

**RECOGNITION OF CONSPECIFIC FEMALES BY MALES
OF *CALOPTERYX HAEMORRHOIDALIS* (VANDER LINDEN)
(ZYGOPTERA: CALOPTERYGIDAE)**

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♂♂ of calopterygid damselflies appear to court ♀♀ of other (related, sympatric) spp. only rarely. Apparently, ♀♀ of this group bear species-specific characteristics that release sexual behaviour in conspecific ♂♂ only. Sympatric *Calopteryx* spp. usually differ conspicuously in pigmentation (colour, transparency, darkness) of their wings. ♀♀ *C. haemorrhoidalis* differ from all other European spp. by the presence of a dark distal zone in the hindwings. — The relative value of various (manipulated) sets of ♀ wings for elicitation of ♂ courtship was assessed using choice experiments. *C. haemorrhoidalis* ♂♂ did not court wingless ♀♀ of their own sp. nor did they court conspecific ♀♀ with wings of the sympatric *C. xanthostoma*. However, the presence of a single wing of a conspecific ♀ was sufficient to elicit courtship behaviour. Choices between 2 ♀ models (presented simultaneously to territorial male individuals) revealed that the presence of a contrasting dark zone was an important distinguishing characteristic, whereas too high a transparency (a single wing as opposed to a set of 2 or 4 wings pressed against each other) greatly diminished the value of a model. The need for the presence of a dark zone will be effective in precluding courtship of ♀♀ of other sympatric spp. The need for sufficiently low transparency will put a check on courtship attempts of immature ♀♀.

INTRODUCTION

It is not uncommon to encounter two or three different species of *Calopteryx* showing reproductive behaviour simultaneously along the same stream. Nevertheless, as in other Odonata, records of heterospecific pairs, and hybrids in particular, are rare (BICK & BICK, 1981; CORBET, 1999). This is remarkable, as morphological traits involved in tandem formation and copulation are almost identical in the various species of Calopterygidae (DUMONT, 1972). Thus, reproductive isolation appears to be achieved by behaviour decisions early in the courtship sequence, which is well developed in this group. Indeed, courtship of females of another species appears to be infre-

quent in most calopterygid species. Apparently, *Calopteryx* males are able to recognise females of the same species (or subspecies) from some distance (BUCHHOLZ, 1955; WAAGE, 1975).

From a distance, individuals of the various sympatric species can be identified by their strikingly differential wing coloration. In Europe, for example, males of *C. splendens*, *C. xanthostoma* and *C. virgo* differ in the proportion and the specific parts of the wing coloured bright blue, whereas wings of male *C. haemorrhoidalis* are brown to black, without any blue. Though the wings of female calopterygids are usually less intensively coloured, they also show species-specific differences. They are uniformly hyaline to greenish in *C. splendens* and *xanthostoma*, uniformly brownish in *C. virgo*, whereas the light brown wings of the females of *C. haemorrhoidalis* show a conspicuously darker brown zone in the distal part of the hindwings.

In calopterygids, differential wing pigmentation appears to play a key role in the recognition of individuals of the same species and as stimuli releasing sexual (and aggressive) behaviour and thus for reproductive isolation. Proper species recognition will be important, as any behaviour directed to a member of a "wrong" species would be a waste of time and effort. In *C. splendens* and its numerous subspecies, BUCHHOLZ (1951, 1955) observed that males respond with courtship behaviour only to models with female wings and that these wings should comply with certain characteristics of size (BUCHHOLZ, 1951) and pigmentation, particularly transparency (BUCHHOLZ, 1951, 1955) to elicit courtship by males of the same (sub)species. Results reported by HEYMER (1973a, 1973b) for *C. haemorrhoidalis* also point to the importance of wing pigmentation, but he disagrees with BUCHHOLZ (1951, 1955) about the decisive significance of wing transparency of female *Calopteryx* wings, because he found that males of *C. haemorrhoidalis* responded also to completely non-transparent female wings which were glued to an opaque sheet of paper. In North America, WAAGE (1975) observed that *C. maculata* males could discriminate between females of their own species and those of the sympatric *C. aequabilis* on the basis of wing pigmentation (darkness of colour).

In all of the above studies, the role of female wing pigmentation in eliciting *Calopteryx* male sexual behaviour stands out. However, proper quantitative data are mostly lacking in the experiments of both BUCHHOLZ (1951, 1955) and HEYMER (1973a, 1973b). Generally, such details as numbers of replicates and exact proportions of positive and negative responses are not stated.

In the present paper, I address the following questions: (1) can males of *C. haemorrhoidalis* (Vander L.) discriminate between conspecific females and those of another sympatric species (*C. xanthostoma* [Charp.]) well before tandem formation, — (2) do female wings play a key role in this early recognition, i.e. are they more important than other female body parts, and — (3) which characteristics of female wings are of particular importance for eliciting male sexual responses? These questions were addressed by choice experiments: altered and unaltered dead females were presented either simultaneously or sequentially to mature males in their territories. In particular choices between simultaneously presented models were applied as a sensitive way to assess the relative value of models and to quantify the relative importance of their different traits.

METHODS

The experiments were performed along a 200-m stretch of the river Massane between Argelès-sur-Mer and Sorède (Dept Pyrénées Orientales, France) in July 1959. At this location, the stream was about 3 m wide, mostly < 0.5 m deep and heavily shaded by trees and shrubs. The population of *C. haemorrhoidalis* was rather dense with 1 to 10 territorial males per 10-m bank length, whereas the numbers of *C. xanthostoma* were about ten times lower and *C. virgo meridionalis* was even less abundant. Though the territories of the species overlapped locally, mating efforts between members of the three different species were never noticed. The total observation time was about 60 man-hours.

Female models were presented in front of individual males that were perched in their territories. These models were tethered dead females with their wings in a position of rest, i.e. their wings were folded closely together. The models were individually tied with their thorax to a thin iron thread of about 20 cm, which stood upright on the end of a 1.5-m long reed-stem. If two such female models were fastened to the end of the same cane, they were positioned closely parallel (the distance between the two models was about 0.5 m). They were offered for 25 or 50 s at a distance of about 30 cm from the head of a number of perched territorial males. A positive response of a male was recorded if the male (usually after a short "arc" courtship display, compare CORDOBA-AGUILAR, 2000) perched on the female wings or thorax and bent his abdomen forward towards the neck of the female. The models were removed if the male had not responded within a certain time (25 or 50 s, see below). In any specific experiment, individual males were not used more than twice (this was easy to check, as territorial males generally stay for several days within the same small area where no other males are allowed; compare BEUKEMA, 2002a). Several different copies of any specific female model were used to avoid spurious effects of individual variation in e.g. pigmentation.

Two kinds of experiments were performed: successive presentations of two models (for 25 s each) or simultaneous presentations of two models (50 s). In the former case, the model deviating most from a conspecific female was offered first. If the male did not respond within 25 s, the presentation of an unaltered dead conspecific female immediately followed. Only if the male responded within 25 s to this "normal" model, it was judged sufficiently responsive to count the earlier negative record. In the case of simultaneous presentations (choice experiments), the model receiving the first positive response was counted. Care was taken to present the two models at equal distances from the males' head.

If not stated otherwise, the wings of the model females were at rest, i.e. right up against each other, and the dark-banded hindwings on the outer side. A "normal" model had two forewings and two hindwings, usually on a female *C. haemorrhoidalis* body. In some models, two or more wings were removed, leaving one or two forewings or one or two hindwings. In other models, two forewings were replaced by two hindwings or two hindwings by two forewings. Other models lacked either the white wing stigmata or the abdomen + head + legs, but were otherwise normal. A special series of models had full or halved female *C. haemorrhoidalis* wings fixed on a female *C. xanthostoma* body.

Wing transparency was measured by a simple device. It compared light intensity (emitted by a small battery-powered light bulb) falling on a photodetector either without any obstacle between bulb and transistor (scale set at 100% of the scale of a microampere meter immediately before any actual measurement) or with one or more wings in between (transmitted light measured on a scale of 0 to 100%; within the range of 20 to 100% the deflection of the pointer proved to be linearly proportional to the amount of light transmitted). The wing area that shaded part of the light had a diameter of about 3 mm. As in the similar apparatus used by WAAGE (1979), this test area was sufficiently small to allow estimates to be made of different part of the wings, but sufficiently large to prevent high variability by the different pigmentation of veins and cells (as recorded by BUCHHOLZ, 1955).

To evaluate the statistical significance of the results, non-parametric tests were used; if not indicated otherwise it was the sign test. Numbers of experiments were usually between 20 and 40, but were limited to 10 if the males consistently responded to only one of the two models.

RESULTS

PRELIMINARY OBSERVATIONS AND EXPERIMENTS
TO ESTABLISH PROPER METHODS

Calopteryx males can respond sexually to a female that either enters his territory flying or is perched within his territory (in oviposition or at some distance from the water surface). In the population of *C. haemorrhoidalis* studied, flying females were only rarely pursued by males and nearly all mature males were truly territorial and generally courted a female only if she was perched within or close to his territory. In other populations of this species, courtship starts in most cases (around 80%) also with the so-called "arc" display in front of a perched female (GIBBONS & PAIN, 1992; CORDOBA-AGUILAR, 2000). Because the male thus sees the female with closed wings (with all four wings pressed against each other) at the start of most sexual encounters, I chose to investigate the releasing value of sets of wings in this closed rest position.

Presentation to males of a simultaneous choice between two models, one with closed wings and one with the same set of wings in a spread position, resulted in a 15 : 4 choice in favour of the closed wing set ($p < 0.05$, sign test). All further choice experiments were performed with sets of closed wings. This is like the experiments by WAAGE (1975), but different from those by BUCHHOLZ (1951, 1955) and HEYMER (1973a,b), who used sets of spread wings or (in most cases) single wings.

Because BUCHHOLZ (1951, 1955), in her pioneer studies on traits of *C. splendens* female wings that elicited sexual responses in males, had indicated that males ignored non-moving models, I moved my models slowly up and down at first in the way she indicated as optimal (about once per 2 s up and down over a distance of about 40 cm, resembling the "butterfly" way of flying of Calopterygidae). However, I realized that such movements would not occur in the natural situation in females with wings folded together in a position of rest. Therefore, I checked whether or not the stated movements did enhance the responsiveness of *C. haemorrhoidalis* males by presenting some models alternately (in random order) moving and non-moving to a high number of males. Positive responses (within 50 s) were observed in 46% of the cases of moving models ($n = 95$) and in also 46% of the 112 cases of non-moving models. The mean time lags (with s.e.) till a positive response amounted to 19 ± 2 and 18 ± 2 s, respectively. Neither difference was statistically significant (χ^2 test and t-test, respectively). Therefore, the movements were abandoned in later experiments.

As HEYMER (1973a, 1973b) rightly remarks, wings look differently when viewed with either primarily incident or primarily transmitted light. Only in the latter case can wing transparency be properly judged. Thus, the position of the sun relative to the wing model and the male should be considered. Pilot experiments with models of similar value to males showed that a position of the model between the male and the sun would strongly favour the choice for this model irrespective of its own characteristics. Therefore, further experiments were performed either in the shadow or with the sun behind the male. Fortunately, males prefer a perch in the shadow during the hottest part of the

day, when they are also most responsive. As far as can be judged from the descriptions of their experiments, both BUCHHOLZ (1951, 1955) and HEYMER (1973a,b) ignored the direction of the sun light.

WING TRANSPARENCY DATA

The dark parts of four-wing sets of adult-male wings transmitted < 20% of the light in the two species. Female wings were much more transparent: in mature females generally between 50 and 60% of the light was transmitted by four-wing sets, whereas this proportion amounted to > 60% in immature females. Average percentages (with standard errors and numbers of individuals used) were: 55.0 ± 1.3 ($n = 7$) in sets of the four greenish wings of mature females of *C. xanthostoma*, 55.8 ± 0.9 ($n = 11$) in the central parts of sets of the four brownish wings of mature females of *C. haemorrhoidalis* and 49.9 ± 1.4 ($n = 11$) in their dark distal zones. With incident light, the apical zones of the female hindwings looked strikingly darker than the remainder of the wings.

Note that over most of the area of their wings the female wings of the two species showed no significant difference in transparency. Only the dark zone at the top of the hindwings of *C. haemorrhoidalis* caused a significant difference with both the other parts of these wings ($p < 0.01$, signed rank test of differences, with $n = 11$) and with the wings of the other species ($p < 0.05$, Wilcoxon test with $n = 7$ and 11).

Single wings (either forewings or hindwings) of *C. haemorrhoidalis* females transmitted about 86% of the light (about 83 % in the dark zone of hindwings) and sets of two wings about 74% (about 69% in the dark zone).

BODY VERSUS WINGS AS FACTORS ELICITING MALE COURTSHIP

C. haemorrhoidalis males did not respond to *C. xanthostoma* female models, though they readily (after 12 ± 2 s, mean and s.e.) responded to models of conspecific females ($n = 10$, $p < 0.05$). Similarly, *C. xanthostoma* males that were responsive to their conspecific female models did not respond to *C. haemorrhoidalis* female models ($n = 10$, $p < 0.05$). Males never responded to wingless female models, though they did immediately afterwards to complete models ($n = 10$, $p < 0.05$). The presence of other body parts than wings was not essential: simultaneous choices between a complete female *C. haemorrhoidalis* model and one lacking a head, an abdomen as well as all legs resulted in an equal number of preferences ($n = 20$ trials, resulting in 10 choices for each model).

The above results suggest that the presence of female wings of the "right" species is essential for eliciting male sexual behaviour. To corroborate this hypothesis, a "hybrid" model was prepared with the body of a female *C. xanthostoma* and the wings of *C. haemorrhoidalis* glued to the remaining stumps of the cut off *C. xanthostoma* wings. Males of *C. haemorrhoidalis* responded positively to this model within 25 s in 8 out of the 11 cases (73%) in which a rapid (< 25 s) positive response followed to a fully conspecific-female model. This 8-out-of-11 record was significantly more frequent than

the 0-out-of-10 record of responses to a model with full female *C. xanthostoma* wings ($p < 0.01$, χ^2 test with $n = 11 + 10$). Note that a 100% response to the conspecific-wing model was not to be expected in this kind of experiment, because males often responded to even the best models only after > 25 s. In 50-s trials with full and completely conspecific models, only 65% of the positive responses occurred within the first 25 s. As this is close to the above 73%, the value of the hybrid model (with the "right" wings but "wrong" body) will have been equivalent to a fully conspecific model.

A female model in which only the distal halves of the *C. xanthostoma* wings were replaced by *C. haemorrhoidalis* ones received 9 positive responses out of 24 trials (38%) with *C. haemorrhoidalis* males. The difference with the 0% found in the case of complete *C. xanthostoma* wings was statistically significant ($p < 0.05$, χ^2 test with $n = 24 + 10$), but the difference with the 73% in the case of complete *C. haemorrhoidalis* wings was not quite significant in a two-tailed test ($0.1 > p > 0.05$, χ^2 test with $n = 24 + 11$).

FEMALE WING CHARACTERISTICS ELICITING MALE COURTSHIP

The relative value of various sets of *C. haemorrhoidalis* female wings for eliciting courtship responses by male *C. haemorrhoidalis* was assessed by experiments in which simultaneous choices were offered between two models. In certain models, numbers of wings were reduced to increase transparency and to reduce "darkness" of the sets, in other models hindwings were either removed or replaced by forewings to evaluate the

Table I

Choices between two female models which were simultaneously presented to territorial males of *C. haemorrhoidalis*. The models consisted of a body of a female *C. haemorrhoidalis* with either a complete set of four wings (C) or a reduced (1 or 2 wings; f = forewing, h = hindwing) or altered set (4 f = four forewings; 4 h = four hindwings, 2h + 2h = two pairs of hindwings arranged to be seen separately; -S = without stigmata). Significance of differences denoted by either n.s. (non-significant), or * ($p < 0.05$) or ** ($p < 0.01$); sign tests with indicated number of trials (n). Lines numbered 1 to 10

Line	models presented	numbers of choices	n	p
1	C vs 1f	18 : 2	20	**
2	C vs 1h	19 : 5	24	*
3	C vs 2f	12 : 0	12	**
4	C vs 2h	27 : 23	50	n.s.
5	2h vs 2f	16 : 4	20	*
6	2h vs 1h	27 : 3	30	**
7	2h vs 4h	17 : 8	25	n.s.
8	2h vs 4f	29 : 12	41	*
9	C vs 2h + 2h	15 : 15	30	n.s.
10	2h vs 2h - S	20 : 17	37	n.s.

value of the dark zone in the distal part of the hindwings (at reduced and approximately normal transparency, respectively).

The results (summarized in Table I) revealed that manipulated sets should contain at least two hindwings to be equivalent to complete sets of two forewings plus two hindwings. One-wing sets (either one forewing or one hindwing) were chosen significantly less frequently than complete sets (Tab. I, lines-1 & -2). As contrasted to two forewings (significantly fewer choices than a complete set: line-3), the presence of two hindwings was sufficient to be chosen (almost) as frequently as a complete set (difference non-significant: line-4). From the above four comparisons with

complete wing sets, a preference for two hindwings over two forewings should follow (this prediction was born out by the results mentioned in line-5) as well as a preference for two hindwings over one hindwing (as indeed shown in line-6).

Thus, at roughly equal transparency over most of the wing sets (two hindwings versus two forewings: line-5), the set that showed a darker zone was strongly preferred to the set without a darker zone. This preference for a set with a darker zone also followed from a comparison of the data shown in lines-4 and -8: the similar preference (27 : 23) of a complete wing set over two hindwings was significantly different ($p < 0.05$, χ^2 test with $n = 50 + 41$) from the low score (12 : 29) of four forewings versus two hindwings. Thus also at lower transparencies (darker four-wing sets than two-wing sets), the presence of a dark zone mattered.

Transparency (darkness) as such appears to be an important trait only at very lightly coloured sets (transparency higher than about 80%), as one hindwing was chosen significantly less frequently than a set of two hindwings (line-6). On the other hand, at lower transparency values (below about 75%: two hindwings versus complete four-wing set, line-4) no significant difference was observed, though there is a suggestion that the transparency of a set of four hindwings might have been too low (see the almost significant difference in favour of two hindwings: line-7). In the case of four forewings which were valued significantly lower than two hindwings (line-8), the preference difference might have been caused either or both by the absence of a dark zone or/and by a too low transparency of the set of four wings. However, because the choice ratios 16 : 4 (line-5: two hindwings versus two forewings) and 29 : 12 (line-8: two hindwings versus four forewings) did not differ significantly ($\chi^2 = 0.6$ only), the presence or absence of a dark zone and not the difference in transparency will have been decisive.

An attempt was made to increase the value of a model over that of a complete set of wings by presenting a "super" female model with two sets of two hindwings which were arranged one behind another so that they were shown to the male as a double surface area of hindwings. This exaggerated model proved to be equivalent to a normal complete model rather than being better (line-9).

Finally, the value of the presence of the white stigmata near the apex of the female wings was tested by comparing sets of two hindwings with and without stigmata. The difference between the numbers of choices was far from significant (line-10).

DISCUSSION

In Odonata in general, reproductive isolation appears to be well-developed (BICK & BICK, 1981). It can be achieved by various mechanisms at early (courtship) as well as late (tandem formation) stages of the behavioural sequence leading to actual copulation. Of course, the earlier the prevention the more cost-efficient the isolation mechanism will be. Interruption of courtship at an early stage demands discrimination from a distance between hetero- and conspecifics, either by females or by males or both.

Females have been observed to show refusal display (quickly opening and closing

of the wings or leaving the territory) e.g. in *C. splendens* and *C. virgo* (BUCHHOLZ, 1951) to courting heterospecific males and in *C. xanthostoma* to courting males with too little wing pigmentation (SIVA-JOTHY, 1999). Also in *C. haemorrhoidalis*, males with well pigmented wings obtain more matings than those with lower proportions of pigmentation (CORDOBA-AGUILAR, 2002). Moreover, *C. haemorrhoidalis* females were observed to refuse males with an abdominal spot of the “wrong” colour (HEYMER, 1973b). However, these females are not usually able to glance at the abdominal spot of a courting male, as most of the courtships start with a head-to-head directed display (GIBBONS & PAIN, 1992; CORDOBA-AGUILAR, 2000). Therefore, the main role in early species discrimination may be played by males in this species.

Males appear to court preferably to conspecific females. As in the present study, *C. haemorrhoidalis*, *C. splendens/xanthostoma* and *C. virgo* males often inhabit the same parts of streams, sometimes even with overlapping territories (DE MARCHI, 1990; own observations) and show very similar courtship displays at the same time of the day. Nevertheless, male courtship to heterospecific females appears to be infrequent in most of such areas (HEYMER, 1973a, 1973b; own observations). Though CORDOBA-AGUILAR (2002) observed interspecific matings between three *Calopteryx* species in Spain and DE MARCHI (1990) could elicit courtship behaviour by model presentation in the (dense) mixed populations he studied in Italy, I could not. However, I could stimulate males of *C. haemorrhoidalis* to court *C. xanthostoma* females by replacing all or part of the wings of the latter species by those of *C. haemorrhoidalis* females. It is thus clear that possession of the “right” (i.e. conspecific) wings was a prerequisite for eliciting courtship in this population of *C. haemorrhoidalis*. In North America, WAAGE (1975) studied a similar situation with strong temporal and ecological overlap of two species: *C. maculata* and *C. aequabilis*. Again visual discrimination based on female wing pigmentation was a component of decisive importance in the reproductive isolation of the two species.

The passive role of females in the courtship of calopterygids makes it easy to study which of the various characteristics of their wings are of particular importance for species discrimination. To this end, female models can be manipulated and preferences can be recorded by offering choices between these models to males. Choices of *C. haemorrhoidalis* males consistently indicated a preference for wing sets that included the dark apical zone of the hindwings (Tab. I). Moreover, the experiments revealed that wing sets should be sufficiently darkly pigmented, i.e. the transparency should not exceed about 80%. The first trait, the presence of a dark zone, is characteristic for females of *C. haemorrhoidalis* and distinguishes these females from those of other European species. The second trait distinguishes mature from immature females, as wing pigmentation increases during the first week of their adult life (compare BEUKEMA, 2002a, 2002b).

HEYMER (1973a, 1973b) observed that males of *C. haemorrhoidalis* did not respond with courtship to a conspecific female forewing nor to the base half of a hindwing, but they did to a full hindwing or to its apical half. Like the results of the present study, these observations indicate that the presence of a dark wing zone is a prerequisite for

elicitation of courtship in this species. He further states that form, size and colour of the female wings play a role as well, but I cannot unequivocally trace back this conclusion from his experiments. In *C. splendens*, BUCHHOLZ (1951) found no effect of wing shape, but size and colour should resemble those of natural wings. Again, it is difficult to judge the validity of these conclusions. Because I found no difference in preference for a double-sized wing set over a normal one in *C. haemorrhoidalis*, males of this species apparently tolerate substantial deviations from normal size and form. In the present experiments, the presence of the white stigmata in the female wings did not add to their value in choice experiments. BUCHHOLZ (1955) reports a similar observation in *C. splendens*, but BALLOU (1984) found that these stigmata play a role in eliciting male courtship behaviour in *C. maculata*.

Rejection of a highly transparent wing of an immature female has also been observed in *C. splendens* (BUCHHOLZ, 1951). She states that an optimal transparency should amount to about 60% in this species. At first sight, this would be in accordance with the value of 55% light transmission I found in complete four-wing sets of the closely related *C. xanthostoma*. However, her statement that this 60% value is typical for one single female wing is inconsistent with my measurements. German female *C. splendens* wings are not that darker than Mediterranean *C. xanthostoma* ones. The transparency values reported by BUCHHOLZ (1951, 1955) are averages of a number of estimates of extremely small areas (roughly less than the width of a vein) at the same wing and such averages may have been biased as compared to (probably more realistic) values obtained by using larger areas for measurements.

Though there is ample evidence that males generally reject female wings that are too transparent, preferences at the lower (darker) end of the range of transparencies are less clear. BUCHHOLZ (1951, 1955) found optimal ranges (mostly between 80 and 60% light transmission) in various (heterochromic) forms of *C. splendens* and complete rejection of fully opaque wings, whereas HEYMER (1973a, 1973b) observed positive responses to such wings (glued on a piece of opaque paper) in *C. haemorrhoidalis*, suggesting that there is no lower limit of transparency effective in courtship in the latter species. My experiments seem to suggest that wing sets that are too dark are often rejected, but unfortunately the preference (mentioned in line-7 of Tab. I) was non-significant.

HEYMER (1973a, 1973b) raises the question whether wing transparency as such can be assessed by *Calopteryx* males (as suggested by BUCHHOLZ, 1951, 1955). In my opinion, it might make more sense to use the less specific term "intensity of pigmentation" to characterize the appearance of more or less transparent wings, because an increasing pigmentation would generally not only reduce their transparency but also enhance darkness of their colour. During their adult life, wings of female *C. haemorrhoidalis* gradually change from nearly hyaline (high transparency, low pigmentation, light colour) to a much less transparent and darker brownish colour, particularly in the strongly pigmented dark apical zone of the hindwings. In males, the initial light-brownish colour changes by increasing pigmentation to a dark brownish-black. Thus, changes in transparency as observed during maturation are closely linked to changes in (dark-

ness of) colour. Unless specifically designed experiments have been done, it will not be possible to discern which single factor (colour, darkness, or transparency) might be decisive in males' choices.

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