

Plebeian Courtship Revisited: Studies on the Female-Produced Male Behavior-Eliciting Signals in *Lycaeides idas* Courtship (Lycaenidae)

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Abstract. The male courtship behavior of *Lycaeides idas* is described. It is shown that males search for mates among females perched in the vegetation with their wings folded. A specimen sitting in the resting position common to lycaenids, with its head facing the ground is more attractive to a male than one facing upwards, and it is suggested that the search image could be a specific pattern on the hindwing. The approach of males to blue objects, common in the lycaenids, is shown to be a behavior response unrelated to mate-search behavior. It is shown that an olfactory cue elicits the touch-down of the male beside the female.

Introduction

The study of butterfly courtship behavior goes far back. The concept of behavior as a sequence of individually elicited steps, however, is of more recent date; the works of Tinbergen *et al.* (1942) and Magnus (1958) are milestones in this field.

In recent years a steady yet very thin stream of studies has been presented on the division of butterfly courtship behavior into separate phases. Numerous papers only treat the function of a certain sensual modality in the courtship, e.g., sight (Magnus, 1958; Lundgren, 1977) or smell (Bergstrom and Lundgren, 1973; Lundgren and Bergstrom, 1975) and thus only give a fraction of the sequence. More extensive attempts to track the importance of the different senses in the courtship behavior among the Lycaenidae have been presented by Douwes (1976a, b) for *Heodes virgaureae* (L.) and by Wago (1978) for *Zizeeria maha argia* (Men.).

The initiation of the present work arose from the studies of Lundgren (1977), published in this journal, where he demonstrated that *Plebejus argus* (L.) males show stronger response to females of the closely related *Lycaeides idas* (L.) than to their conspecifics. The males were presented the wing upperside of the females and the results were deduced to have originated from the males' attraction to blue color. Lundgren concluded that there must be another reproductive barrier to counteract this effect. This conclusion seems somewhat enigmatic: such a constant mistake by the male (i.e., always to prefer a nonsuitable mate) is energetically very

expensive. A male who can differentiate some other way will have several advantages: he will not have to waste energy on extra searching within a non-rewarding category, and he is furthermore likely to find the proper mate before any of his less talented congeners. The increased fitness conferred on efficient males would predict that such male's offspring would flood the entire population within a few generations.

My observations and experiments concentrated on two questions. First, is the blue coloration of critical importance in the mate-search flight? Second, is there any indication that a possible female scent plays a part in the elicitation of (at least) part of the male courtship behavior?

Materials and Methods

In the course of a study on the male androconial secretions of some plebejine species in 1978, I had the opportunity to observe the courtship behavior of both *L. idas* and *P. argus* repeatedly. Both species occurred sympatrically at a site on the island of Oland (southern Sweden; N56°42' E16°31'). The locality is believed to be the one where Lundgren performed his experiments. The locality is a sandy pine-forested area. About half of the ground is covered by a dense mat of *Calluna vulgaris*. The flight period of *idas* began on July 5th, and lasted until August 1st. No extensive records were made in 1978.

In 1980 observations and experiments were performed at a locality in central Sweden, 18 km NNW of Orebro (N59° 25' E15°04'). This locality (Figs. 1 & 2) consists of an artificially cleaned roadside. The vegetation consists mainly of *Calluna vulgaris* and a number of grasses. Surrounding areas are dry spruce forests and a pine-forested bog, respectively. At this locality *argus* was entirely absent. (Despite intensive sampling I never encountered *argus* in the area within the radius of one kilometer from the experimental site). In 1980 the first male *idas* was observed on July 11, and the first female on July 14. Bad weather conditions prevented systematic data gathering during much of the flight period, and only scant information on the courtship sequence could be added before July 28. The weather then improved and four days of intensive experimentation on the possible scent emission were possible. Beginning August 1 there was another 10 days of rain, during which only a few remaining specimens of both sexes were observed sitting in the vegetation, occasionally making short flights to forage on nearby flowers. After that no more specimens were seen that year.

The experiments were run between 1200-1600 hours for periods of about two hours each. The weather was relatively constant throughout the experimental period: approximately 22-25°C, wind velocity 2-5 m/s, degree of cloudiness 2/8-4/8 (mainly cumulus clouds).

In the experiments on the possible existence of female scents, two types of specimens were used: half of the specimens were freshly killed (never used for more than one hour *post mortem*), and half old specimens



Fig. 1. The locality where the experiments were performed. The area was cleared a number of years ago; dense spruce forest on left, pine forested bog on right.

Fig. 2. Close up view of the experimental site. The track going from the chair and stones to the birch was a route frequently patrolled by males.

collected at the same locality in 1970 and 1971. All specimens had their wings tightly folded above the thorax in the usual resting position of blues (= the posture held by females courted successfully by males). All specimens were mounted on ordinary black insect pins, with the pin head only slightly above the thoracal surface so that it was not visible between

the wings. Only female specimens were used in the experiments. In each experiment four specimens were pinned with their heads facing the ground on erect heather stems, in a spot known to be regularly routed by mate-searching males. This position in the vegetation is typical of resting *idas* females. In the experimental setup two of the specimens were freshly killed, and the other two were old ones. The specimens were arranged with specimens of the same age placed diagonally to each other at a distance of 15-20 cm to the nearest specimens. The specimens were moved one step counter-clockwise every $\frac{1}{2}$ hour in order to nullify anomalies that might possible appear due to different visibility.

In another experimental series two old specimens were placed each with their heads facing upwards and downwards, respectively. This was done to determine the importance of orientation of the specimen.

Male courtship pattern was arbitrarily categorized into six phases depending upon the level of advance in the sequence at which it was ended. The division is by no means meant to represent an exact description of phases individually elicited; they are merely a means by which to quantify how far the crude steps had advanced. The phases were numbered 1-6, the key feature(s) of each phase is described below.

- Phase 1: The patrolling/searching flight of the male is clearly arrested, and the male approaches to examine the specimen observed. Stronger expressions of this phase include fluttering around the specimen, whereas in some cases it becomes no more than a dip in the route flight.
- Phase 2: The male flutters for several seconds around the specimen usually at the same level at which the object is situated. It does not, however, touch it.
- Phase 3: The male flutters intensively around the specimen, frequently touching its counterpart with its wings. In the final stage the male tries to alight in close proximity to the female.
- Phase 4: The male alights by the side of the female. Almost instantaneously he begins to vibrate his wings over the body plane very rapidly. Meanwhile he walks up to a position parallel to the length axis of the female.
- Phase 5: The male bends his abdomen with its claspers extruded and widely apart, toward the genital region of the female. Often the fluttering behavior of the male continues throughout much of this phase.
- Phase 6: The male clasps the female genitalia.

The response of all males that showed any of the steps described above were recorded. In cases where the male made subsequent approaches toward more than one dummy these were recorded as separate approaches. The response patterns achieved were statistically compared using the chi-

square test for homogeneity with one degree of freedom at the 0.05 level of significance.

Description of the Foraging and Mate-search Behavior of Males

Two major types of activity are easily recognizable in *idas* males: foraging and mate-search. When in the mate-search phase, the male performs a rather low, rapid, frequently interrupted flight. My observations indicate that they often follow routes along vegetational strips, e.g. along a border of heather at a roadside. These routes are patrolled for the entire period of mate-search flight, i.e., several hours. This behavior is dependent upon temperature and sunshine: whenever the temperature falls below ca 20°C and/or the sun is covered by clouds for a minute or more the behavior become interrupted and fragmentary. The males rest in the vegetation, and will only occasionally fly short distances, and then at very low speed. Often the behavior in such microclimatic changes will gradually change to foraging. An important characteristic of the latter is that the males almost completely lack the approach response to blue so heavily expressed while in the mate-search phase. The presence of strong attraction of males to blue coloration resulting in male-male interactions is a well-known phenomenon, but no case was found in the literature where emphasis has been put on the fact that this behavior only occurs in one "mood" of the male. However, in his dissertation, Robbins (1978) described a similar phenomenon among eumaeine hairstreaks.

When the butterflies forage they are often seen sitting in numbers on inflorescences, there being no aggressive tendencies. It should also be noted that it is during foraging the butterflies most frequently expose their wing upperside (Fig. 4). During the mate-search flight, however, males will approach any blue object present along or close to the route being patrolled (e.g., the author's blue jeans were an object thoroughly investigated by the male blues).

The first step toward courtship is the male seeking a proper mate. He does so by searching in the vegetation, where females sit quiescent on a stem. When a Lycaenid alights on a stem it immediately turns around so that it faces the ground. It is of importance to notice that all specimens sitting in this manner have their wings folded (Fig. 3). The upperside of the wings is not visible. Hence, it is not possible to distinguish the sexes by sight alone. Females that are found on flowers where they may be foraging or sunbathing (thermoregulating ?) frequently sit with their wings more or less open. They are often approached by mate-searching males, but always respond negatively under such circumstances (first bending the abdomen upwards, and if persistently courted, also vibrate their wings rapidly or escape).

After his initial approach, the male will perform at least parts of, sometimes the entire, courtship sequence. The extension of the courtship

behavior of the male is completely dependent upon signals elicited by the female.

Results

The total number of approaches as well as the number of courtships performed to a given level was higher for fresh specimens in all categories as shown by the data in Table 1. The difference is statistically significant in



Fig. 3. Female sitting in resting posture on a heather stem.

Fig. 4. Male sitting in typical posture with wings apart, sunbathing.

TABLE 1. Behavioral responses of *L. idas* males to fresh and old female dummies. For further explanation see text.

Phase Dummy	1	2	3	4	5	6	Σ
F	18	31	16	9	17	2	93
O	13	11	2	0	0	0	26

χ^2	.81	9.52	5.44	9.00	17.00	2.00	37.22
P	> .3	< .005	< .05	< .005	< .0005	> 1	< .0005

all cases except phase 1 (the initial approach). Analysis of the data shows that the difference in discrimination between the two types is strongest between phase 2 and 3. This indicates the point at which a crucial cue is lacking.

Observations on courtship established that the initial approach of the male is elicited by visual stimuli. It was hypothesized that the position of the resting lycaenids, to which group the receptive females belong, might be a part of the search image of the male. However, the experiments on this part of the study, with the dummies facing upwards or downwards, became fairly restricted as to the numbers recorded (due to weather conditions). From the values obtained for the total observations, Table 2, the preference for the specimen facing downwards is statistically significant at the 0.005 level.

Discussion

The observations reported above on male behavior in the courtship of *L. idas* indicate that it is practically identical with the major sequences in other Lycaenids previously studied. [*Lycaeides argyrognomon* Brgrstr. (Lundgren, 1977), *Zizeeria maha argia* (Wago, et al., 1976; Wago, 1977, 1978), and *Heodes virgaureae* (Douwes 1976a, b)].

Wago et al. (1976) emphasized that males search for females sitting in vegetation with their wings folded. The fact that the males actually search for females with this presentation, and approach towards specimens sitting, e.g., on flowers with their wing uppersides well exposed to passing males, is an otherwise released behavioral response, will be shown below.

In his comprehensive studies on *Zizeeria maha*, Wago showed that the wing underside is visually similar in all parts of the visible spectrum. He showed that males approach dummies of both sexes at about the same frequency. Wago concluded that it is the color of the underside that elicits the primary approach towards the female. The undersides of the sexes of *idas* are visually indistinguishable to the human observer (they co-vary

with respect to color). There is no reason to believe that there are differences in the visual attractiveness in any other part of the spectrum either, although this was not tested. Based upon the assumption, I excluded all male dummies from my experiments. The experiments did show that orientation is of utmost importance in the attractiveness of the resting insect. Those female dummies with their heads facing upwards did not provide the optimal visual signal, and consequently no responses after phase 1 were recorded. The specimen facing the ground elicited the complete visual stimulus phase 2, however, but did not possess the olfactory cue critical for the release of phase 3. Considering the fact that practically all receptive females are found in this latter position, such a finding is not surprising. Hence there is not only the question of wing color, as suggested for *Z. maha* by Wago *et al.* (l.c.), there must be a specific pattern recognition; be it the contours of the specimen, the position of the antennae, possibly some part of the hindwing pattern such as the row of bright-colored spots along the border, or some other feature. Whatever the case, the data suggest that the high level of specific discrimination among the males is a response entirely different from the very unspecific attraction to blue coloration. Such a "double entry" to a typical behavior is furthermore evolutionarily unlikely: as mentioned above, practically all receptive females sit in the resting posture. Females foraging on flowers or otherwise sitting with their wings exposed to the sun are practically

TABLE 2. The effect of age and resting position of female dummies on male behavioral responses of *L. idas*. F = fresh specimen, O = old specimen.

Phase Dummy		1	2	Σ
F₁	↑	4	0	4
F₂	↑	2	0	2
O₁	↑	1	0	1
O₂	↓	4	11	15

χ^2	.22	11.00	4.63
P	> 50	< .005	< .05

already mated. A male wasting his time and energy on approach and courtship of such females would thus have a much lower fitness than his conspecific males searching for unmated females only. A strong selective pressure would be expected for the ability of males to search for mates among the folded-wing resting type only, as approaches toward open-wing females will not result in mating. The approach to blue coloration is a phenomenon of general occurrence among the blues as mentioned by Lundgren (1977). It deserves mention that in the case of *Plebicula dorylas* (Schiff.) the males do not approach the entirely brown upperside-exposing females, but retain the response to blue coloration as such (Pellmyr, unpubl.).

In one experiment Lundgren (1977) investigated female color preference by males of *P. argus*. In this experiment he used various combinations of dried and spread specimens of *idas* and *argus*. He measured the difference in approach to brown versus blue coloration. The results showed that the number of approaches were lowest for the mainly brown specimens, that it was significantly higher for the partially blue females, and even higher for the entirely blue males. The female of *argus* is on average much more brown than female *idas*, and in his experiments Lundgren consequently achieved a high number of cross-specific approaches. He concluded that there must be another factor responsible for the reproductive isolation than the color of the female wing upperside. When put in the light of the discoveries of Wago *et al.* (l.c.) and myself, the experimental design used by Lundgren was clearly inadequate for the measurement it was meant to produce. What he actually studied was the male's response to blue coloration. As shown above, this signal is completely different from that of the mate-search response eliciting stimulus. The parameter studied is of no importance in the courtship behavior, and could hence not be correctly considered among the possible reproductively isolating factors between *argus* and *idas*. Other cross-specific approach experiments would reveal the value of the initial visual signal as a specific recognition factor. In experiments with *Z. maha* and the closely related *Zizina otis* (F.) Wago (1977) showed that the males of *maha* responded equally well to the undersides of both species, and that the specific recognition factor hence must be another characteristic or response (e.g., some part of the female's response to the male's approach).

The approach to blue coloration and the first phase of the male courtship are superficially similar, but the evidence presented of their different initiation indicates that minor dissimilarities may occur when inspected more closely.

My experiments on fresh versus old females clearly indicate a difference in their attractiveness to the approaching males. Several of the sensory abilities that may differ between the two categories can be ruled out: thus tactile as well as visual are similar in both categories, but the existence of

an olfactory cue seems to be confirmed by these results. Further, the results show that the first two phases are elicited at about the same rate for both old and fresh females (Table 1). The step from phase 2 to phase 3 appears as the step in the courtship behavior wherein the difference between the fresh and old specimens becomes significant. It should be noted, that both of the approaches that elicited phase 3 toward old females were recorded from males previously excited by persistent approaches toward fresh dummies (approach values for these = 5) a few seconds earlier. The major step in the interval between phase 2 and 3 is touchdown of the male beside the female. It is thus suggested that touchdown is the primary response elicited by the olfactory cue of the female. The origin and nature of the female scent is unknown. No identifiable scent scales are present on the wings of the female. Preliminary gas chromatographic analyses of female *idas* wings revealed a complete absence of volatile compounds (Bergstrom & Pellmyr, unpubl.). It is thus believed that the source is located somewhere on the body, possibly the abdominal glands. In both cases where the male coupled the dead female in the experiments I only separated them using brute force. Doing this the female's genitalia were drawn out due to the very obstinate grip of the male, and they were therefore cut off before further experimentation. At first encounter the male had no problem whatsoever to move up and couple with the female, but after the genitalexomy the male would search for a suitable grasp on many sites on the female in vain (e.g., at the costa). The same thing happened with all subsequent courting males. The intensity of their courting remained unaltered, and the longest courtship ever seen was actually recorded for one of these males: 5.5 minutes. Male sense of orientation toward the abdominal tip, however, was completely lost.

From his experiments on *Heodes virgaureae*, Douwes (1976b) concluded that an olfactory cue was present either on the forewings or on the thorax.

Acknowledgments. I wish to express my sincere thanks to Professor Bertil Kullenberg for providing working facilities at the Ecological Station on Oland; Dr. Gunnar Bergstrom of the Dept. of Ecological Chemistry, University of Goteborg, for financial support during the 1978 field work; the financial support of the Biological Society of Orebro for the field work in 1980 is gratefully acknowledged. Thanks are due to Robert Robbins for valuable criticism of the manuscript, especially the mathematical part. I wish to express my warm gratitude to Mrs. Inga Thomasson for the final drawings, and to Mr. Nils Ryrholm for kind loan of the photograph for Fig. 3. I am indebted to Mrs. Christina Backman-Martinsson for linguistic revision of the manuscript.

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