

Colour variation and crypsis in relation to habitat selection in the males of the crab spider *Xysticus sabulosus* (Hahn, 1832) (Araneae : Thomisidae)

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ABSTRACT. The crab spider *Xysticus sabulosus* (HAHN, 1832) is a sit-and-wait predator, typical for sandy habitats in Europe and Flanders. In the Flemish coastal dunes, the species is very abundant in grey and blond dunes. Its abdominal and cephalothorical colour varies from almost completely white to dark brown. During autumn 2001, we investigated crypsis as a function of the occupied micro- and macrohabitat. Our results indicate that (1) Colouration differs between the populations. The species is darker in a grey dune completely covered with dried (brown) mosses and in a humid dune slack covered with algae, than in populations from a sea inlet and from a blond dune. The colouration of a population from a grey dune with mosses, lichens and bare sand is intermediate. (2) Individual cephalothoracal colouration is, in contrast to abdominal colouration, related to microhabitat selection : individuals with darker cephalothoraxes occupy hunting sites with a higher coverage of mosses, while those with a pale one are found in microhabitats with a high amount of nude sand. The observed spider colour-environment covariation between populations is probably the result of natural selection or colour alteration during the juvenile development. Further research on these possible underlying mechanisms remains, however, necessary.

KEY WORDS : Coastal dunes, microhabitat, foraging, predation.

INTRODUCTION

Colour variation within the same species is a characteristic of many invertebrates. Especially in molluscs, butterflies, grasshoppers and spiders, this phenomenon has been studied within the framework of apostatic selection (ALLEN, 1988, ENDLER 1988, 1990), sexual selection (HAUSMANN et al., 2003), thermoregulation (WHITMAN, 1988; FOSMAN, 2000) and crypsis (ENDLER, 1981, 1984, 1988).

According to ENDLER (1991), colour pattern is cryptic if it resembles a random sample of the visual background as received by its predator at the time and place at which the prey is most vulnerable to predation. In the case of predators, crypsis should, hence, also occur in the situation where predation efficiency strongly depends on the visual perception of prey. This colour matching in relation to the substrate can result from a rapid, physiological response or from a slow, morphological adaptation (MORETEAU, 1975), more specific from ontogenetic colour adaptation (GRAF & NENTWIG, 2001), sometimes induced by the diet (SCHMALHOFER, 2000) or by natural selection in the case of colour pattern inheritance (ENDLER, 1983). There is a general consensus that crypsis increases the species' survival chances by reducing its own predation rate (i.g. STIMSON, & BERGMAN, 1990; ENDLER, 1991; GÖTMARK, 1994; KINGSOLVER, 1996; FORSMAN & APPELQVIST, 1999). Documented studies on benefits resulting from an increased foraging success are, however, rare. In the case of the latter, foraging and reproduc-

tive success are highest if the animal colour pattern matches the colour of the substrate (FRITZ & MORSE, 1985). In a web-building spider, ontogenetic colouration changes were related to changes in web-structure, presumably as an adaptation to reduce intraspecific competition (GRAF & NENTWIG, 2001).

In spatial heterogeneous environments, colour polymorphism induces the use of different microhabitats, as demonstrated for grasshoppers in mosaic grasslands (CALVER & BRADLEY, 1991), for juvenile crab spiders and flower inflorescence selection (SCHMALHOFER, 2000), and for marine isopods in macro-algal vegetation (MERILAITA & JORMALAINEN, 1997).

Our study animal, the crab spider *Xysticus sabulosus* (HAHN, 1832) is a ground-active sit-and-wait predator, typical for sandy habitats in Europe and Flanders (MAELFAIT et al., 1998; ROBERTS, 1995). In the Flemish coastal dunes the species is abundant in grey and blond dunes (BONTE et al., 2002). Males are active in autumn, while females are characterised by an activity peak in autumn and spring. Its abdominal and cephalothoracal colouration varies from almost completely white to dark brown, and is constant during the adult phase (BONTE, pers. obs.). Ontogenetic changes in colouration during juvenile development have not yet been investigated.

In this contribution we investigate how spider colouration varies between several populations and if colouration is adapted to the habitat (i.e. substrate). We hypothesise that in sandy habitats (Marram dunes, sea inlet), *X. sabu-*

losus should be coloured paler than in grey dunes with a heterogeneous moss, lichen and sand coverage, and that colouration should be darkest in dune vegetation dominated by mosses, which colour brown during dry or dark green during wet weather conditions. Additionally, we investigate if microhabitat selection in the heterogeneous grey dune is induced by the spider colouration. By comparing relations between the abdominal and cephalothoracal colouration and the patterns of microhabitat selection, potential crypsis-inducing patterns are investigated. We especially question whether crypsis is the result of a predator-avoiding strategy or if optimal foraging induces it.

MATERIAL AND METHODS

Study area and sampling methodology

Five populations were sampled in the coastal dune complex of De Panne, Bray-Dunes and Ghyvelde, at the French-Belgian Border. The sampled habitats differed in soil- and vegetation structure, ranging from completely nude sandy habitats (Marram dunes, sea inlet), through moss- and lichen grey dune with a substantial amount of bare sand, to completely moss (*Campylopus intraflexus*)-dominated dunes and a dune slack covered with a dark algae layer. This habitat variation corresponds with the colouration of the substrate: pale white to grey coloured in the case of the first two habitats dominated by bare sand, intermediately (grey-brown) coloured in the case of the grey dune with *Cladonia* lichens and dried mosses (*Tortula ruralis* and *Hypnum cupressiforme*) and dark grey to black coloured in the case of the *Campylopus* vegetation and the dune slack.

In each habitat we sampled spiders during September 2001, with five pitfall traps (diameter 9 cm, filled with a formalin-soap solution). A total of 136 males were collected in the five sampled habitats: 22 in the Marram dune, 21 in the Sea inlet, 24 in the dune slack, 38 in the lichen-grey dune and 31 in the *Campylopus*-dominated grey dune.

In a second experiment, 100 small pitfalls (diameters 3 cm, same fixative, distance between traps: 30 cm) were placed in a grid in one habitat, the varied grey dune. Around each trap, the coverage of bare sand, lichens and dried mosses was estimated. The latter set-up was used to study the possible effect of colouration on the microhabitat selection. Here, 174 individuals were sampled.

Colour determination

Dorsal digital photographs of each specimen were taken with a high quality digital camera (2800000 pixels), placed on a binocular microscope with magnification 10x, under standardized lighting conditions. The mean pixel value in the Red-Green-Blue (RGB channels) spectrum was determined by using the software Corel Photo-Paint, version 7.373. The brightness of each pixel was determined and averaged for, respectively, the abdominal and cephalothoracal parts. Pixel values range from 0 (black) to 255 (white). Colouration of the macro- and microhabitat was determined in the same way from, respectively, digital aerial photographs (taken from an aeroplane, flying 50 meters above the habitats) and digital photographs

taken from 1-meter height above the surface. Photographs were taken on the same day within a short time span, so light conditions were similar. Macro-habitat substrate colouration values were (means \pm SD) 203.11 \pm 38.57 for the Marram dune, 217.50 \pm 13.38 for the sea-inlet, 103.45 \pm 15.70 for the dune slack, 188.15 \pm 28.27 for the lichen-grey dune and 95.38 \pm 4.66 for the *Campylopus*-dominated grey dune. Since both habitat and spider colouration vary within the range white-grey-brown-black, mean values of the RGB channels are a good quantification of the substrate and animal colour.

Data analysis

General results. The relationship between cephalothoracal and abdominal colouration was investigated by Pearson correlation since all spider colouration data were normally distributed. Principal component analysis was applied for the detection of covariances between the estimated coverage of mosses, lichens and bare sand. The relationship between component scores (one significant axis; see results) and microhabitat colour were again analysed with Pearson correlation.

Colour variation between the sampled populations. Only colouration data from males were used, since only eleven females were caught during the sampling period. Since variances were unequal, a Kruskal-Wallis ANOVA was applied for the analysis of colour variation between the five populations (habitats). Mann-Whitney U-tests, Bonferroni-corrected for multiple testing (P-level of 0.0041), were used as post-hoc tests for the determination of colour differences between the specific habitats.

Colour variation and microhabitat-selection. Spearman rank tests were used for the analysis of microhabitat selection as a function of component scores, related to the coverage of bare sand (very pale substrate), lichens (grey substrate) and dried *Tortula* mosses (dark brown substrate). P-values were again Bonferroni-corrected (P<0.025).

Analyses were performed with Statistica 5.5 (Statsoft 2000).

RESULTS

General results

Colouration values of the cephalothorax ranged from 54.32–137.36, with a mean of 99.787; those from the abdomen ranged between 50.23–157.84, with a mean value of 91.66. Both values are significantly correlated ($r_{309}=0.102$; P<0.0001). The colouration was in general analogous for the cephalothorax and the abdomen, but slightly darker on the latter. Three examples of spiders with different colouration are given in Fig. 1.

The proportional coverage by *Tortula* mosses, *Cladonia* lichens and bare sand was related to one principal component. Component loadings (r_{99}) were -0.801 for moss, -0.668 for lichen and 0.999 for sand coverage. Component scores hence reflect the transition from moss to bare sand dominance and are correlated with the microhabitat colouration ($r_{35}=0.268$; P<0.001). The moss, lichen and sand coverage range gives thus a good reflection of the microhabitat colouration.



Fig. 1. – A light (left), intermediate (middle) and dark (right) coloured individual *Xysticus sabulosus*. Carapax colouration scores (mean \pm SD) : 136.44 ± 37.89 , 95.33 ± 35.13 and 60.38 ± 37.74 , respectively.

Colour variation between the sampled populations

The mean values of both the cephalothoracal and abdominal colouration, with 95% confidence intervals are visualised in Fig. 2. Results of the Kruskal-Wallis ANOVA revealed significant inter-population variation for the cephalothoracal (Kruskal-Wallis test : $H(4, N=136)=68.012$; $P<0.0001$) and the abdominal colouration (Kruskal-Wallis test : $H(4, N=136)=12.719$; $P=0.0127$). Bonferroni-corrected post-hoc Mann-Whitney U-tests only indicate significant differences in the abdominal colouration between the population from Marram dunes and the one from the *Campylopus*-dominated grey dune ($P=0.002$). Differences between populations (habitats) were more pronounced for the colouration of the cephalothorax : only the population from the Sea inlet did not differ from those from Marram dunes ($P>0.05$) or from the sandy, lichen-rich grey dune ($P=0.006$, NS after Bonferroni-correction).

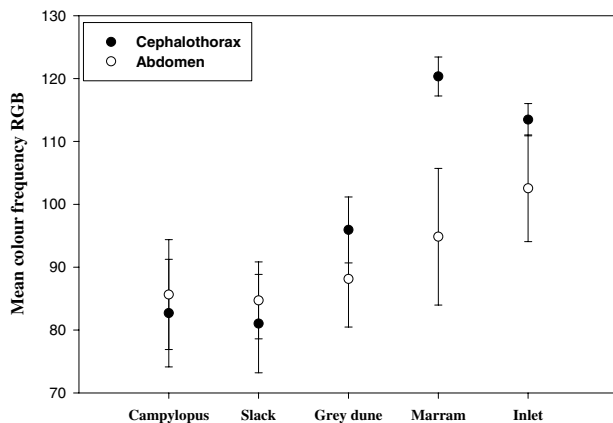


Fig. 2. – Variation in spider colouration between the five populations (mean values and 95% confidence intervals). Legend : *Inlet* : Sea inlet; *Marram* : Marram dune; *Grey dune* : heterogeneous moss-sand-dominated dune; *Slack* : pioneer dune slack; *Campylopus* : dark mosses-dominated grey dune.

Colour variation and microhabitat-selection

Correlation of the abdominal and cephalothoracal colour with the substrate principal components revealed significant results for both ($R_{abd,173}=0.159$; $P=0.036$; $R_{Ceph,173}=0.217$, $P=0.04$: Fig. 3). The relationship between abdominal colouration and the substrate component is, however, not significant after Bonferroni-correction.

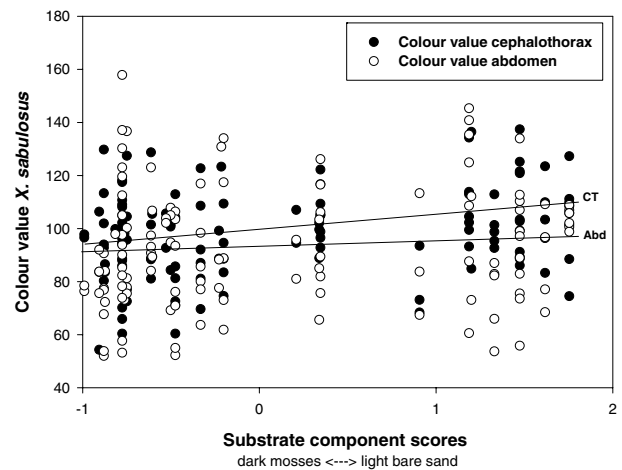


Fig. 3. – Relationship between substrate colouration (as revealed by substrate component scores) and spider colouration (cephalothorax and abdomen).

DISCUSSION

Body colouration of the crab spider *X. sabulosus* gradually varies between whitish and dark brown, with a high frequency of intermediate-coloured individuals. Cephalothoracal and abdominal colouration covary significantly, although pale individuals with dark abdomen and vice versa do occur. Crypsis was observed for both body parts between macrohabitats, but was only significant for the cephalothoracal colouration in the case of microhabitat selection.

Colouration of the cephalothorax and abdomen showed distinct differences between the sampled populations, although only for the first could significant differences be detected as a function of the habitat : spiders with a dark cephalothorax were significantly more abundant in the dune slacks and the moss dune dominated by *Campylopus intraflexus*. Intermediate-coloured spiders were found in the heterogeneous grey dune, while pale individuals occurred in the dune habitats, dominated by nude sand. Crypsis was, therefore, detected between spider and substrate colouration. Interdemic variation in colouration can result from natural selection (ENDLER, 1983) or from ontogenetical morphological adaptations (MORETEAU, 1975; GRAF & NENTWIG, 2001). Unfortunately, the possible underlying genetic mechanisms have not yet been studied in this species. Studies on colour variation in another crab spider indicate that morphological colour changes are induced by the diet (SCHMALHOFER, 2000)

and the substrate during juvenile development (HOLL, 1987). This mechanism for colouration changes during juvenile development in a related crab spider allows us to assume that natural selection during the juvenile development may be an explanation for the observed colour differentiation, although only during the early developmental stages, in which spider colouration is not yet adapted to the substrate.

In the adult phase, colouration is fixed (BONTE, pers. observ.), and in spatially heterogeneous environments is responsible for the observed related microhabitat selection. Selection of suitable microhabitats for crypsis may be induced by one or more of three possible mechanisms (which also underlie natural selection): avoiding predation, increasing foraging success (which is directly related to fitness) or optimal thermoregulation (ENDLER, 1991). The temperature on moss is only significantly higher than on bare sand during warm summer days. During colder days (the period in which our species is adult and active), temperatures do not differ between these locations (GHESQUIERE, pers. comm.). Crypsis will hence not result from thermoregulatory processes since substrate choice would not enable certain colour forms to heat up faster than others.

Avoidance of predation is the second possible reason for the observed crypsis. This implies that predators should be visually orientated. Crab spiders are however sit-and-wait predators with a low cursorial activity and are slightly conspicuous for potential predators. Although scarcely documented, Pompililidae and Ichneumonidae wasps (FITTON et al., 1987), which detect prey possibly by olfactory stimuli (as detected for the parasitoid *Gelis festinans*, VAN BAARLEN et al., 1996) can be regarded as their most important predators in coastal dune ecosystems (NOORDAM, 1998). Since abdominal crypsis is less pronounced, avoidance of predation is probably of minor importance for the elucidation of the observed crypsis. By contrast, both the passive hunting strategy and the highly significant covariation between substrate and cephalothorax colouration indicate that crypsis is related to optimal foraging. Since prey have to approach the crab spider as closely as possible, an optimally-camouflaged cephalothorax should be beneficial for prey capturing. In heterogeneous environments, such as the investigated grey dune with lichens, mosses and bare sand, individuals are, on average, intermediately coloured, but considerable intraspecific variation occurs. This variation results in differential microhabitat use, dependant of the colouration. Possibly, this microhabitat selection results from previous experience or from certain inherited behavioural responses, in which the spider is able to link its own body colouration to the selection of suitable hunting sites.

Crypsis is thus obvious in populations of the crab spider *X. sabulosus* in the Flemish coastal dunes and linked to microhabitat selection in a spatially-heterogeneous grey dune. The underlying evolutionary mechanisms for the observed interdem variation (the result of natural selection or from ontogenetic changes?) and the observed relationship to microhabitat selection (inherited behavioural response or the result of earlier experience?) remain unclear and need to be elicited in future research.

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