ANIMAL BEHAVIOUR, 2002, **63**, 175–182
doi:10.1006/anbe.2001.1878, available online at http://www.idealibrary.com on IDEAL®

Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae)

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(Received 6 March 2001; initial acceptance 5 April 2001; final acceptance 9 September 2001; MS. number: 6871R)

Giant wood spiders, *Nephila maculata* (Fabricius 1793), typically have a greenish cephalothorax and a dark abdomen decorated with striking yellow bands and spots. However, in Taiwan and neighbouring coastal islands we also found some morphologically indistinguishable individuals that were totally dark. As insects are attracted to ultraviolet (UV) light, we compared the UV reflectance property and insect-catching ability of the two morphs to see whether variation in colour affected foraging success. We also examined the population genetic structure to estimate indirectly the level of gene flow between these two colour morphs. Body surface UV reflection rate was measured from six areas of the spider with a spectrometer. To compare the insect-catching ability of different morphs, we recorded the spiders' body colour, orb size and insect-interception rates. The typical morph of *N. maculata* reflected significantly more UV in four of the six areas examined and caught significantly more insects than the melanic morph. We estimated population genetic structure by allozyme electrophoresis, using 20 loci from 17 enzymes. The population differentiation index (F_{ST}) derived from all eight polymorphic loci was 0.023, indicating a minimum level of genetic differentiation. These results indicate that the two morphs of *N. maculata* may be members of an interbreeding population, and melanics have lower foraging success because of a lower body surface reflectance.

Although melanism is currently being studied intensively in various fields, how the ratio of melanics to other morphs is maintained in various species is still under debate, even in the intensively studied peppered moths, *Biston betularia* (Majerus 1998). The mechanisms determining the frequency of melanics in various species of ladybird beetles have received much study. Although the evidence is still equivocal, colour-associated thermal properties (the so-called 'thermal melanism', reviewed by Majerus 1998) and nonrandom mating (de Jong et al. 1998; Ueno et al. 1998) are currently considered as two potential major driving forces.

Compared with peppered moths and ladybirds, melanism in spiders is less well known. Gunnarsson (1987) found that the melanic morphs of the sheetweb spider *Pityohyphantes phrygianus* were more active than nonmelanics at low temperatures. Based upon this result, Gunnarsson (1993) conducted a field experiment testing whether bird predation was a selective agent for the low but stable frequency of melanic *P. phrygianus* in the population. However, absence of predation did not increase the frequency of melanics, indicating that variation in body colour was not associated with differential predation pressure.

Even in several well-studied polymorphic spider species, it is not clear how variation in body colour affects behaviour and thus leads to the observed morph ratios. Gillespie & Tobashnik (1990) reported a stable morph frequency and a negative correlation between morph frequencies and residence time in the happy-face spider, *Theridion grallator*, and they proposed that frequency-dependent selection by bird predation may be involved. Gillespie & Oxford (1998) compared population genetic differentiation values derived from colour and allozyme loci and concluded there was a balancing selection pressure, which they also proposed was bird predation. They also found that when the morph frequency was

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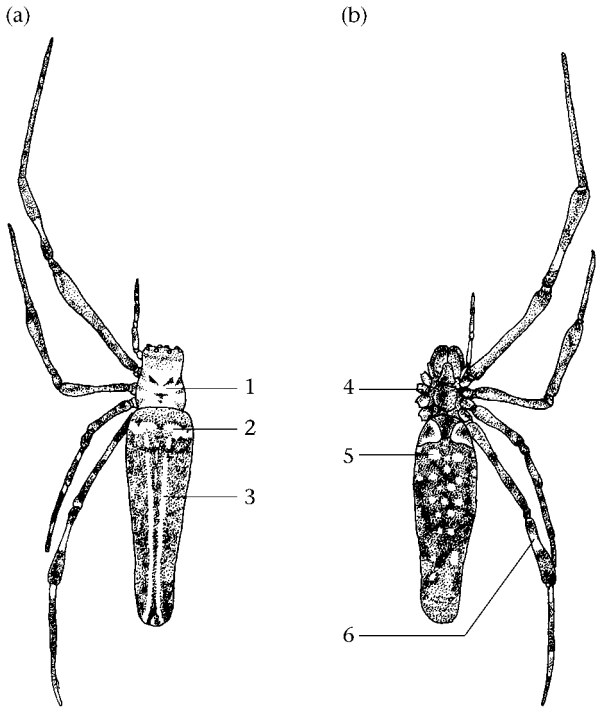

Figure 1. Illustrations showing the colour patterns of (a) the dorsum and (b) the ventrum of the giant wood spider, *Nephila maculata*. Ultraviolet light reflectance data were recorded from areas 1–6.

perturbed, females tended to mate with males of the rare morph. Greco & Kevan (1999) found that different morphs of *Enoplognatha ovata* prefer different habitats and suggested that polyethism in hunting strategies might be responsible for maintaining the observed morph ratios. All these studies suggest that colour variants of a polymorphic spider may experience differential selection pressures (but see Reillo & Wise 1988). However, the behavioural mechanisms mediating selection are still not clear.

Recently, we discovered that the largest orb-weaver in Taiwan, the giant wood spider, *Nephila maculata* (Fabricius 1793), varies in body colour. Typical female *N. maculata* have an olive green prosoma and a yellowish black abdomen decorated with a transverse white band, two longitudinal yellow bands and numerous yellow spots (Fig. 1). However, some sympatric females are darker. Body colour in spiders, especially in orb weavers, is important for prey catching. Craig & Bernard (1990) found that the conspicuous body coloration of *Argiope argentata* reflected ultraviolet (UV) light and could thus attract insects. Craig & Ebert (1994) further showed that the UV-reflecting dorsal surface of *A. argentata* attracted more pollinating insects than the spiders' brown ventral surface. These studies led us to hypothesize that body colour variation may result in a difference in UV reflectance and thus affect the insect-catching ability of giant wood spiders. We tested this hypothesis by comparing (1) the UV reflectance intensity of the body surface and (2) the insect-catching rate of typical and melanic spiders.

We also examined *N. maculata*'s population genetic structure to see whether the variation in body coloration is associated with a certain degree of genetic differentiation. The level of genetic differentiation among polymorphic individuals of a population is rarely examined. Results of the few existing studies suggest that sympatric polymorphic individuals may be members of different subspecies. For example, Steiner et al. (1977) examined the genetic structure of three colour morphs of an isopod *Asellus brevicauda* and found a strong colour-dependent pattern. As fixed differences were found at two loci between two morphs, Steiner et al. (1977) concluded that sympatric individuals of different colour should be regarded as different subspecies. This result indicates that reproductive isolation may occur between different morphs of a polymorphic species. If reproductive isolation also occurs between colour variants of *N. maculata*, it will be inappropriate to interpret the behavioural mechanisms investigated on the basis of polymorphism. The most direct way to evaluate the existence of reproductive isolation is to do breeding experiments. However, males found on webs of both typical spiders and melanics were of the same coloration (bright orange). Consequently, breeding experiments could not be used to judge whether *N. maculata* of different colours can interbreed. An indirect approach is to estimate the level of genetic differentiation between two morphs. If reproductive isolation does occur and for long enough, the accumulated changes in genetic material can be revealed by various molecular techniques (Hillis et al. 1996). Although lack of genetic differentiation does not necessarily mean that reproductive isolation does not occur, this indirect approach at least provides a preliminary understanding of the reproductive status between two morphs. Therefore we estimated the colour-associated genetic structure of *N. maculata* using starch gel electrophoresis to investigate if these morphologically similar but chromatically distinctive individuals were polymorphic members of one species.

METHODS

Frequency of Melanic Morph

To determine whether the frequency of melanics in the population was stable over time, we conducted censuses on the population on Chung-Ai bridge, Orchid Island, Taiwan (22°N, 121.5°E) on 10 December 1997 and 3 August 1999. The study site is described in Tso & Severinghaus (1998). During the censuses, we recorded the body length and coloration of the spiders. We used a chi-square test to compare the morph frequencies obtained from the two censuses.

UV Reflection Rate

We measured UV reflection rate as specular reflectance with a spectrometer (S2000, Ocean Optics, Inc., Dunedin, Florida, U.S.A.). For each measurement, the illumination leg of a reflection probe (with six illumination fibres) was attached to a light source (450-W, Xenon arc lamp), and the read leg (with 1 read fibre) to the spectrometer. the

end of the probe was placed 5 mm above (90°) the part of the spider being measured. The reference spectrum (R_λ), dark spectrum (D_λ) and reflection spectrum (S_λ) were taken following the operation manual. Based on these spectrum measurements we calculated the UV reflection rate (%R_λ) as:

$$\%R_\lambda = \frac{S_\lambda - D_\lambda}{R_\lambda - D_\lambda} \times 100\%$$

We measured five typical and five melanic individuals. For each individual we recorded reflectance data from the following areas of the dorsum (areas 1–3) and ventrum (areas 4–6): (1) the cephalothorax; (2) the transverse white band on the fore-end of the abdomen; (3) the longitudinal yellow band; (4) the coxa; (5) the yellow spot on the abdomen; and (6) the yellow spot on the distal end of the femur. The range of wavelengths used was 340–430 nm (increment 0.3 nm), because recent reviews have concluded that the potential prey of *N. maculata* (Diptera, Hymenoptera and Coeloptera) were most sensitive to this range (Silberglied 1979; White 1985; Hardie 1986; Menzel & Backhaus 1991; Stavenga 1992). For each wavelength (300 in total), we measured reflection rate 10 times and we plotted the mean against wavelength. To compare the reflection properties of typical and melanic morphs, we first calculated a mean reflection rate from the 300 data points recorded between 340 and 430 nm for each area of each individual. Then for each area, we compared the mean reflection rates of the two morphs (five individuals each) using a two-tailed Mann–Whitney *U* test.

Insect-catching Rates

To examine whether melanic *N. maculata* catch fewer insects than the typical morph, we conducted an experiment between 3 and 6 August 1999 on Chung-Ai Bridge, Orchid Island, Taiwan. We marked the web sites of 39 typical and 20 melanic spiders by fastening a plastic strip in the vegetation nearby. During the study we visited the spiders once each hour each day between 0800 and 1800 hours. In the first survey of the day we measured the orb radius from four cardinal points and used the 'adjusted radii–hub' formula of Herberstein & Tso (2000) to calculate catching area. The formula assumed a circular approximation treating each web half as a semicircle, but it adjusted the vertical radii by taking the horizontal diameter into consideration:

$$\text{Catching area} = \left[\frac{1}{2}\pi r_{au}^2 - \frac{1}{2}\pi (Hr_u)^2\right] + \left[\frac{1}{2}\pi r_{al}^2 - \frac{1}{2}\pi (Hr_l)^2\right]$$

where r_{au} is adjusted upper radius, r_{al} is adjusted lower radius, Hr_u is upper hub radius, Hr_l is lower hub radius. The adjusted upper and lower vertical web radii are calculated as follows:

$$r_{au} = \frac{r_u + \frac{d_h}{2}}{2}, \quad r_{al} = \frac{r_l + \frac{d_h}{2}}{2}$$

where d_h refers to the horizontal diameter of the orb. Beginning from the first survey of the day, once every hour we recorded the number, size (in mm) and taxa (to order) of insects trapped by the web. We also removed kleptoparasitic spiders (mostly *Argyrodes lanyuensis*, Yoshida et al. 1998) to prevent them from reducing the orb size during our recording (Tso & Severinghaus 1998). We analysed the effect of colour variation on insect-catching rate, taking into account the spider orb's catching area and the interaction of these two variables, using the following general linear model: Insect catching rate=constant+A × coloration+B × catching area+C × coloration × catching area.

Since catching rates and catching area were not normally distributed even after transformation (Lilliefors test: $P<0.001$), we estimated the parameters of the model by maximum likelihood approximation as in Craig (1994); Craig et al. (1996) and Tso (1998). In this approach, the effects of colour, catching area and their interaction can be evaluated by examining whether the corresponding parameters A, B and C are statistically different from 0 by two-tailed Student *t* tests. After estimating the parameters A, B and C by SYSTAT 5.2 (Wilkinson et al. 1992), we divided the parameters by their standard errors to generate Student *t* values, then evaluated the significance levels with $N-k-1$ degrees of freedom (N=sample size, k=number of parameters). We also used a two-tailed Mann–Whitney *U* test to determine if catching area differed between typical and melanic morphs.

Population Genetic Structure and Gene Flow

We examined the level of gene flow between typical and melanic morphs by comparing allozyme frequencies using starch gel electrophoresis. In August 1999 we collected 48 typical and 39 melanic morphs from a population on Chung-Ai Bridge, Orchid Island. They were transported live to the laboratory in the Department of Biology, Tunghai University, and were preserved at −80°C before subsequent processing. As a preliminary study comparing the allele frequencies of cephalothorax, appendages and abdomen indicated no tissue-specific alleles (I-M. Tso, unpublished data), we used the abdomen only because it was the easiest to extract enzymes. We used 17 enzyme systems to assay the samples, which yielded 20 loci. Of these, the following were polymorphic and were used in the population genetic analysis: asparate aminotransferase (AAT, E.C. 2.6.1.1); glucose-6-phosphate dehydrogenase (G6PDH, E.C. 1.1.1.49); malate dehydrogenase (MDH, E.C. 1.1.1.37); mannose-6-phosphate isomerase (MPI, E.C. 5.3.1.8); phosphoglucomutase (PGM, E.C. 2.7.5.1); esterase (EST, E.C. 3.1.1.-∞) and L-lactate dehydrogenase (LDH, E.C. 1.1.1.27). Wright's *F* statistics (Wright 1978) were used to analyse the electrophoresis data. We estimated the degree of population differentiation by calculating F_{ST}, the fixation index, and gene flow between typical and melanic morphs by calculating N_m, which is equal to:

$$\frac{(1 - F_{ST})}{4F_{ST}}$$

All calculations were conducted by Popgene 1.2 (Raymond & Rousset 1995).

RESULTS

Frequency of Melanic Morphs

In the 1999 census we measured spiders of all size classes but in the 1997 census only individuals greater than 7 mm. We recorded 127 typical and 28 melanic females from the 1999 census. No melanics were found among individuals smaller than 7 mm, suggesting that the spiders did not become dark until they reached a certain developmental stage. The frequency of melanics was 18.1% for all size categories pooled and 27% for individuals larger than 7 mm. We recorded 82 individuals from the 1997 census and among them 27 were melanics. None were smaller than 7 mm, so we used individuals larger than 7 mm in the 1999 census to compare the frequencies between the two censuses. A two-tailed chi-square test showed no significant difference in frequency of melanics between the two censuses (χ^2_1=0.240, NS).

UV Reflection Rate

UV reflectance of typical morphs differed significantly from that of melanics in four of the six areas examined. In the typical morph, the white band at the fore-end of the back of the abdomen (area 2) reflected the most UV (Fig. 2b), and significantly more than that of melanics (U=25.00, N_1=N_2=5, P<0.01). Compared with area 2, the longitudinal bands on the abdomen (area 3) reflected less UV (Fig. 2c), but still more than the same area of melanics (U=25.00, N_1=N_2=5, P<0.01). UV reflection of the greenish cephalothorax (area 1) of the typical morph was relatively low (Fig. 2a), but significantly higher than that of melanics (U=23.00, N_1=N_2=5, P<0.05). The yellow spots on the distal end of the femur (area 6) also reflected a considerable amount of UV (Fig. 2f), and more than that of melanics (U=25.00, N_1=N_2=5, P<0.01). Although this area, the coxa (area 4) and the ventral abdominal spots (area 5) were similar in colour and intensity to human eyes, the latter two areas showed little UV reflectance, and were not statistically different from those of melanics (area 4: U=17.00; area 6: U=15.00, both N_1=N_2=5, NS; Fig. 2d,e).

Insect-catching Rates

When colour, catching area and their interaction were incorporated in the model, only the corresponding parameter of colour was significantly different from 0 (Table 1). The interaction term was not significantly different from 0, suggesting that there was no dependence between colour and catching area. We then excluded the interaction term from the model and re-estimated the parameters. The parameters of both variables were significantly different from 0 (Table 1), which indicated that both were significant determinants of insect catching rates. While the typical morphs were shown to catch significantly more insects than melanics (Fig. 3a), no significant difference was found between the catching areas of the two morphs (Mann–Whitney U test: Z=0.45, N=88, NS; Fig. 3b). Among all the captured insects recorded, 78.8% were dipterans, 15.1% were hymenopterans and 6.1% were coelopterans; all were potentially sensitive to UV light.

Population Genetic Structure and Gene Flow

The number of alleles per locus, frequency of polymorphic loci and heterozygosity values were similar between typical and melanic morphs (Table 2). Among the 20 loci examined, eight were polymorphic (Table 3). Estimated from all polymorphic loci the fixation index was low and gene flow was high (Table 3), indicating a minimum level of genetic differentiation according to the reference values given by Wright (1978).

DISCUSSION

This study shows that body coloration may affect the foraging success of polymorphic predators by altering their UV reflectance. The average insect-catching rate of the typical morph was almost twice that of the melanic morphs. Since the two morphs inhabited the same study site, built orbs of similar size and caught UV-sensitive prey (hymenopterans, dipterans and coelopterans; Silberglied 1979), the difference in foraging success probably resulted from their chromatic variation. Our results also corroborate those of Craig & Ebert (1994), who showed that the bright dorsum of *Argiope argentata* is more attractive to insects than the dark ventor, although the UV reflectance was not measured directly. However, photos taken from a camera mounted with a filter that removed wavelengths greater than 400 nm showed that the distinctive dorsum of the spider was bright under UV, while the dark ventral surface reflected little UV (Figure 2 in Craig & Bernard 1990). In our study we measured the UV reflectance of *N. maculata* directly. In the typical morph, the back of the abdomen as well as the spots on the femurs reflected a considerable amount of UV. The UV-reflecting spot on the femur is especially interesting. When spiders are hanging in the forest understorey with eight legs extended, the spots are arranged in a ring. Whether this arrangement plays a role in attracting insects deserves further study.

The electrophoresis data suggest a minimum level of genetic differentiation between the two morphs of giant wood spider populations on Orchid Island. Estimated from all polymorphic loci, the observed heterozygosity was 0.042 and polymorphism was 40%, which were similar to values reported from other invertebrates, including spiders (reviewed by Ramirez & Fandino 1996; Ramirez & Haakonsen 1999). In both morphs the genetic variation averaged 1.5 alleles per locus. The genetic structuring between typical and melanic *N. maculata* is in accordance with that reported from populations with a high level of interbreeding (Wright 1978). Therefore, the two colour variants seem to be members of an

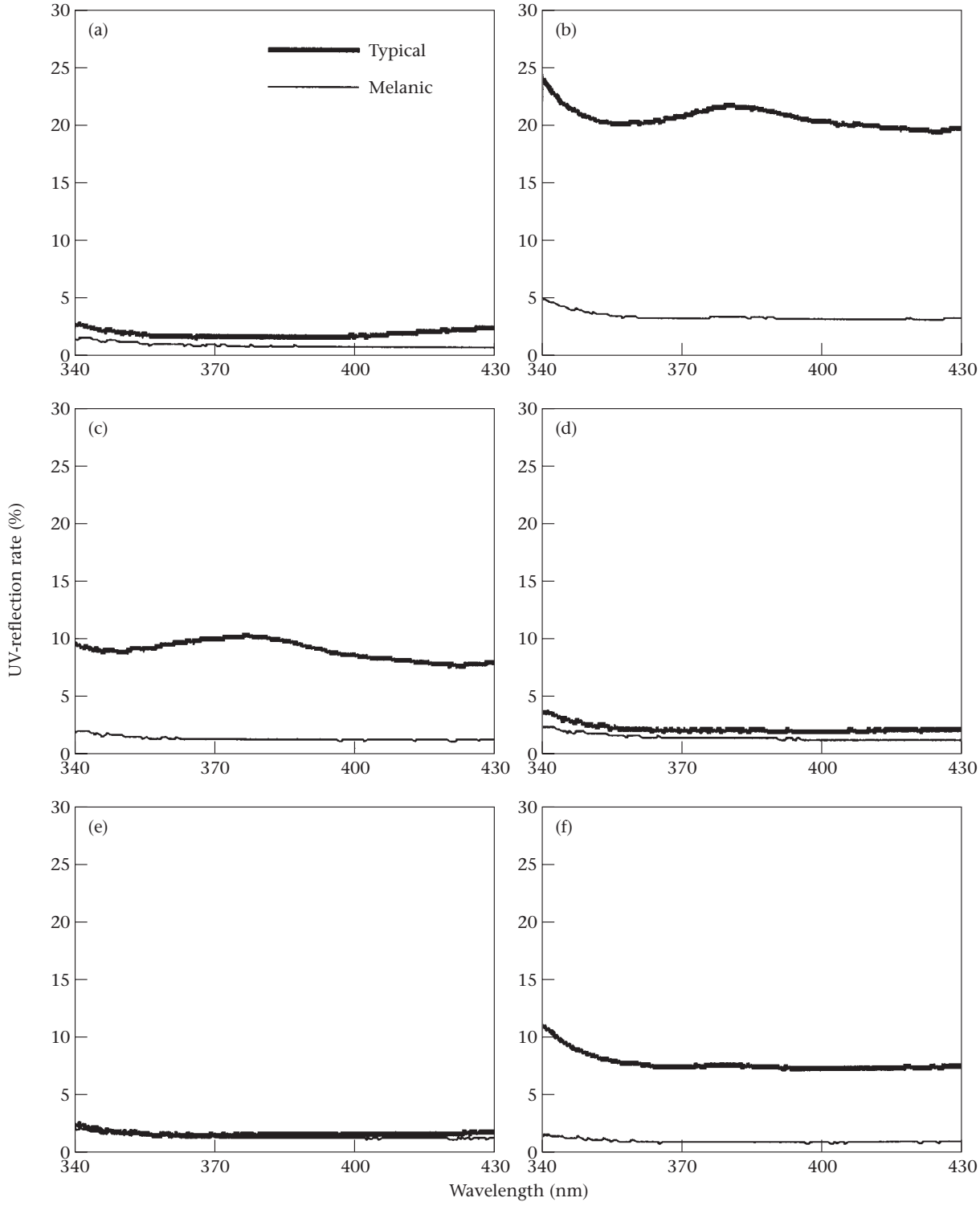

Figure 2. Ultraviolet light reflectance intensity measured from six areas of typical and melanic morphs of *Nephila maculata*. (a–f) correspond to areas 1–6, respectively; see Fig. 1 and text for descriptions of each area.

interbreeding species, without any reproductive isolation between them.

Nevertheless, it is possible that the colour variation is environmentally induced. *Nephila maculata* is abundant at low elevations in East and South-East Asia (Yaginuma 1986; Barrion & Listinger 1995), but the melanic morph has not been mentioned before in the literature. However, we found melanic individuals in virtually all populations in Taiwan and neighbouring coastal islands (I-M. Tso, unpublished data). In a review, Oxford & Gillespie (1996) concluded that body colour variation in spiders can be caused by either genetic mechanisms or

Table 1. Results of maximum likelihood approximation estimating the parameters of the model: insect catching rate=constant+A×coloration+B×catching area+C×coloration×catching area

Effect	Parameters	Estimate	SE	*t*	*P*
With interaction term					
Colour	A	−0.314	0.153	2.052	<0.025
Catching area	B	−0.003	0.007	0.471	NS
Interaction term	C	0.007	0.005	1.396	NS
Without interaction term					
Colour	A	−0.111	0.047	2.362	<0.01
Catching area	B	0.005	0.002	2.500	<0.01

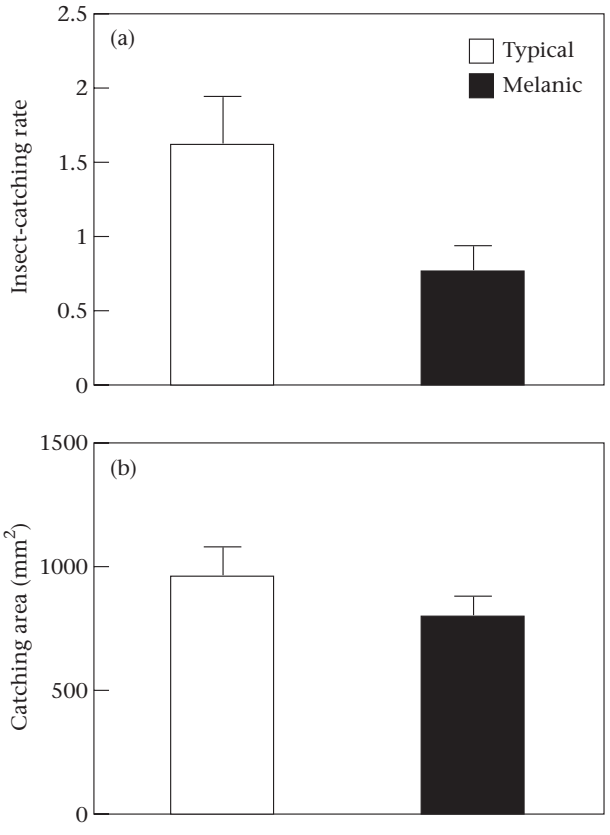

Figure 3. (a) Insect-catching rate (number of insects caught per spider) and (b) catching area of orbs built by typical and melanic *Nephila maculata*. Means are given+SE.

environmental parameters. To gain a preliminary understanding of the mechanism of colour variation in *N. maculata*, we brought several spiderlings of the typical coloration pattern (body length smaller than 7 mm) back to the laboratory and kept them in the same environment. While the majority of individuals grew into typical females, two became increasingly darker after successive moults (I-M. Tso, unpublished data), and did not revert to the typical coloration. Since the majority of the induced colour changes in spiders involve changes in intensity and are reversible, the darkening of the body colour is not likely to result from environmental parameters, such as food or background reflection patterns (Oxford & Gillespie 1996). It is also hard to imagine that environmental factors experienced by the spiderlings before they were brought to the laboratory could have such a long-lasting effect and cause such a marked colour change. An ontogenetic study is currently underway to understand the nature of the mechanisms responsible for melanism in *N. maculata*.

The results from the 1997 and 1999 censuses indicated that the frequency of the melanic morphs was more or less stable over time. The marked difference in foraging success between the two morphs may be partially responsible for the higher frequency of the typical morph in the population. However, since the distribution of insects varies in time and space, the effect of colour variation on foraging success may fluctuate over time. To evaluate further the effect of colour-associated foraging variation on morph frequencies in *N. maculata*, a long-term study comparing the reproductive success of these two morphs is needed. Besides, although the lower foraging success of the melanic morph correlates with a lower UV reflectance, there is no direct evidence that the latter is the cause of the former. The foraging success of orb-weaving spiders is affected by numerous factors and melanic individuals might catch fewer prey because of factors unrelated to chromatic properties. An important determinant of foraging success in orb-weaving spiders is the size of the catching area (Brown 1981; Higgins & Buskirk 1992; Herberstein & Elgar 1994). In our study, since the

Table 2. Genetic variability measures ($\bar{X}$±SE) of typical and melanic *Nephila maculata*

Population	*N*	No. alleles/locus	% Polymorphic loci	Heterozygosity	
				Observed	Expected
Typical	48	1.450±0.605	40.0	0.046±0.102	0.075±0.151
Melanic	39	1.450±0.605	40.0	0.039±0.099	0.070±0.135
Total	87	1.500±0.688	40.0	0.042±0.093	0.073±0.141

Table 3. Population differentiation index (F_{ST}) and gene flow (N_m) of eight polymorphic loci

Loci	F_{ST}	N_m
G6PDH	0.0023	108.9
PGM	0.0894	2.5
MPI	0.0003	981.7
MDH-3	0.0138	17.8
LDH	0.0037	67.8
EST-1	0.0049	50.9
EST-2	0.0005	490.9
AAT	0.0003	981.7
Mean	0.0231	10.6

catching area of the typical morph did not differ significantly from that of the melanic morph, unequal web size is unlikely to explain our result. However, only a manipulative study can show if a lower UV reflectance is responsible for the observed lower foraging success in the melanic morph of *N. maculata*.

Even if a manipulative study shows that lower UV reflectance is responsible for the melanic morph's foraging disadvantage, we should also examine the advantages enjoyed by melanics that might be responsible for their stable persistence in the population. Thermal properties associated with dark coloration have frequently been reported to be advantageous to many temperate ladybird species (reviewed by Majerus 1998). However, in a tropical area such as Orchid Island with a mean annual temperature of 22°C (Chen 1982), better heat-focusing ability is unlikely to enhance the fitness of the melanic spiders. One advantage that melanic individuals may have is improved survival. Losey et al. (1997) provided evidence that a matching of body coloration with the environment increases the survivorship and frequency of the green morph pea aphid, *Acyrthosiphon pisum*. Giant wood spiders, as the name implies, usually inhabit low-elevation tropical or subtropical forests with dense overhead canopy and low ambient lighting (Robinson & Robinson 1973; Yaginuma 1986). In such habitats, a dark coloration may render the spiders less visible to visually oriented predators. In addition to prey insects, the UV-reflecting typical morph may also attract visually oriented predators such as birds and parasitoid hymenopterans. Many species of birds have UV vision (Burkhardt 1982; Jacob 1992; Maier & Bowmaker 1993; Bennett & Cuthill 1994) and some species use UV to detect and capture their prey (Viitala et al. 1995). Parasitoid hymenopterans, such as Sphecidae and Pompilidae, may prey upon spiders to provision their larva (Coville 1987), and orb weavers are specifically preyed upon by some species (Coville 1978; Evandro & Brescovit 1999). Since hymenopterans have UV vision (White 1985; Menzel & Backhaus 1991; Stavenga 1992), perhaps the UV-reflecting typical morph is easier for them to find. On the other hand, melanic individuals may benefit merely from their low frequency in the population. The higher frequency of the typical morph, resulting from their higher foraging success, may enhance the formation of a search image by predators (Allen 1988; Endler 1988). Further field manipulative studies on colour-associated mortality and relative strength of the different selection pressures will help determine the mechanisms generating the frequency of melanic *N. maculata* in a population.

Acknowledgments

We thank Dr S. C. Lee for support and Dr H. C. Lin, Dr L. K. Lin, Mr J. W. Lee, Miss C. M. Chu and Miss I. J. Yeh for assistance in logistics, field experiments, electrophoresis techniques and genetic data analyses. This study was supported by National Science Council (Taiwan, R. O. C.) grants to I.M.T (NSC88-2311-B-029-003, NSC89-2311-B-029-002) and an NSC Undergraduate Summer Research Grant to P.L.T. (NSC89-2815-C-029-004-B).

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