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Industrial albinism in females of a webspider, *Neottiura bimaculata* (L.) (Araneae: Theridiidae) – insights from a long-term field study, 1981–2006

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Abstract. The density and sex-specific colour polymorphism in the webspider *Neottiura bimaculata* (L.) were studied in three natural sites in 1983 (used as reference sites) and a heavily polluted site near a phosphate fertilizer factory in Thuringia, Germany, during the emission phase (1981–1983) and two regeneration phases (1994–1996, 2005–2006). About 2.220 individuals collected by quantitative sweep-net sampling were classified into inadults, subadult and adult males and females, and four colour morphs ranging from brown to white. During the emission phase and 4–6 years after closing of the plant the spider density was high and the colour morph spectrum in females distinctly shifted towards white individuals. For this phenomenon we introduce the term 'industrial albinism'. In males, during the emission phase a shift to brown-white was registered. Already after 15 years of regeneration the density decreased to a level in unpolluted meadows and the colour morph spectra in both sexes slowly approximated to those of natural reference populations. The probable selective nature of this observed colour polymorphism is discussed.

Colour polymorphism, density, industrial albinism, pollution, sex, Theridiidae

INTRODUCTION

Over recent decades, pollution effects on the colours and patterns among individuals of a wide range of taxa have been observed and studied, prominent insect examples including moths and ladybird beetles, both of which show an increase in melanistic forms with increasing industrial emissions (summarized by Kettlewell 1973 and Majerus 1998). In contrast to this well-known industrial melanism, pollution-related albinistic effects are rare and seemingly affect few individuals (rather than the majority of a population), as mainly reported in small mammals and especially birds, where the causes for albinism are many, and often environmentally influenced and linked with diet, injury, disease, shock and age (Sage 1962). The most recent example is the barn swallow (*Hirundo rustica*) from Chernobyl/Ukraine where, years after the disastrous nuclear accident in 1986, several abnormalities were detected, including partial albinistic plumage in about 14% of thousands of individuals studied (Møller et al. 2007).

In webspiders, all forms of colour variation related to one sex or both occur inter- and intraspecifically, ranging from environmentally-induced, reversible changes based on genetically fixed reaction norms up to completely genetically controlled individual variation, with combinations of both in between (reviewed by Oxford & Gillespie 1998). For example, in the tropical orb-weaving *Eriophora fuliginea* (C. L. Koch) (Araneidae) considerable colour changes in the course of ontogenesis occur with a change of behaviour as well (Graf & Nentwig 2001). Some transition was detected in two common European orb-weaving araneids. In *Araneus diadematus* Clerck the opisthosomal colouration depends on the lightness of the surroundings, which is visible for the spider. In contrast, *A. marmoreus* Clerck has three genetically-based colour morphs, modified by environmental cues, a phenomenon, interpreted as an additional chance to adapt to specific surroundings (Blanke & Merklinger 1982). In the sheetweb spider, *Pityohyphantes phrygianus* (C. L. Koch) (Linyphiidae), three main phenotypic colouration classes can be distinguished, despite a continuous variation in dark colouration, explained as a polygenic system (Gunnarson 1987). Within the Theridiidae, in the candy-stripe spider, *Enoplognatha ovata* (Clerck), three main colour morphs exist, but despite a plethora of studies including population genetics since the 1930th their selection significance (a thermal selection is argued) is yet to be fully understood (Oxford & Gunnarson 2006). In the endemic Hawaiian happy-face spider, *Theridion grallador* (Simon), populations exhibit an extreme colour polymorphism, and morph frequencies may be maintained by some form of apostatic balancing selection, perhaps mediated by bird predators (Gillespie & Oxford 1998, Oxford & Gillespie 1996, 2001).

In the present study we describe the example of the two-spotted theridiid, *Neottiura bimaculata* (L.), with a predominating frequency of albinistic females found in a highly polluted site near a phosphate fertilizer factory in mid-Germany. Here from 1980–2006, intensive investigations were performed to examine the effects of dust emissions on soil, vegetation and numerous arthropod taxa, both during the period of aerial pollution and following cessation of the plant in 1990 during the regeneration period (e.g. Heinrich et al. 2001, Perner et al. 2003). In the webspider *N. bimaculata* this gave rise to comparative studies on colour polymorphism in natural, unpolluted areas as well as to a long-term monitoring over three periods during fertilizer production (emission phase) and after closing of the plant (two succesive regeneration phases).

STUDY SITES

The study was performed in the Saale-river valley around Jena/Thuringia, Germany (50° 56' N, 11° 35' E). On the S/SW--exposed slopes (10–15° inclination) species-rich semi-dry grassland (Onobrychido-Brometum) has developed, a habitat type suitable for *N. bimaculata* (Malt & Schäller 1998). As a reference unmanaged plots were sampled at three natural sites (Kernberge, Sonnenberge, Leutratal – all about 250–300 m a. s. l.) with a *Bromus*-dominated vegetation. From April till October 1983, *N. bimaculata* was recorded on these three sites on 24 days (Krieger, unpubl.).

As a polluted site the vicinity of a former cement plant (up to 1957) and later phosphate fertilizer factory (from 1969/70 to 1990) near Dornburg-Steudnitz (51° 00' 46" N, 11° 40' 51" E; 13 km N of Jena) was used. Here on an E-exposed slope, a transect of differently polluted plots was established from the valley floor to the upper slope (140–210 m a. s. l.) during the period 1980–2003. In mid-slope (170–180 m a. s. l., 2–10° inclination) *N. bimaculata* was especially common. In this region, most of the shrubs had died off whilst the green plants were covered with a grey dust layer, only briefly washed down by rain. In 1980/81, at the beginning of the study, the grassland at the heavily polluted plots had been affected for a decade by the emissions of the nearby fertilizer factory, mostly apatite, sand and soda. Since the early 1970s and during intensive production (100,000 t/year), the monthly input of dust near the factory amounted to 35 g/m² (Heinrich 1984). In April 1981 the mean amount of dust on leaves of *Agropyron* reached around 8 g/m² (Köhler 1984). Due to the long dust input, the K, Na and P content of the soil was very high (26–121 g/kg) and maintained over a long period. These strong alkaline emissions have led to considerable changes in the soil properties (at pH 8.0 to >9.0) of the surrounding area. Although production was stopped in 1990, pollution levels in the surface soil layers thereafter remained high, and compared to natural meadows, concentrations of the aforementioned elements were significantly higher (Metzner et al. 1997, Langer & Günther 2001).

MATERIAL AND METHODS

Study species

The two-spotted theridiid, *Neottiura bimaculata* (Linnaeus, 1767), is holarctic in distribution and common throughout Germany up to the subalpine zone. It lives in a variety of habitats, ranging from humid and dry grassland and herbage formations to apple orchards and sunflower fields (Wiehle 1937; Locket & Millidge 1975; Heimer & Nentwig 1991; Pekár 1999, 2005). With a body length of 3.5 mm (♀) and 3.0 mm (♂) it belongs to the smaller wed-spider species (Wiehle 1937). In the study area, the web is preferably built in the middle and upper herb layer of semi-dry grassland, where the spider can be readily swept. *N. bimaculata* is found throughout the season as a euryoecic meadow spider (Malt & Schäller 1998). Eight instars have been distinguished: five inadult (juvenile), two subadult and the adult (Pekár 1999). At the study

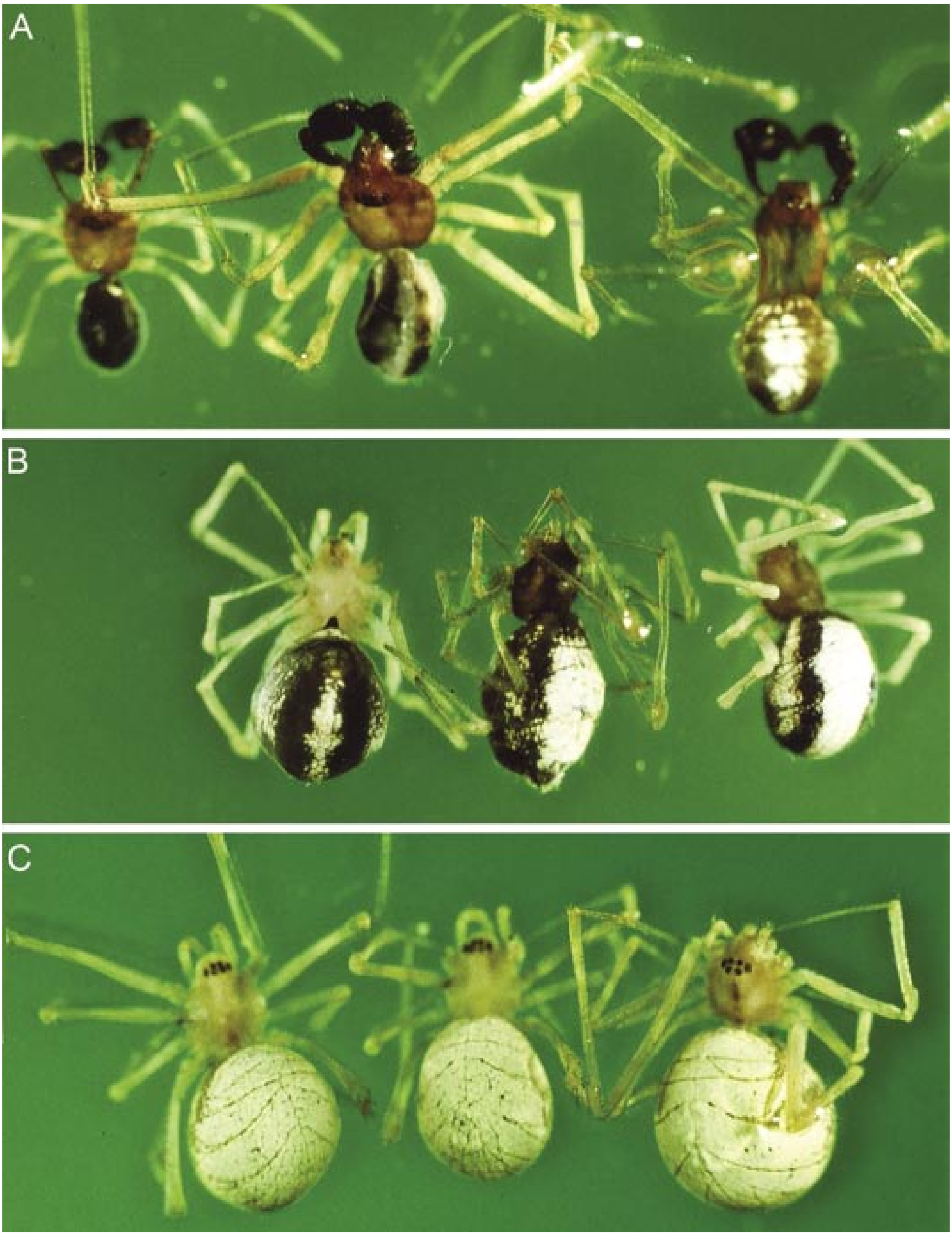

Fig. 1. Colour morphs of *Neottiura bimaculata*. A – adult males (brown, brown-white). B – adult females (brown-white, white-brown). C – adult females (white). Body length 3–3.5 mm.

sites, the young spiders began to hatch in August and reached an inadult maximum in October. These inadults hibernate and develop in the following April/May into subadults and mainly in June/July to adult males and females (Fig. 1a–c), which die after egg-laying up to the beginning of August. In our studies, the populations were so spread that in every month from April–October inadults occured. In May–June, subadults and in June, adult spiders of both sexes dominated. Whereas adult males peaked only during a short time in June (with few individuals in May and July), females declined in numbers up to October.

Sampling method
On dry and sunny days standardized sweep-net samples were taken according to Witsack (1975), with 10x10 double sweeps (d.s.) per day and plot, out of two natural sites with 13x10 d.s./day. The swept material (10 d.s.) was put into plastic bags, killed with ethylacetate and stored in a refrigerator at 5–7°C for 1–2 days. Thereafter, samples were sorted into taxa and preserved in 70% ethanol, in which the colour morphs of *N. bimaculata* retain their pigmentation over long periods. On the three natural sites in 1983 a total of 154 *N. bimaculata* was swept on 24 days, as taken to represent reference populations (see Table 1), whilst on the polluted site over 8 years (1981–1983, 1994–1996, 2005–2006) a total of 2.072 *N. bimaculata* was swept on 55 days (see Table 2), comprising 2.226 individuals (1.210 inadults, 265 subadult and adult males, 751 subadult and adult females) included in the present analysis.

Instar, sex and colour type
The sex-specific variability in the body colour of *N. bimaculata* is well-known, with males presumably of dark-brown to brown-white, and females mainly ranging from brown-white to completely white (Simon 1881, Wiehle 1937, Locket & Millidge 1975, Roberts 1985). The alcohol preserved *N. bimaculata* were classified into three instar groups (inadult, subadult and adult) and according to sex (in subadults and adults). We use the term ‘inadult’ instead of the fewer precise ‘juvenile’ or ‘immature’, and because of the specific spider ontogenesis. The individual colour morph according to the dark-light-distribution can already be distinguished in inadults from the 3rd instar onwards and the pattern does not differ considerably from stage to stage; only in the earliest inadult instars 1 and 2 are individuals not fully pigmented (Pekár 1999). We use the term ‘colour morph’ despite some transitions in between, focussing on the dorsal surface of the opisthosoma (O) and prosoma (P), where four colour morphs were distinguished (Fig. 1a–c, Fig. 2a–h).

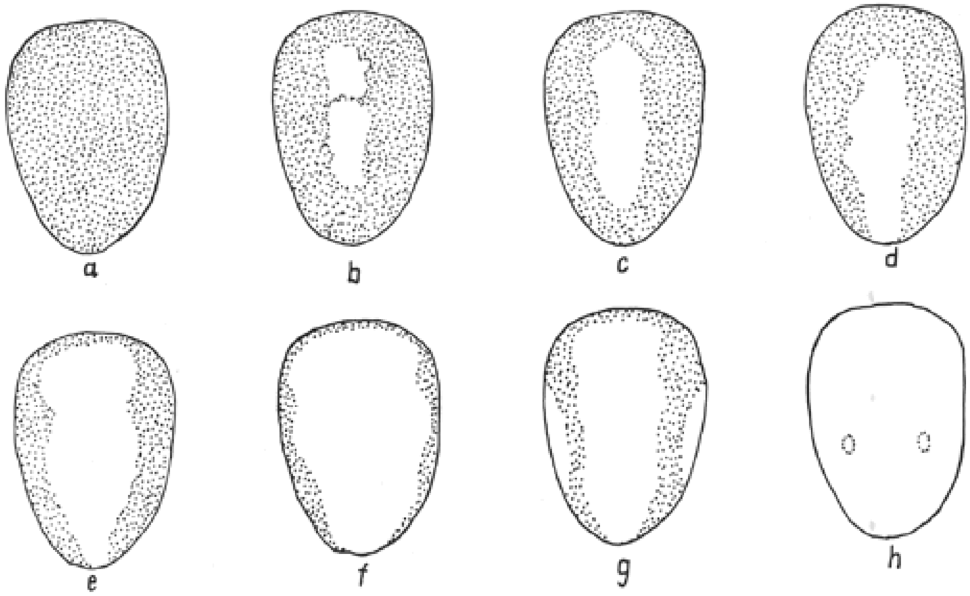

Fig. 2. Colour morphs of *Neottiura bimaculata* showing the brown-white distribution on the dorsal opisthosoma: brown (a), brown-white (b–d), white-brown (e–g), white (h). Drawing: C. Krieger.

Table 1. Frequency of colour morphs in *Neottiura bimaculata* around Jena (Germany), pooled for three natural semi-dry grassland sites. Quantitative sweep-net samples, April–October 1983

stage / sex	n	colour morph			
		brown	brown-white	white-brown	white
inadult (♂, ♀)	81	0.20	0.60	0.20	–
♂ (subadult, adult)	23	0.96	0.04	–	–
♀ (subadult, adult)	50	0.04	0.70	0.24	0.02

- Brown (b): O brownish to dark brown, at most central with a lighter oak-leaf drawing (which can more or less disappear) and a dark line pattern. P dark (than the dark central line disappears) to light brown. This morph is mainly male (Fig. 1a), seldom female (Fig. 2a).
- Brown-white (bw): O predominantly dark-brown, the light long-stretched central patch is (much) less than half of the surface area, a broad brown band laterally and partly dorsally. P darker to lighter brown. Occurs in both sexes (Fig. 1a, b; Fig. 2b–d).
- White-brown (wb): O predominantly light, the cream-coloured area occupies more than half of the upper surface, the dark-brown lateral band is narrow. P lighter to darker brown (than central line invisible). Occurs mainly in the female (Fig. 1 b, Fig. 2e–g), seldom in male.
- White (w): O cream-white with a fine dorsal furrow and 3–4 laterally branching furrows, in between net-like structured. P yellowish, amber-coloured or light-brown, with striking black eyes, and a dark central line (also partly or lacking). Occurs only in the female (Fig. 1c, Fig. 2h).

RESULTS

Populations in natural sites

In natural, unpolluted meadows *N. bimaculata* was widely spread, but with relatively small populations and sweep-net densities of 4–9 ind./100 double sweeps over the vegetation period. In the three populations investigated the two dark colour morphs dominated, with brown males (frequency of 0.96), brown-white females (0.70) and brown-white inadults (0.60). Consequently, white-brown spiders were in the minority, both in females and in inadults, but completely missing in males. In the white morph, only one adult female was recorded at a natural site (Table 1).

Table 2. Frequency of colour morphs of *Neottiura bimaculata* during three phases of pollution, 1981–2006. Quantitative sweep-net samples, May–October (1–2 days/month)

phase, years stage / sex	n	colour morph brown	 brown-white	 white-brown	 white
emission phase, 1981–1983					
inadult (♂, ♀)	157	0.11	0.26	0.43	0.20
♂ (sub, ad)	118	0.36	0.54	0.10	–
♀ (sub, ad)	272	0.02	0.13	0.15	0.70
regeneration phase I, 1994–1996					
inadult (♂, ♀)	930	0.18	0.23	0.20	0.39
♂ (sub, ad)	107	0.62	0.30	0.08	–
♀ (sub, ad)	356	0.01	0.10	0.24	0.65
regeneration phase II, 2005–2006					
inadult (♂, ♀)	42	0.07	0.43	0.38	0.12
♂ (sub, ad)	17	0.59	0.41	–	–
♀ (sub, ad)	73	0.02	0.22	0.67	0.09

Population in a polluted site

Emission phase

At the beginning of the monitoring near the fertilizer factory in 1980 and 1981, the spider association (sweep net sampling) in the herb layer was dominated by the theridiid *N. bimaculata* with about one third (0.34) of swept spiders and a mean sweep-net density over the vegetation period of 41 ind./100 double sweeps, the manyfold of natural sites.

In 1981–1983, in females the white morph predominated with 0.70 (Table 2, Figs. 1c and 4). It was striking that already in the inadult instars there were many white (0.20) or white-brown individuals (0.43, perhaps females), so that the lightening could not have developed during the inadult phase as a direct consequence of the various emissions. Subadult and adult males remained brown-white and brown, but also in a noticeable frequency white-brown individuals occurred (Table 2, Figs. 1a and 3). In comparison with the colour morphs on natural sites with a striking majority of dark spiders, the colour spectrum in the polluted area was distinctly switched to lighter spiders, mainly in females and to an extent also in males (Figs. 3, 4).

Regeneration phase I

After closure of the fertilizer factory in 1990 and the sudden ceasing of emissions, the mean sweep-net density of *N. bimaculata* during this beginning regeneration phase (1994–1996) amounted with 40 ind./100 d.s. still as high as during the emission phase (1981–1983). At about 5 years without dust emission, the white morph still predominated both in female (0.65; Table 2, Fig. 4) and in inadult spiders (0.39), whereas the males removed their maximum frequency to brown and the rest to brown-white (Table 2, Fig. 3).

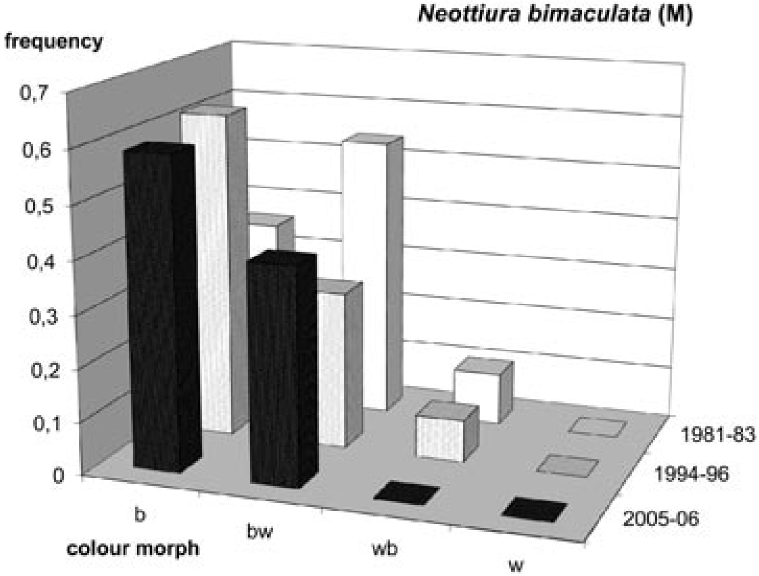

Fig. 3. Frequencies of colour morphs of male *Neottiura bimaculata* at the polluted site during the emission phase (1981–1983), regenaration phase I (1994–1996) and II (2005–2006). Subadult and adult males summarized (n=241).

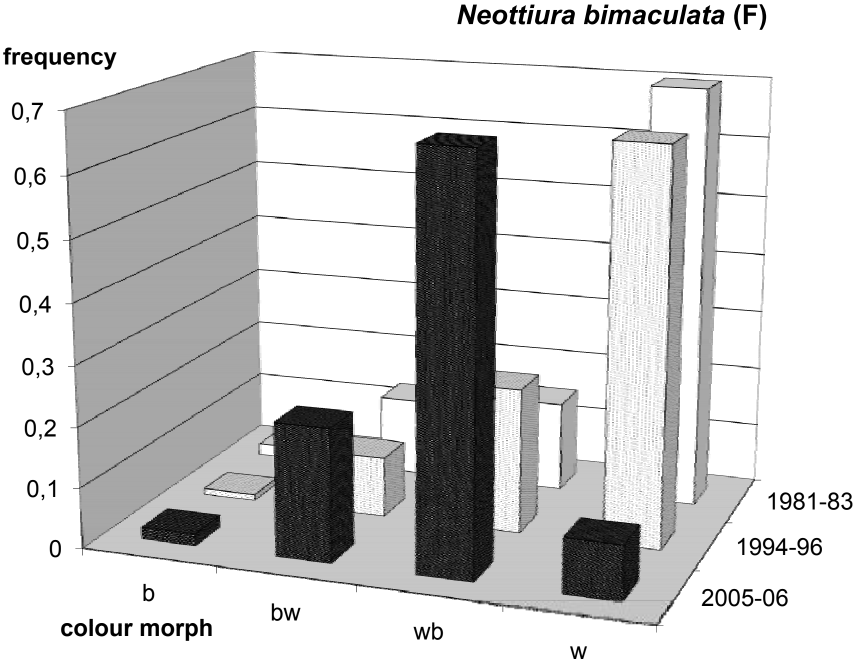

Fig. 4. Frequencies of colour morphs of female *N. bimaculata* at the polluted site during the emission phase (1981–1983), regeneration phase I (1994–1996) and II (2005–2006). Subadult and adult females summarized (n=701).

Regeneration phase II

In 2005–2006, fifteen years after suspension of fertilizer production, the population density of *N. bimaculata* decreased considerably to an average sweep-net density (May–July) of 11 ind./100 d.s. and approximated to the normal densities in the natural sites.

At the same time, the colour morph spectrum in females shifted to a white-brown maximum (0.67), whereas completely white individuals were seldom (Table 2, Fig. 4). In both years, in the inadults slightly predominated brown-white, and males occurred mainly in the brown, but also in the brown-white morph (Table 2, Fig. 3). It was striking that males returned in direction of the natural colour morph spectrum more rapidly and already during the first regeneration phase, whereas the females removed more slowly and to white-brown individuals during the second regeneration phase, indicating sex-specific selection modes.

DISCUSSION

In the course of the studies on *N. bimaculata* in the polluted area of a fertilizer factory over 26 years (1981–2006), with a period before and two periods after suspension of production, the colour morph spectrum shifted in females slowly from the dominance of white (till 4–6 years after suspension of the pollution) to that of white-brown individuals (15–16 years after suspension), and in males rapidly from brown-white to brown, respectively. This phenomenon of predominating albinistic *N. bimaculata* (frequency of 0.70 in females) is here described as ‘industrial albinism’ in contrast to the well-known 'industrial melanism'. But this is only justified if the mechanism is based on the same main factors as observed in the industrial melanism and resulting from positive and negative selection for given colour morphs (e.g. Majerus 1998). Furthermore, besides a significant and continuous amount of pollution, the species in question should have a genetically-based colour polymorphism, with different morphs being differentially cryptic, and selectively hunted by predators (Brakefield 1987, 1988). These premises may be pertinent in relation to our observations and results in the case of *N. bimaculata*. A further more detailed look provides three strong clues which indicate a mainly genetically controlled polymorphism, as known from related theridiid species.

(1) Phenotypic classes in colouration are well-known in female *N. bimaculata*. Simon (1881) was the first to classify five colour variations in French populations, compatible with our separate classification into four morphs. Therefore, colour-expressing genotypes should occur in the populations despite some visible transitions. As described in the literature and shown by own observations, under natural, unpolluted conditions the darker types (mainly brown-white) dominate in populations, but also few light or creamy individuals can be found, indicating that this genotype is also present at very low frequency (Simon 1881, Wiehle 1937, Locket & Millidge 1975, Pekár 1999). It is also noteworthy that in one of our three natural populations studied, a single white female was collected.
(2) Already in the inadults, the later distribution of dark and white colouration on the opisthosoma becomes apparent, indicating that the colour morph is expressed in the young spiderlings after hatching. As rearing experiments in *N. bimaculata* have shown, during the course of development the individual colouration is to a large extent stable (Pekár 1999). According to the colour morph distribution in our samples in the early and middle instars, white inadults must develop into white subadult and adult females. Obviously the same is valid for brown inadults, developing predominantly into brown subadult and adult males. These findings were confirmed mainly by our phenological series of *N. bimaculata* in 1994–1996, where the white colour morph predominated from June to October, involving inadult and adult females.
(3) Both during extensive pollution and for 4–6 years after its cessation in 1990, the majority of female *N. bimaculata* near the fertilizer factory stayed of the white morph. This is a further argument for selection on genotypes, which react at most in females over a longer time interval than any direct environmental cues. After 10–15 years following closure of the factory, the colour polymorphism of *N. bimaculata* slowly approximated to values normally found in unpolluted areas, with an increase in the frequency of brown males (to 0.62 resp. 0.59) and white-brown females (to 0.24 resp. 0.67), but yet not reaching the proportions occurring in the surrounding natural populations.

So far, this interrupted long-term monitoring over 26 years allowed the detection of selection effects on colour polymorphism due to changed habitat conditions. But there was no accompanying study investigating the decisive selection pressure behind this phenomenon observed. As known from many other taxa, the existence of colour phenotypes in webspiders is most commonly explained as being related to the avoidance of predation, mainly by crypsis (camouflage), but also by mimicry and aposematism, but the selective advantage of this variation is often far from clear (Holl 1987, Gunnarson 1993, Foelix 1996, Oxford & Gillespie 1998). So in *Pityohyphantes phrygianus* the removal of bird predation increased considerably the mean spider density, but the proportion of melanics did not change (Gunnarson 1993). In *N. bimaculata* also the cryptic property of body colour may be the main factor against potential predators including besides birds some Vespid wasps, which search for webspiders in the herb layer of semi-dry grassland. In this respect, in natural meadows the mixed-coloured spiders (brown-white) should have an advantage because of a better camouflage within the species-rich grass and herb vegetation. In contrast, within heavily polluted vegetation covered with a dense light-grey layer of dust, the darker morphs are much more striking and pose a greater predation risk, whereas the white morph is more invisible in this environment and less vulnerable to direct selection.

The sixfold higher density of *N. bimaculata* on polluted plots during (in 1981–1983) and after pollution (in 1994–1996) can be explained by a more dense vegetation, in which a higher humidity enables a greater hatching success. The other argument that white females have a higher fecundity than dark females was not investigated, but can be neglected because of the broadly similar body sizes of females of different colour morphs (G.S., pers. experience).

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