) where plenty of attachment sites for the scaffolding of the orb-web are available. The female is the largest sex and reaches a length of 10 to 18 mm (Roberts 1995). Adulthood is reached in late-summer-autumn and the female dies a few days after the deposition of the eggsacs (Dahl 1931). Offspring emerge in spring, disperse through ballooning and settle in a new location till adulthood (Foelix 1982; Preston-Mathan & Preston-Mathan 1996). The web consists of energetic-costly proteins and is therefore recycled (eaten) every day (Sherman 1994). The species' web design variability and functionality is well documented (e.g. Witt 1963, Vollrath 1986, Rhisisart & Vollrath 1994, Vollrath et al. 1997, Schneider & Vollrath 1998; Zschokke 2002). In agricultural landscapes, webs are preferentially located in trees in field margins (Dahl 1931; Ludy 2007). Its prey-spectrum on field margins is dominated by larger Diptera (Ludy 2007 and references here-in). Herbivorous pest species like *Sternorrhyncha* including aphids are also caught in large numbers (Ludy 2007).

Assessment of prey availability:

Prey abundance in relation to landscape composition was independently assessed with 37 white-colored pan traps that were located randomly within the landscape. Diameter of the traps was 5 cm and filled with a formaldehyde-water-detergent fixative. All traps were placed at a height 1.2-1.5 meter above the ground surface and attached on solitary trees. By using these traps, we are able to assess activity pattern of flying arthropods that are the main prey for *A. diadematus* in agricultural landscapes (Diptera; Ludy 2007). Although these traps consist of an activity-based sampling methodology, activity levels reflect patterns in abundance (Saint-Germain et al. 2007). Traps were operational from September 20th till October 15th. The numbers of prey were counted in the lab and their size was approximated by measuring body length and body width (Sample et al. 1993).

Assessment of web building behaviour and fecundity

A total of 155 female *A. diadematus* were located in solitary trees in September-November 2006 during 21 days within a heterogeneous agricultural landscape in the proximity of Ghent (see further). Of each individual web, we measured the following web geometrical features: web and capture area width (geometrical radius in 4 sectors), number of sticky spirals (*sensu* Zschokke 1999) counted along a primary radius (*i.e.* a radial thread; Zschokke 1999) in the capture area, web orientation, web inclination and web height. Distance to the nearest vegetation was measured as the closed distance to plant branches perpendicular to the web. Hub diameter and the hub spiral density were measured because they may, like special web decorations, reduce predation risk due to a decreased visibility towards predators or attract potential prey (Herberstein et al. 2000). From these, we calculated web asymmetry (lower vertical web geometrical radius *minus* upper vertical geometrical radius) and the total capture thread length

$$CTL = \frac{\pi}{16}(N_v + N_h)(D_{o.v} + D_{i.v} + D_{o.h} + D_{i.h}) \quad \text{(eq.1)}$$

according to Venner et al. (2001). Here N depict the number of vertical (N_v) and horizontal (N_h) sticky spirals as counted along respectively the vertical and horizontal primary radii, while D_o

and D_i denote respectively the outermost (from one outermost spiral to the opposite outermost spiral) and innermost (corresponding to the free zone around the hub without spiral turns) diameter of the capture area (for horizontal and vertical positions). Because web-building appears to be plastic in response to daily changes in meteorological conditions, the species' phenological state and the size of the spider (e.g. Vollrath et al. 1997), on average 7.8 occupied webs (by female spiders) were randomly located within the entire region at the same day. We measured web design parameters *in situ*; cephalothorax width of the collected spider (preserved in 80% ethanol) was measured under a binocular microscope as a surrogate for body size. Size and the number of eggs were assessed after dissection of the abdomen. Total reproductive output was calculated as total number of eggs x average egg size. For spiders collected in the period prior to their eggsac deposition, no eggs could be counted or measured because they were completely imbedded in abdominal tissues.

Landscape composition

The study area was situated in the alluvial planes of the river Scheldt near Ghent (Belgium). It is a heterogeneous landscape, consisting of intensively used agricultural fields and biologically valuable habitats like marshes, elder bush and hayfields. All fields were conventionally treated with herbicides, fungicides, insecticides and fertilizers in summer. Cattle on intensively used pastures were treated with ivermectin, which is known to have a lethal effect on coprophilic arthropods (Madsen et al. 1990). The study site is approximately 12 km², which is within the range of the species' dispersal capacity through ballooning (Johannesen & Toft 2002, Thomas et al. 2003), consequently assuring sufficient gene mixing and the presence of a panmictic population (Johannesen & Toft 2002). Web-design properties, body size and fecundity were related to landscape composition (proportion of specific habitat types) at five landscape scales with radii 25, 50, 100, 250 and 500 meters around each target individual. As prey are known to be negatively affected by the amount of intensively used agricultural area (being maize and winter wheat crops and heavily fertilized pastures in the study area) and positively affected by the amount of biologically valuable habitat (flower rich pastures, hedges, forests and marshes) (e.g. reviews in Vickery et al. 2001; Tscharntke et al. 2005), we calculated the percentage of crops, intensively grazed pastures and biologically valuable habitat (here-after abbreviated as BVH) from recent digital biological value maps (De Saeger et al. 2006) within the predefined radii around the position of each focal spider.

As in other methodologically similar studies (Steffan-Dewenter *et al.* 2002; Schmidt et al. 2008), landscape properties within the distinguished radii were highly intercorrelated. The within-habitat-type correlations between the smallest and the largest scale had coefficients between r = 0.51 (% pastures) and r = 0.63 (% BVH). The intercorrelation between different habitat types within predefined radii was significantly negative (r ranging from -0.14 (% BVH – pastures at the 25 meter scale) to -0.66 (% crops – pastures at the 250 meter scale)). Intercorrelations between the total amount of BVH and the total amount of arable (intensively managed pastures + crops) habitat showed the strongest correlation (r between -0.75 to -0.87). The area of intensively used crops and BVH ranged from 0-100%, with median values 48 - 69% for crops and 15-20.5 for BVH.

Statistical analysis and inference

Prey availability

Number of prey items in relation to the amount of biologically valuable habitat was tested by Poisson-regression (Proc Glimmix, SAS). We tested the size distribution of prey in relation to landscape properties by univariate null models (EcoSim 6.0; Gotelli & Entsminger 2006). By means of this randomization technique, expected patterns with respect to slope of the regression (more large prey with increased amount of natural habitat), shape (points are concentrated in a defined left triangle with increased amount of natural habitat), an the possible presence of an ecological boundary (right-upper corner of the bivariate plot prey size-amount of natural habitat is unusually empty) were tested against the null hypothesis that the observed pattern makes part of a random ordering of the measurements. The observed pattern was compared to the null model by generating 1000 randomizations by reshuffling the observed x and y variables.

Web building behaviour and fecundity

General model structure

Linear models were run for web building and fecundity measurements in relation to the proportion of BVH within each of the five predefined radii around the located web as main fixed effect. Because we conducted five analyses simultaneously to infer (instead of testing multiple null-hypotheses; Johnson & Omland 2004) how and on which spatial scale behaviour and fecundity were influenced by landscape composition, we used Akaike-criteria (with corrections for small sample sizes; AIC_c Burnham & Anderson 1998) for linear models to assess the reliability of the different competing models. We subtracted the minimum AIC_c-value from each AIC_c-value and rescaled the resulting values Δ_I such that Δ_I=0 for the model with minimal AIC_C.

Rules of thumb, provided by Burnham & Anderson (1998) suggest that models with $\Delta_I \geq 7$ strongly support the model with the smallest Δ_I, models with $2 < \Delta_I \leq 5$ sufficiently support the model with the smallest Δ_I and those with $\Delta_I \leq 2$ do not support one single model at all. All analyses were conducted with SAS (proc glm, proc glimmix).

Model structure for web building behaviour

Capture area radius (only lower radius length was analysed due to strong intercorrelation), hub diameter, web location height, distance to the vegetation, inclination, web asymmetry (radius above *minus* radius under) and capture thread length measurements were analyzed by linear models. Numbers of spirals in the hub and capture area were analyzed with generalized Poisson models, which were corrected for overdispersion. Spiral density within the hub and the capture are was tested by including their width (respectively radius and diameter) as a covariate.

Body size, date and meteorological conditions (wind velocity, aerial humidity, precipitation and average temperature the day before sampling) were included as covariates in the full model. Because temperature and date showed negative colinearity ($r=-0,45$; $N=20$; $p=0,044$), we retained the latter in the analysis because Sherman (1994) and Vollrath et al. (1997) showed that phenology (state of fecundity) had larger impacts on web-building behaviour than small changes in temperature. Since covariation of precipitation, aerial humidity and wind velocity were not significant in any model (see results), we retained only body size and date as covariates in the reduced models for different web size traits, web asymmetry and capture thread length.

Model structure for fecundity

Because all fecundity measurements showed a positive relationship with body size, the latter was retained as covariate within all analyses. As for web building traits, linear regressions were applied for egg size, clutch size and total reproductive output in relation to the proportion of BVH within the predefined radii.

Results

Prey availability

Total numbers of prey did not show any relationships with landscape properties at any scale (all $F_{1,36} < 2.11$; $P>0.05$). Prey size, however, showed significant distributional patterns according to the amount of biologically valuable habitat. The regression of the slope was significantly higher than after randomization for the data points at the scales between 25-250 meters (BVH 250 meters: observed slope=0.173; expected slope after randomization=0.000). Data points were also significantly distributed in the right triangle at these scales, but boundary effects were only observed at the scale of 250 meters (Table 1). As depicted from Fig. 1, large prey appears to lack from samples which were located in landscapes with biologically valuable habitat beneath 40 percent in the 250 meter radius.

Web building properties

Covariation among factors

The radius of the lower capture area was significantly related to date of sampling (β=-0.110 ± 0.003 SE; $F_{1,151}$=14.28; P=0.0002) and with body size (β=0.659 ± 0.367 SE; $F_{1,151}$=3.22; P=0.075). The number of spiral threads in the capture area was positively related (β=0.038 ± 0.003 SE; $F_{1,152}$=125.22; P<0.0001) with the radius of the capture area (slope estimates and statistics are average responses for the four web sectors). Capture thread length was positively related with body size (β=371.60 ± 115.26 SE; $F_{1,151}$=10.39; P=0.0015) and negatively with date (β=-32.318 ± 4.76 SE ; $F_{1,150}$=22.69; P<0.0001). Web asymmetry only showed positive covariation with web diameter (β=0.401 ± 0.06 SE ; $F_{1,151}$=37.91; P<0.0001).

Similar patterns for the number of spiral threads in the hub were found in relation to its diameter (β=0.10 ± 0.02 SE ; $F_{1,150}$=29.71; P<0.0001), but significant covariation with date was additionally found (β=-0.005 ± 0.001 SE; $F_{1,150}$=14.52; P=0.0002). The diameter itself showed strong covariation with body size (β=0.351 ± 0.069 SE; $F_{1,151}$=25.35; P<0.0001), but a positive relationship with sampling date was retrieved for the latter (β=0.021 ± 0.005 SE; $F_{1,151}$=15.07; P=0.0002). No covariation of precipitation ($F_{1,150}$<0.01; p<0.92), aerial humidity ($F_{1,151}$<0.05 p<0.82) and wind velocity ($F_{1,149}$<1.41; p<0.22) were found for any factor.

Effects of landscape composition on web design at different spatial scales

After controlling for above mentioned covariation, negative effects of the proportion of BVH were found for the number of spirals and the geometrical radius of the lower web capture area (Table 2). These effects were significant at the spatial scale of 100 and 250 meters for the number of spirals and at the spatial scale of 25 and 250 meters for capture area radius. Models at these spatial scales are equally reliable according to Akaike criteria (Δ_I < 2). No effects for capture area spiral density were found (all $F_{1,152}$-values < 3.43, P>0.05).

Accordingly, similar negative additive effects of the amount of surrounding BVH were observed for capture thread length (controlled for body size; Fig. 2). These effects appeared only significant for the proportion of BVH within 100 and 250 m around each target web, and nearly significant within 25 and 50 m (Table 2). AIC_c-values were not sufficiently different to distinguish between effects at 25-250m. The model was less reliable (Δ_I > 2; P>0.3) at the spatial scale of 500 meter. No effects for the proportion of BVH at any of the considered scales were found for height of the web, distance to the nearest vegetation and web inclination ($F_{1,152}$ ranges [0.02-2.11], all P>0.05). Negative effects on web asymmetry were pronounced, though only at a radius of 250 meters (Fig. 3; Table 2). According to AIC_c-values, however, alternative models remain possible, despite non-significant contributions.

No landscape-scales affected hub diameter (all $F_{1,150}$<1.49; P>0.05), but negative effects on hub spiral density were found for the proportion of BVH at a radius of 250 and 500 meters (Table 2). Effects at both spatial scales were equally reliable ($\Delta_I < 2$)

In conclusion, web design properties were negatively affected by the proportion of biologically valuable habitat at different spatial scales, but with overall convergence at the spatial scale of 250 meters (Table 2). Increased overall investments in capture thread length, especially within the lower web sector and in the central hub are consequently prevalent when the proportion of natural habitat decreases at larger spatial scales.

Body size and fecundity

No effects of landscape properties were found on body size ($F_{1,152}$ ranges [0.02-4.19], all *P>0.05).* Relative investments (i.e. controlled for body size) in total number of eggs and reproductive output were positively correlated with investment in capture thread length (r_{31}=0.406; P=0.018 and r_{31}=0.357; P=0.036; Fig. 4), but not with egg size (r_{31}=0.234; P>0.05). Despite this positive relationship, the proportion of BVH within 250 and 500 m scales positively affected reproductive output (corrected for capture thread length and body size; Table 2).

Discussion

The common orb web spider *A. diadematus* adapted its web building strategy to landscape simplification. The availability of potential larger prey also decreases with decreasing availability of biological valuable habitat. The observed functional response in web building is suggested to be adaptive (i.e. beneficial; Gothard & Nylin 1995) towards lower prey availability because (i) foraging investment is increased due to increased silk production in the web capture area and (ii) foraging efficiency is increased due to increased web asymmetry. Subsequent negative effects on fecundity in relation to increased investment in produced silk were recorded. According to model selection criteria, behavioural responses were especially pronounced at median spatial scales.

Intraspecific variation in dispersal ability and subsequent dispersal limitation at different spatial scales is acknowledged to generate biodiversity loss when agricultural intensification manifests at large spatial scales. Generalist predators like orb web spiders are highly mobile in the early juvenile life phases through aerial dispersal, but largely immobile when adult (Foelix 1982). These organisms possess pest-controlling services in crop-dominated landscapes through direct consumption of pest species and by inducing high levels of wasteful killing of non-food, often smaller, pest species like aphids within webs (Sunderland et al. 1999). For orb web spiders in particular, depletion of prey (especially essential prey like larger Diptera; Venner & Casas 2005, Ludy 2007) are yet empirically documented to induce functional changes in web building behaviour, with increased investments in capture area or foraging efficiency under laboratory conditions (Vollrath et al., 1997). Our results therefore suggest prey deprivation as the underlying mechanisms. However, because the potential spider prey spectrum and quantity does not necessarily reflect the actual prey of the spider (Ludy 2007) alternative explanations (e.g. changes in prey quality; Sigsgaard et al. 2001) cannot be excluded.

For *A. diadematus*, we found evidence of increased investment in web-building in intensively used agricultural landscapes. Fitness costs suggest that increased investments in silk thread production (Venner & Casas 2005) are not fully compensated, despite the fact that orb webs are recycled on a daily basis (e.g. Sherman 1994). Possibly non-recyclable energetic investments in silk web production and higher energetic losses under web damage cause these patterns, but causes related to changes in prey spectrum and its nutritional quality (Sigsgaard et al. 2001) can again not be excluded. Because fitness consequences are not expressed through changes in clutch or egg size but in total reproductive output within a single panmictic population, environmentally-cued adaptive plasticity is considered to be prevalent. Although this flexibility does not necessarily imply any adaptive functionality, observed shifts towards increased foraging investment (silk length thread) and efficiency (web asymmetry) do indicate beneficial modifications of the species' behaviour. Only for increased hub spiral density, adaptive underlying mechanisms are uncertain. Although no empirical evidence is available, increased thread density of the spider's resting place, may provide increased protection against predators due to reduced visibility, as is the case for silk decorations (Herberstein et al. 2000). Mechanistic modifications related to increased lower web areas provide, however, a valuable alternative explanation (Heiling & Herberstein 2000).

Because shifts in web-building and fitness properties converge in response to the availability of biologically valuable habitat (or inversely to the presence of intensively used arable habitats) at the spatial scale of 250 meter, and because prey limitation appears to be strongest at this scale, we propose that environmental properties at intermediate spatial scales, rather than local conditions affect the species' life history, behaviour and condition. This study subsequently generates new insights that not solely numerical responses of arthropods (e.g. Tscharntke et al. 2005), but also behaviour of species is affected by the spatial structure of the agricultural landscape. The correlative nature of our study, however, requires some precaution with respect to interpretation of the observed patterns since other environmental factors like wind velocity, aerial humidity and temperature may induce plastic responses in web-building as well (Vollrath et al. 1997). Because we collected data on web-building for spiders experiencing both natural and intensively used landscapes on the same day, we were able to control for these potential confounding effects. No relationships with meteorological conditions were found, and neither did we record any differences in microsite selection (height of the web location, orientation and distance to the vegetation) in relation to landscape properties. Correlated responses of microclimate to landscape properties do consequently not attribute to the observed variation. Only a relationship with ambient temperature was detected. However, this is mainly due to collinearity with the species' phenology, and patterns with respect to landscape structure became clear after correction for the latter. This covariation consequently confirms reduced investment in web-building in relation to the species reproductive state, and timing of eggsac production (Sherman 1994, Heiling & Herberstein 2000)

In conclusion, changes in the complexity of agricultural landscapes not solely induce shifts in abundances and diversity of arthropods (Kremen et al. 2007), they also influence individual behaviour of predators. Because these changes are here recorded for web building, our results suggest that landscape composition may also affect the functionality of immobile species that are potentially important for pest-controlling services.

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Table 1: *P*-values generated by null model randomization tests (Gotelli and Entsminger 2006) for slope, right triangle shape (concentration of data-points within the shape) and upper-left boundary (are data points significantly sparse in the indicated corner of the bivariate space).

Radius	**slope**	**shape**	**boundary**
25 m	0.001	0.056	0.063
50 m	0.000	0.007	0.067
100 m	0.000	0.001	0.117
250 m	**0.000**	**0.003**	**0.012**
500 m	0.201	0.095	0.252

Table 2: Slope estimates, F-statistics and P-values for general(ized) linear model analyses of the radius and number (N° of spiral threads in the lower web section, capture thread length, web asymmetry, hub spiral thread density and reproductive output (residual values of total number of eggs x average egg size, controlled for body size) in relation to the proportion of Biologically Valuable Habitat in five predefined radii around each focal *A. diadematus*-web. Grey shading indicates alternative reliable models according to Akaike-criteria (Δ_I-values ≤ 2).

	Radius Capture Area Under			***N Capture Area Under***			***Capture thread length***		
Radius	**Slope (SE)**	**$F_{1,150}$**	**P**	**Slope (SE)**	**$F_{1,152}$**	**P**	**Slope (SE)**	**$F_{1,150}$**	**P**
25	**-0.015 (0.009)**	**4.71**	**0.031**	-0.0006 (0.0004)	2.72	0.092	**-3.56 (1.88)**	**3.57**	**0.061**
50	-0.015 (0.008)	3.58	0.060	-0.0008 (0.0004)	3.86	0.052	**-3.89 (2.16)**	**3.24**	**0.074**
100	-0.018 (0.010)	3.44	0.065	**-0.0014 (0.0005)**	**7.35**	**0.007**	**-5.51 (2.58)**	**4.53**	**0.034**
250	**-0.029 (0.013)**	**5.01**	**0.026**	**-0.0017 (0.0006)**	**6.91**	**0.009**	**-6.69 (3.44)**	**3.97**	**0.048**
500	-0.027 (0.019)	2.02	0.157	-0.0014 (0.0009)	2.23	0.137	-4.44 (5.07)	0.77	0.387
Radius	***Web asymmetry***			***Hub spiral density***			***Reproductive output***		
Slope	**(SE)**	**$F_{1,151}$**	**P**	**Slope (SE)**	**$F_{1,150}$**	**P**	**Slope (SE)**	**$F_{1,30}$**	**P**
25	-0.011 (0.006)	3.09	0.081	-0.001 (0.000)	1.64	0.22	0.48 (0.31)	2.29	0.141
50	-0.012 (0.007)	2.74	0.100	-0.001 (0.000)	0.94	0.333	0.63 (0.36)	3.12	0.087
100	-0.015 (0.008)	2.93	0.089	-0.001 (0.000)	3.41	0.062	0.85 (0.43)	3.83	0.059
250	**-0.026 (0.011)**	**5.16**	**0.024**	**-0.002 (0.000)**	**5.78**	**0.017**	**1.74 (0.63)**	**7.67**	**0.009**
500	**-0.027 (0.017)**	**2.58**	**0.110**	**-0.002 (0.000)**	**4.73**	**0.031**	**2.52 (0.75)**	**11.20**	**0.002**

Figure Legends:

Fig. 1: Distribution of prey size within pan traps in relation to the proportion of biologically valuable habitat in a radius of 250 meters. Null-model parameters by which randomized data distributions were tested (Gotelli and Entsminger 2001) are indicated: slope; right triangle shape (concentration of data-points within the shape) and upper-left boundary (are data points significantly sparse in the indicated corner of the bivariate space?).

Fig. 2: Estimated investment in capture thread length for web building in relation to the proportion Biologically Valuable Habitat and spider size (CT-width). Because the represented model is corrected for date-effects, observed data cannot be plotted.

Fig. 3: Observed (dots) and estimated (plain) web asymmetry in relation to the proportion Biologically Valuable Habitat at different spatial scales and web radius.

Fig. 4: Relationship between fecundity (reproductive output and number of eggs) and CTL-length. Due to covariance with body size, residual values are represented.

Fig 1

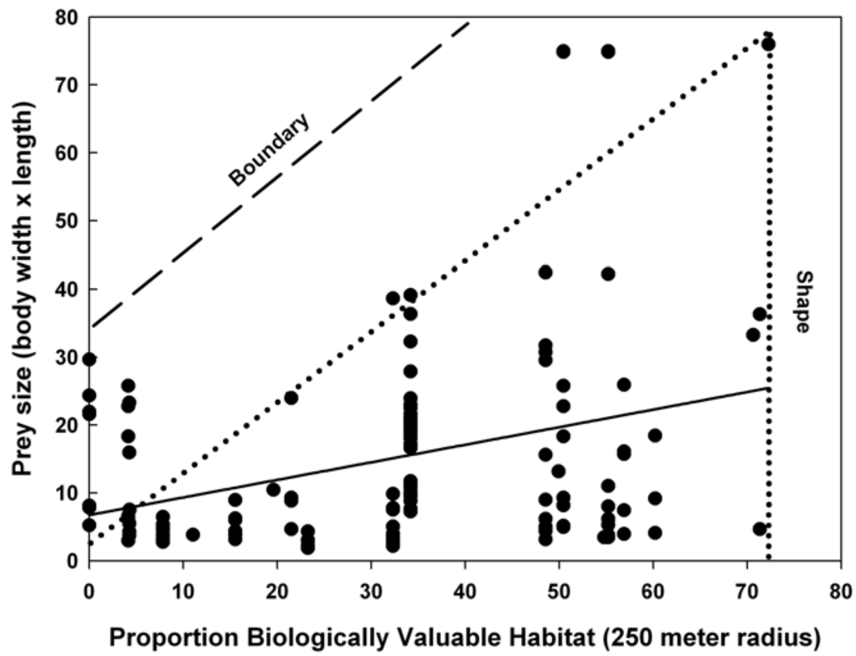

Boundary
Shape
Prey size (body width x length)
0
10
20
30
40
50
60
70
80
Proportion Biologically Valuable Habitat (250 meter radius)

Fig. 2

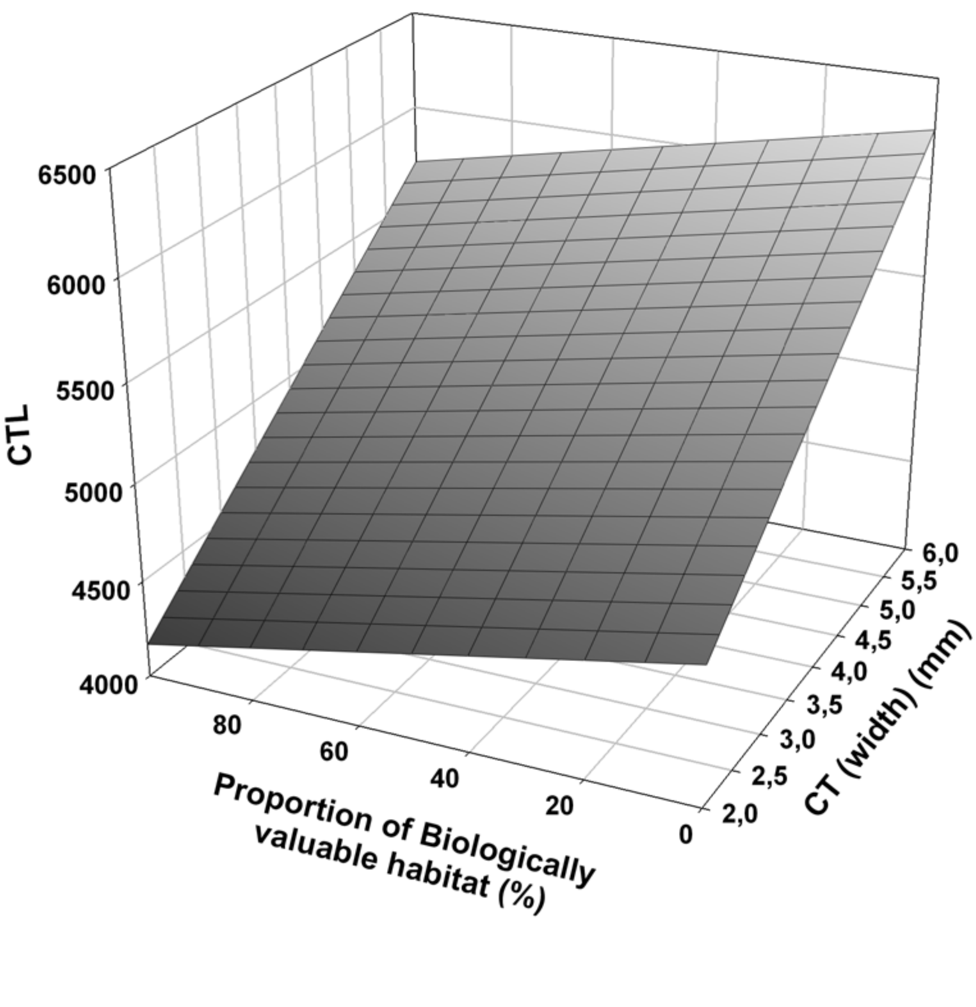

CTL
6500
6000
5500
5000
4500
4000
80
60
40
20
0
Proportion of Biologically valuable habitat (%)
6,0
5,5
5,0
4,5
4,0
3,5
3,0
2,5
2,0
CT (width) (mm)

Fig. 3

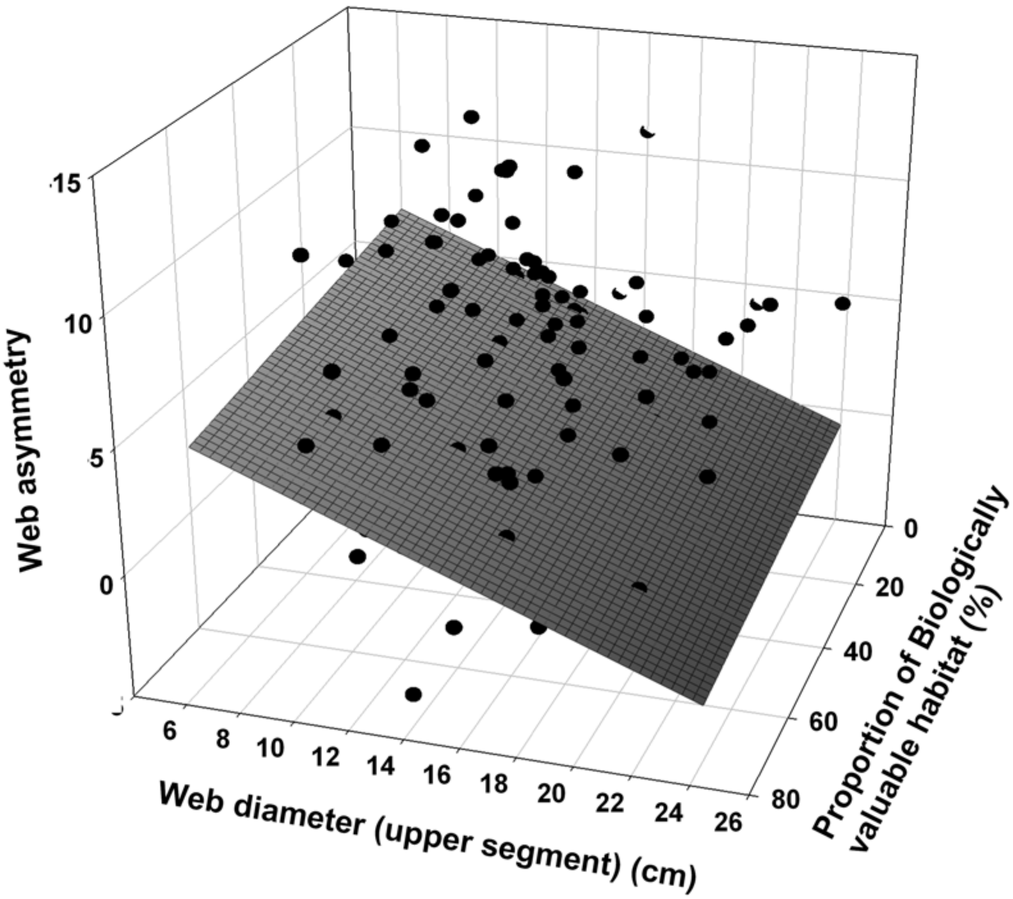
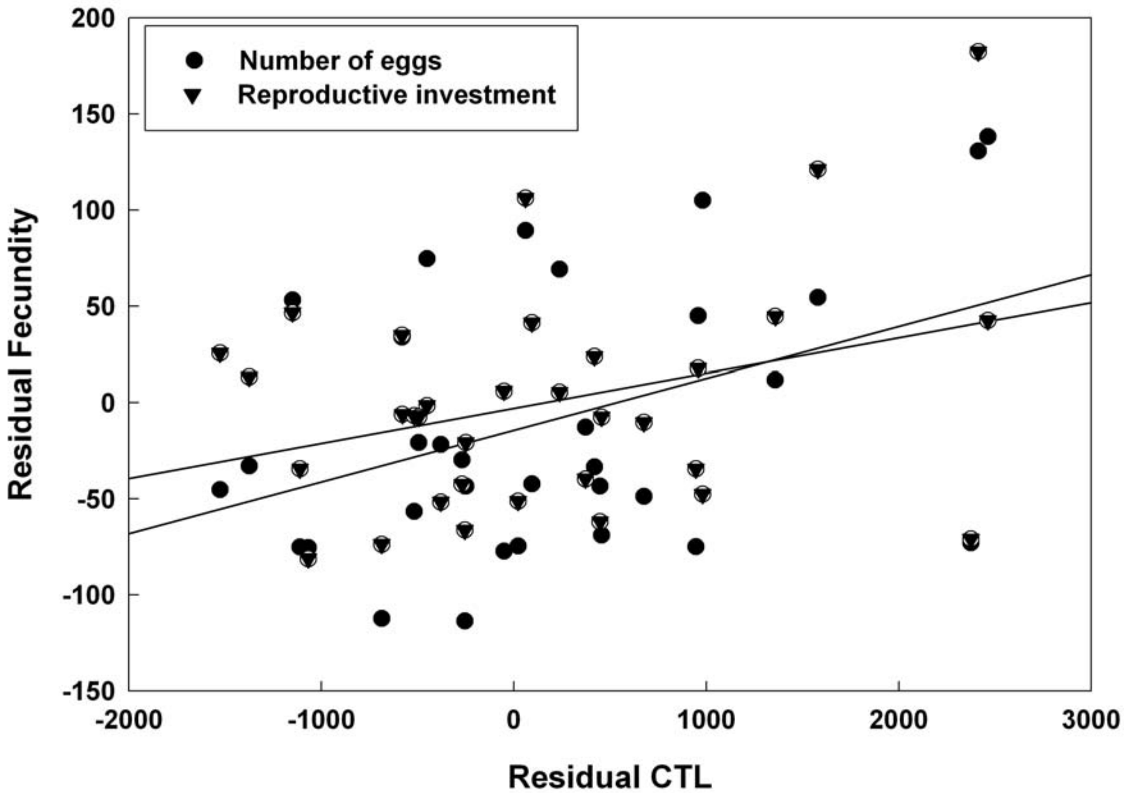

Web asymmetry
15
10
5
0
6
8
10
12
14
16
18
20
22
24
26
Web diameter (upper segment) (cm)
0
20
40
60
80
Proportion of Biologically valuable habitat (%)

Fig. 4


Number of eggs
Reproductive investment
Residual Fecundity
Residual CTL
200
150
100
50
0
-50
-100
-150
-2000
-1000
0
1000
2000
3000