EDITORIAL

Since the death of Dr. Hovanitz, I have assumed the role of acting editor of this Journal as directed by the trustees of the Lepidoptera Research Foundation. We are seeking someone who will take the position permanently, but are faced with numerous problems in so doing. No small consideration is the physical one of having our entire publishing facility, technical editing, and business location in one place. Another is the sheer responsibility of the job description, an item well expanded upon by Stan Nicolay in his presidential message to the Lepidopterists' Society (1977 *Jr. Lep. Soc.* 31:217-222). In the meantime, the mechanics of publishing so well established by Bill Hovanitz are well oiled. The JRL has the financial prospects and will continue as long as appropriate manuscripts need a home.

Although short papers, reviews, habitat descriptions, etc. will be accepted, the value of the JRL lies in the longer, well illustrated articles we prefer. These articles should emphasize research on environmentally and genetically induced variation, patterns of distribution, population structure, behavior, comparative morphology, phylogenetic and phenetic systematics and comparative physiology. In a word, on evolution as the central theme of biology as applied to Lepidoptera.

The liberal use of color plates has been an important adjunct, made possible by Bill's ability to coordinate a printer in Pasadena and a color separation firm in Missouri. Thus an apparent extravagance is permitted on our very limited budget. We are studying setting up typesetting with our own automatic composing equipment. This step would be undertaken jointly with other societies who also must find alternatives to the high costs from "turn key" publishers. Such a move would also ease editorial work both by propinquity and elimination of more layout efforts.

The basic policy of the Foundation will continue to be the publication of the JRL with few minor changes. Bill had intended to standardize formats of all papers, and this will be done in Volume 17. Changes will include providing more information in the space available. Instructions to authors will be specified on the back inside cover. The notice section will be separately printed in a "newsletter" form which will permit and encourage increased communication among members. The notices section

is open to all members; we hope you will feel free to more extensively use the service. Lastly, if we receive sufficient favorable comment we will start a section of abstracts of papers of more than usual interest which have not appeared in the regular Lepidoptera press. Accordingly, we should solicit your aid in providing reprints or notices of such papers. Our objective is to increase both membership and member participation to both better serve you and ease the load on us. The latter will occur with being able to purchase outside help. We will have publication up to date before the end of 1978 (Volume 17 completed). We invite your comments, criticisms, and help.

Barbara Hovanitz will continue to give generously of her time in the position of secretary-treasurer. She will handle all business matters including subscriptions and memberships. Karen Nielson Hovanitz as assistant editor is responsible for formatting, layout, coordination of printing, illustrations, publications, and mailing. Scott Miller has become a second competent assistant editor and colleague. Serendipity has provided an able team. Bill would be proud of us.

R. H. T. Mattoni

THE USE OF α-ECDYSONE
TO BREAK PERMANENT DIAPAUSE
OF FEMALE HYBRIDS BETWEEN
PAPILIO GLAUCUS L. FEMALE AND
PAPILIO RUTULUS LUCAS MALE

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PREVIOUSLY WE HAVE SHOWN that both males and females can be produced by the cross female *P. rutulus* X male *P. glaucus* (Clarke and Sheppard, 1955) but the reciprocal cross only produces males, the females remaining in permanent diapause until they die.

In order to examine the phenotype of the F1 females for genetic purposes we attempted to use ecdysone (Clarke, Sheppard and Willig, 1972) in order to get the female adults to eclose. Although a number started to develop only one was sufficiently advanced to score the phenotype, and that did not emerge. The present paper reports the successful use of -ecdysone and describes the phenotype of the F1 females when the female *glaucus* parent was the black form.

METHOD

α-Ecdysone was purchased from Simes, Milan. The hormone was dissolved in ethanol and diluted with distilled water to give a final concentration of 7.0 μg/ml in 10% ethanol-water. The pupae (1.4 g) were injected with 20 μl each of this solution (100 ng α-ecdysone/g w.w) through the intersegmental membrane of the abdomen, avoiding piercing the pupal gut, nervous system or spiracles. The injections were repeated every second day, each pupa receiving six in all. The butterflies emerged 24 days after the first injection.

RESULTS

Two female insects which were similar to one another were

produced from the two pupae injected. It will be seen from the plate (bottom right) that they are intermediate between the black and yellow forms in that the normal yellow pattern is present but heavily suffused with black scales. The suffusion is almost complete in a triangular area at the base of the forewing, extending out as far as the proximal black bar in normal yellow *rutulus*. A corresponding black area is to be found in the hind-wing extending from the inner margin to the proximal black line running through the cell towards the anal angle.

A similar female, together with a number of others showing less yellow, right through to black *glaucus*, was obtained by back crossing males of the F_1 to black *glaucus*.

On the ventral surface the F_1 females are also suffused with black but to a much lesser degree, so that the general appearance is rather like a sooty yellow form.

DISCUSSION

The use of α-ecdysone opens up the possibility of studying the genetics of species differences. In the case of the present cross this seems particularly likely as the F_1 hybrid females had their full complement of developed ova.

The black and yellow female forms of *P. glaucus* are controlled by a locus on the Y chromosome, apparently associated with a cytological marker (Clarke, Sheppard and Mittwoch, 1976). The inheritance of the black form is therefore maternal since the female is the heterogametic sex. The presence of an intermediate F_1, plus similar insects in the back cross using male hybrids, demonstrates conclusively that *rutulus* carries an autosomal or perhaps X-linked gene (or genes) which modifies the effect of the Y-linked allelomorph controlling black. This finding has interesting implications with respect to the evolution of the black form, which mimics *Battus philenor*. *P. rutulus*, although it flies with *B. philenor* in a number of places, including the coastal range of California, has never evolved a mimetic form. It seems possible that in the *rutulus* gene complex the Y-linked black allelomorph if it arose would be so suppressed (the F_1s having only half the *rutulus* gene complex) that it would not produce a phenotype sufficiently close to *Battus* to have any advantage.

With the new technique we hope to get a series of back crosses to *rutulus* to test this hypothesis.

TEXT FOR PLATE

Top left: *Papilio glaucus* female, black. Top right: *Papilio glaucus* female, yellow. Bottom left: *Papilio rutulus* male. Bottom right: F1 hybrid female, ex black *P. glaucus* female X male *P. rutulus*.

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THE ROLE OF INTRA- AND INTERSPECIFIC MALE:MALE INTERACTIONS IN *POLYOMMATUS ICARUS* ROTT. AND SOME OTHER SPECIES OF BLUES (LYCAENIDAE)

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INTRODUCTION

THE MALES OF POLYOMMATUS ICARUS START TO EMERGE and fly before the females. The males show a greater flight activity than the females. In addition, they mostly fly higher above the ground vegetation and are more easily observed. The more or less zigzag-formed patrol flight of the males has in other butter-flies (e.g. *Argynnis paphia* L., Magnus 1956) been interpreted as a typical appetite behaviour, a sexual search flight which brings the male into contact with the stimuli of females. A complete courtship is seldom observed. It is most often the vigor-ous mate refusal behaviour of the female or sometimes a pair in copula that catches the sight. In fact it was the astonishing frequency of male:male interactions that first struck me when I started to study this species. During the patrolling the males perpetually meet, whirl around and often pursue each other in a straight fast flight. Such "male chases" of more than 25 meters are not rare.

The aim of this paper is to discuss the role of the intra- and interspecific male:male interactions in the light of our pres-ent knowledge of natural regulation of number in populations. A survey of theories in this field is given by Dajoz (1974).

The investigation of the approach reaction of the males was performed in 1963 and in 1964, some complementary experiments in 1966.

The field observations brought about the following ques-tions:

1. Are all butterflies visually equally attractive to the *P. icarus* males?
2. Is the approach reaction of the *P. icarus* males released to the same extent by conspecific males and females?
3. How attractive are the blue males of other species of blues compared to *P. icarus* females and *P. icarus* males?

MATERIAL AND METHODS

Spanned and dried butterflies were used as dummies to release the approach reaction of the males. The dummies were hanging freely close over the vegetation in a thin black thread from 1 meter long hazelrods obliquely stuck in the ground. The position of the dummies was randomized by arranging the "angle rods" in a Latin square. A simultaneous testing of e.g. 5 types of dummies required consequently 5 x 5 rods placed at a distance of 1 meter from each other. A moderate clearing of the area was made to remove tall plants which could conceal a dummy. Futher details about the experiments are summarized in Tables I - IV.

The responses of the males were classified as approach-reactions and fluttering around reactions. The approach reactions were recorded as a "D", alluding to the fact that the response often was a fast dip movement against the dummy. It was in practice hard to distinguish between D and F reactions (fluttering around) though two observers were always recording the responses. D was much more frequent than F. The experimental method was best suited to comparing the approach tendency of the males to various visual dummies. At the compilation of the results the D and F reactions were put together.

If the same male when flying through the square responded to more than one dummy, this was recorded as well as the order of the approaches. The proportions of the results were not changed when the repeated responses were excluded.

RESULTS

The field observations showed that butterflies are strikingly more attractive to the males of *Polyommatus icarus* than other insects are. This preference has in other species been explained by the typical way of movement of butterflies.

1. Are all butterflies visually equally attractive to the *P. icarus* males?

In five experiments (Table I) 4 dummies were various blue-winged blues but the 5th alternative was another type of butterfly also occurring in the habitat. The choice of species was partly determined by the supply of spanned and dried butter-

flies. It is obvious that the *P. icarus* males did approach blue colored blues far more often than other butterflies. The greater attractiveness of the copper, *Palaeochrysophanus hippothoe* L. (Lycaenidae) and the fewer approaches to the brown lycaenid females (*Cyaniris semiargus* Rott.) can also be noted.

2. Is the approach reaction of *P. icarus* males released to the same extent by conspecific males and females?

The experiments show (Table II) that the males are as easily attracted to specimens of their own sex. The brown females of this species are more or less flushed with blue scales. The dummy females used were intermediate blue. Out of 156 females collected on Öland in 1965, 10 were classified as blue-shimmering at the wing base, 55 were blue almost to submarginal lunules, and 91 were blue almost to the black marginal line. No completely brown females with or without orange lunules were caught. The blue females are of course over-represented as they can be more easily seen.

3. How attractive are the blue males of other species of blues to the *P. icarus* males as compared to *P. icarus* females and *P. icarus* males?

The answer to that question is that the males of the tested species (*Cyaniris semiargus* Rott., *Lysandra icarus* Esp. and *Lysandra argester* Bgstr.) successfully compete with *P. icarus* butterflies of both sexes about the approach reactions of the *P icarus* males (Table II).

Even if the experimental method only tested the initial approach stage of the male chase, the experiments have shown that intra- and interspecific male:male interactions are two characteristic ways of behaviour in *Polyommatus icarus*. Table III illustrates the same behaviour in *Plebejus argus* L.

4. What stimuli release the approach responses of the males?

The experimental squares were set up in wind-protected parts of the habitat. As a rule only the upper side of the dummy wings was exposed to the males. In the first experiment the spanned butterflies were first hanged 30 centimeters above the vegetation. Most of the males flew below the dummies. Between 9:20 a.m. and 2 p.m. 19 nonresponses and 8 approaches were registered. The dummies were then lowered to hang close over the vegetation. Between 2 and 5:10 p.m. only 2 out of 37 males passed through the area without taking notice of the dum-

mies. This behaviour indicates that colour signals from the upper side of the wings are the active stimuli. An objection is that the under side of the dummy wings is shaded. This was not the case when a spanned and dried male was rotated around the body axis. The rotating dummies were fixed to a thin steel axis running through a 2 m long hollow spinning rod. The rotational velocity could be varied with the spinning reel which drives the axis. The alternating flashes of upperside and underside colour from a male dummy with a "fluttering speed" which seems normal to our eyes did not increase the atractiveness of the male as compared to when presented not rotating.

To examine the reaction of the male to a larger blue wing surface "giant males" (3 x) were made by covering a butterfly silhouette of stiff paper with the wings from 3 males. The giant males got almost as many responses as the normal *P. icarus* males (Table II). As similar experiments have already been made (Tinbergen 1942; Magnus 1956) no further experiments were made to see if the ordinary size of the male is optimal. The reactions to deformed males suggest that the shape of the coloured object is unimportant to the males as in other species of butterflies which have been investigated in this respect.

In many species of blues e.g. *Polyommatus icarus* and *Lysandra icarius* the ground colour of the females varies from brown to more or less blue. The readiness of the males to approach blue objects ought to lead to a selection in favour of the blue colour genes. The grey-green mutant colour form valesina of *Argynnis paphia* is heriditary dominant expressed only in females. Magnus (1956) has shown that one explanation of its rareness is a sexual preference by the males for the normal yellow-brown colour of the female.

The two species *Plebejus argus* and *Lycaeidas idas* are very similar and often hard to distinguish without examination of the genitalia. The *P. argus* females are brown but the *L. idas* females more or less blue and rarely completely brown. The square experiments have confirmed (Table III) the existence of interspecific male approaches between these species.

P. argus and *L. idas* are consequently suited objects for an investigation of the female colour preference of the males. Fortunately, I had in my possession some blue and some brown spanned female specimens of *L. idas*. The most eligible locality found in the neighbourhood was an area in a pine forest clearcut some years ago, with *Calluna vulgaris* as a dominant in the

herb layer. 60 males were caught and released again, 28 were *P. idas* and 32 were *P. argus*. As it is impossible to determine with certainty to which species the approaching males belong without catching the butterflies a pure population of *L. idas* would have been better.

The supply of spanned females permitted only a 3 x 3 square with: 1 *L. idas* brown female, 2 *L. idas* blue female and 3 *L. idas* male. The result (Table IV A) is very interesting. Males of both species respond to the dummies which was verified by catching some of the reacting males. The experiment indicates a visual preference selection of blue *L. idas* females. Even the *P. argus* males are more easily attracted to the blue *L. idas* females than to their own brown females. This remarkable fact was further supported by two experiments in a locality where only *Plebejus argus* were flying (Table IV B).

A similar visual interspecific female preference has earlier been found in other species. According to Petersen et al. (1952, 1954, 1963) the white males of *Pieris bryoniae* Hübner prefer the white females of *P. napi* L. to their own yellow females. This may be a secondary effect of intra- and interspecific male:male interactions released by the white male colour of *Pieris*. The *P. bryoniae* males do more often approach each other than their own females. Males of *Papilio rutulus* Boisduval are in the beginning of the courtship more often attracted to female *P. multicaudus* Kirby than to their own females (Brower, 1959). In this case the explanation can be quantitative differences. To human vision the females have the same yellow colour, but the yellow area on the wings of *P. multicaudus* is larger.

Sign stimuli are mostly qualitatively optimal. One of the phenomena which the dummy experiments have revealed to the ethologists is the existence of supernormal stimuli. Various selection pressures often prevent the realization of quantitatively optimal stimuli in the organism. It must yet be considered as remarkable that in two sympatric species or two allopatric species with a contact zone the females of one of the species have got supernormal sign stimuli to the approach reaction of the males of the other species. It is necessary to ask for the compensating isolating mechanisms. Brower found a partial season isolation and a difference in altitude preference in *Papilio multicaudus* and *P. rutulis*. Petersen established that where *Pieris bryoniae* and *P. napi* appear as different species habitat

isolation and a bad hybrid vitality were active. An understanding of the isolation of *P. argus* and *L. idas* needs further investigations. Although they morphologically are very similar species the male genitalia are strikingly different (according to Chapman the most different in tribus *Plebejini*). Sengün (1944) showed that curtailed males without the whole copulation apparatus including aedeagus are capable of fertilizing the females. As Petersen (unpubl.) has pointed out such experiments are only indicating. Small quantitative differences in male copulation success can have a considerable isolating importance. *Plebejini* is characterized by female genitalia deviating from those of the main part of *Rhopalocera*. The vaginal orifice is situated on the tip of an extrudable organ (hypostema + heina) behind the 7th sternite. As I have failed to handpair these butterflies it seems that the female copulation apparatus is not extruded reflexably when the valves of the male grip the abdomen tip. It may function as an effective refusal apparatus against males which do not present the right stimuli.

5. Are the male:male interactions the defence part of a territorial behaviour?

Gently following males of *Polyommatus icarus* in various localities did not indicate that the male:male interactions are concerned with the defence of an area through chasing or leading the intruder away from a domain to which the male returns. Every male was followed until it was lost. The most frequent reason was interference with another male. The males were frequently lost during the flight chase or it was impossible to identify the traced male afterwards.

During observations of another species I spent some whole days on a 200 meters long rectangular meadow. In this locality the first *icarus* males emerged on the 11th June in the year 1966. The male resided all the day in a well defined area in the east part of the meadow. The size of the domain was estimated to 1/3 of the length and 1/8 of the width of the meadow. On the 13th June male No. 2 appeared. The first male was still flying in the same area as before. Male No. 2 spent the whole day in a less well-defined domain west of the flight area of No. 1. In the afternoon a sustained "fluttering around" was observed near the ground in the contact zone between the domains followed by a fast chase to the west end of the meadow. Later on both males were again observed in their respective areas. On

the next day several males were flying. The population was in constant restlessness. The male chases were frequent.

Without individual marking one can not be absolutely sure that defended territories do not exist but my field observations indicate that the *P. icarus* males locate their mates by patrolling according to the terminology of Scott (1972). Tendencies to perching are observed at low population densities but male:male interactions not attributable to the defence of a defined area to which the defender returns are much more frequent.

A 16 mm colour film on the biology of *Cupido minimus* L., *Maculinea arion* L., *Lycaeides argyrognomon* Bgstr., *Aricia allous* H-Gbg., *Cyaniris semiargus* Rott., *Polyommatus icarus* Rott., *Lysandra icarius* Esp. and *L. argester* Bgstr. has been made and it is filed in the Department of Entomology at the Institute of Zoology, at Uppsala university, together with a scenario in English. In this film (1,5 hrs) male:male interactions as well as feeding behaviour, courtship and egglaying are documented.

DISCUSSION

I find it very unsatisfying to explain the male:male interactions as the result of a poorly characterized releasing mechanism for the sexual appetite flight. There ought to have been a selection against unnecessary approaches as indicated by the few approaches to other butterflies. The selective disadvantage of "timewaste" during the search for females measured as reduced fertilization rate has been demonstrated (Parker, 1970) in a dung fly (*Scatophaga stercoraria* L.)

What evolutionary advantages have maintained the high level of intra- and interspecific interactions between blue males? There must also have been a selection for epigamic recognition. That is why the males' chasing of each other seems too sustained only to be a mate recognition behaviour. The explanation can be that the male:male interactions are agression concerned with the defence of an area. Perching behaviour is defined by Scott (1972) as a mate-locating method in which males sit at characteristic sites and dart out at passing objects in search of females. This type of behaviour is frequent in butterflies but I know of only two investigations focused on the return of the male to the same area, the defended territory. A comparison between these is made in Table V.

According to Baker (1972) the benefit of the territorial be-

haviour of the nymphalid butterflies, *Aglais urticae* L. and *Inachis io* L. is an increased female quota for a territory-occupying male. The optimum territories have an edge or corner site where the stream of females is more intense. The study area is not more closely described but the localities seem not to be isolated. Both species are migrant. Voluntary male displacement occurs between the territorial periods. The distance covered during a fine day is about 1 km in *Aglais urticae* and 0.5 km in *Inachis ino*. Without physically injuring the intruders the territorial defence is rather elaborate involving in *I. ino* defence by the very presence of a male in the territory, chasing or leading the intruder away, and demonstration of better manoeuverability and thus as a consequence seemingly potential superiority in a coming courtship contest about the same female. A low territory: male ratio, i.e. the ratio of suitable territories to the number of males, is suggested to select for a break-down of the territorial system. Tendencies in that direction are shown by *A. urticae* through the increasing readiness of the incoming males to share a territory with males already established rather than to continue to search for an unoccupied territory.

Douwes (1975 b) has investigated the territorial behaviour in *Heodes virgaureae* L. as a part of a detailed study of the ecology and ethology of the adult stages of this species. The study area was a well isolated, fairly small locality of the species with a low migration and a low territory: male ratio. Only a few males defend a couple of optimal territorial sites (perching areas). Douwes' results indicate that territorial *H. virgaureae males* are inferior to non-territorial ones in the competition for females and nectar resources, since females and suitable flowers occur principally in the open field at some distance from the male territories. The selective advantages of this territorial behaviour is hard to understand but Douwes suggests it might be that it makes the males cover the habitat better in their search for females. Tendencies to territorial behaviour occur also outside the territories preferred. The few males which occupy the preferred territorial sites due to their superiority in competition seem to "sacrifice" themselves for the best of the population. The consequence ought to be a lower female quota and a negative selection which work to eliminate this behaviour. A solution of these difficulties might be to look upon the preferred territorial sites as located not "at a distance from" but

"on the route to" feeding and oviposition sites. According to the description they can be edge territories similar to the ones in *I. ino* and *A. urticae*. That only one female was observed in the territories could perhaps be explained by the more unobtrusive behaviour of the females and by the fact that the territorial study was performed before the peak of the female number. The distribution study (Douwes, 1975 a, Fig. 5) shows that the territorial sites lie at intense traffic routes. In addition they lie close to two of the three most loco-climatically favourable sites and two places with abundant Tubuliflorae flowers. Douwes also studied thoroughly another population which virtually lacked territorial sites and territorial males at least with the characteristics defined from the other locality. Such a habitat-adapted behavioural polymorphism is conceivable. Chitty (1967) writes about intraspecific competition: "If we can expect that interference has severe effects on survival and reproduction it is less reasonable to assume that all genotypes suffer equally than to assume that they are affected non-randomly".. Through the work of Gilbert and Singer (1973) we know that in the butterfly *Euphydryas editha* "the longstained selection pressure associated with the detailed ecology of each population can produce intraspecific genetic differentiation in dispersal tendency such that even populations with abundant resources may differ in dispersal behaviour". Douwes (1976 a) found that also in the non-territorial population the colour responsible for the attraction of the male to the female is less strongly expressed in the female than in the male. This means that the male:male interactions must be frequent also in the non-territorial population.

Breakdown of territorialism at least in the butterfly species discussed here does not lead to breakdown of the male:male interactions. The intraspecific competition seems to have different expressions at different population densities in the same way as has been found in e.g. *Mus musculus* (Anderson, 1961) with the exception that when territorialism breaks down when the population density rises, no social hierarchy is established in the butterflies in absence of ability to individual recognizing.

The male:male interaction are truely. density-dependent. If the variations in behaviour as a function of population density are summarized (Table VI), it seems highly probable that the male:male interactions are the feed-back part of the natural regulation of population density. All females are initially unwill-

ing. Small differences in persistance are aimed to affect fecundity.

According to Magnus (1963) performing of "mistake" approachflights in *Argynnis paphia* gives a lowered stimulus threshold and a sexual over-excitement. The males' chasing of each other may contribute to maintain the sexual mood especially in the beginning of the flight period when females are rare as the males begin to hatch earlier than the females.

Why are the male butterflies more brilliantly coloured? This problem has been discussed by many authors, e.g. Scott (1972) and Douwes (1976 a). Is it because sexual selection is more important in the males whereas in the females there is a counter selection against predation? On the other hand male colour is not exposed during the decisive stages of the courtship. The existence of polymorphism mainly restricted to the females speaks for sexual differences in selection. One suggested explanation is genetic (Magnus, 1963). If male:male interactions have the vital importance for population regulation, which is suggested in this paper, male colour is meant for other males. This may also include chemical male signals. Douwes (1975 b) found a gap between the male response to conspecific males in *H. virgaureae* and to other butterflies which cannot only be explained by differences in visual stimuli. In the Latin square experiments with *P. icarus* odor-males painted with a chloroform extract of fresh males got more approach responses than non-odor males (Table I). These results may indicate that male odor is à signal in the male:male interactions.

Color similarity and color unimportance at the end of the courtship mean selection for chemical and tactile specificity. The main components of the male wing volatiles have been identified (Lundgren & Bergstrom, 1975) only in one species of blues (Lycaeides argyrognomon). Since then the methods for isolation and concentration of the odor substances as well as the sensivity of the GLC-MS instrument have been improved. A GLC of the volatiles from the male wings of the same species (Fig. 1) shows a very complicated peak pattern, representing more than 120 components with rich possibilities of species specificity of the male scents. *Polyommatus icarus, Lysandra icarius, L. argester* and *Cyaniris semiargus* have partly overlapping spectra of larval host plants. They also share the nectar resources. Nectar is continually produced but Wynn-Edwards (1970) emphasizes correctly that all supplies of food are finite
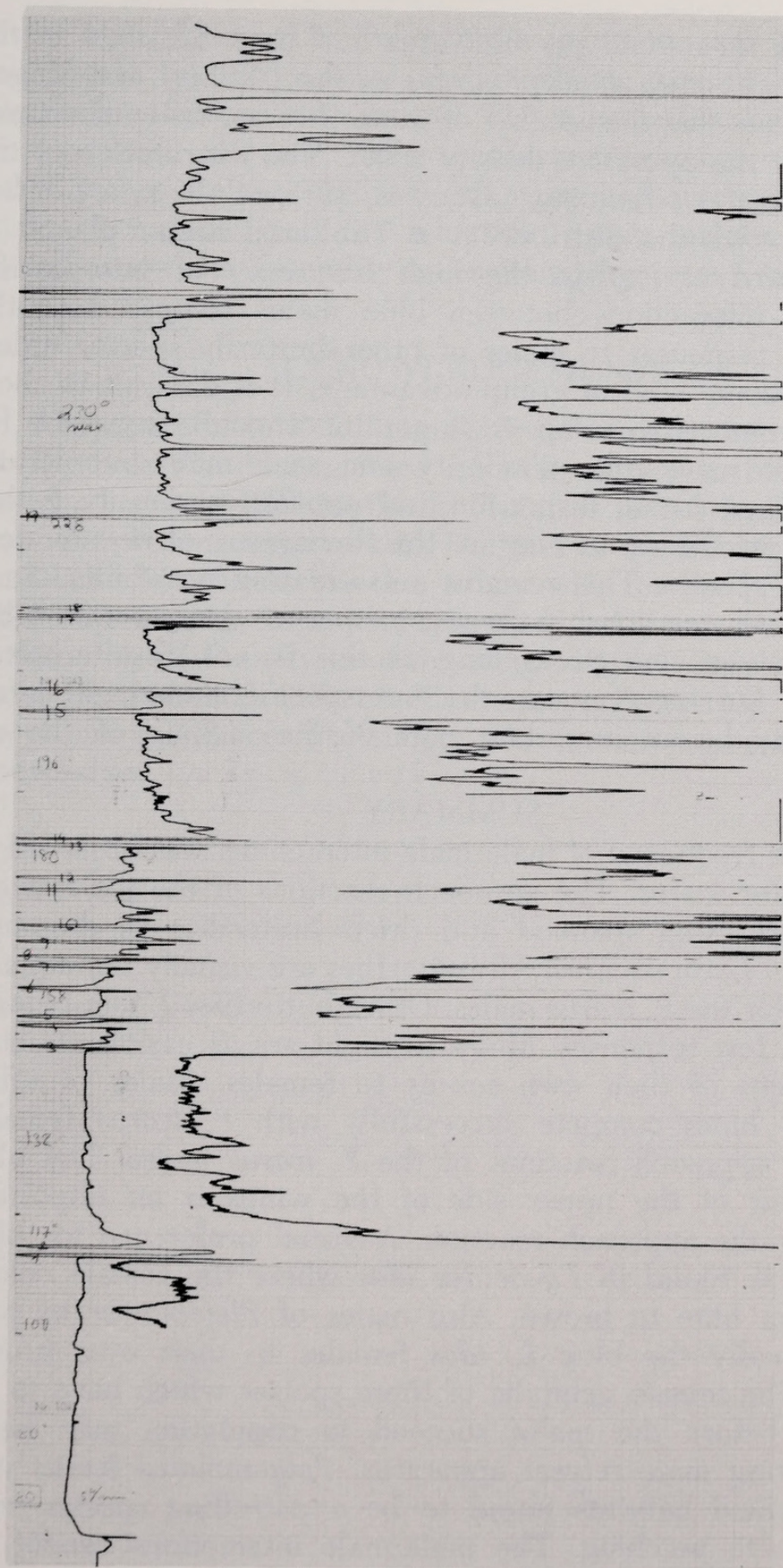
Fig. 1.
Capillary gas chromatogram of the volatiles from the wings of two males of *Lycaeides argyrognomon*. Ionization at 70 eV electron energy and 200μA electron voltage. Temperature programmed with 5°C/min from 80 up to 230°C. More than 120 components are separated. Scot column 65 m, SE-30.

in terms of their yield per unit area and time. Changes in the population structure of *Euphydryas editha* (Gilbert and Singer, 1973) indicate that the number of butterflies per unite of volume of nectar is the operative density index. The distribution of the lycaenid *Heodes virgaureae* (Douwes, 1975 a) shows a positive correlation with the distribution of Tubifloral nectar plants.

It is hard to explain the high frequency of interspecific male:male interactions between blue males compared to the number of responses to males of other butterfly species unless it involves some kind of group advantage. It is difficult to show that the resource overlap is important enough to select for interspecific male color similarity and male:male interactions capable of regulating dispersion and population density within the group in the same way as this behaviour obviously does within the species. This remains a fascinating possibility. Such an ecological relationship between species does not conflict with the niche concept as long as this is not misinterpreted as spatial. On the contrary the interspecific male:male interactions may be an important part of the niching of the resources.

SUMMARY

An high frequency of male:male interactions was observed in *Polyommatus icarus*. The approach reactions of the males were investigated using spanned and dried butterflies as dummies arranged in Latin squares. All butterflies are visually not equally attractive for the *P. icarus* males. Other butterflies ("non-blues") got only a few responses. Males in flight are as easily attracted to specimens of their own sex as to females. Males of other species of blues compete successfully with *P. icarus* females about the approach reactions of the *P. icarus males*. The blue wing colour of the upper side of the wings is an important stimuli for the approach reaction. A visual preference for blue females was found in *Lycaeides idas* where the female colour varies from blue to brown. Also males of *Plejebus argus* preferred visually the blue *L. idas* females to their own brown females. The female genitalia of these species which have to be extruded before the males succeed in copulation may be a compensating mate refusal apparatus. *Polyommatus icarus* was in the studied habitats found to be a patrolling species with tendencies to perching. The male:male interactions cannot be merely "mistake" approaches meant for females. True territorial behaviour occurs in butterflies but male:male interference persists after the breakdown of territorial behaviour at low ter-

ritory:male ratios. The following suggestions are made: The male:male interactions are the feedback part of the natural regulation of population density. The more brilliant male colours and perhaps also the male scents are primarily directed to other males. Colour similarity of males and interspecific male:male interactions may be adaptive within species complexes by adjusting the fecundity to overlapping resources.

ACKNOWLEDGEMENTS

Table I

Polyommatus icarus. Male approach responses to some other butterfly species compared to responses to blues of the species *P. icarus* (P.i.), *Cyaniris semiargus* (C.s.), *Lysandra icarius* (L.i.) and *L. argester* (L.a.). Dried and spanned butterflies. Latin square 5 x 5. The odor dummies were painted with a chloroform extract from 5 fresh male or female specimens.

Exp. No.	1	2	3	4	Other butterfly species	
		Blues				
	P.i. ♀	P.i. ♀ (odor)	P.i. ♂ (odor)	P.i. ♂		
1	12	27	37	44	Argynnis paphia ♂	2
2	16	20	18	30	Brenthis ino ♂	2
3	39	49	57	63	Palaeochrysopanus hippothoe ♂	17
	P.i. ♀	P.i. ♂	C.s. ♂	L.i. ♂		
4	20	19	16	14	Coenonympha pamphilus ♂	0
	P.i. ♀	P.i. ♂	C.s. ♂	L.a. ♂		
5	22	21	33	27	Cyaniris semiargus ♀ (brown)	2

Table II

Polyommatus icarus. Interspecific male responses to males of other species of blues compared to conspecific butterflies of both sexes. Dried and spanned butterflies. Latin Square 3 x 3 and 5 x 5. Species name abbreviations the same as in Table I.

Exp. No.	1	2	3	4	5
	P.i. ♀	P.i. ♂	C.s. ♂		
1	8	23	12		
	P.i. ♀	P.i. ♂	C.s. ♀	L.i. ♂	P.i. ♂ (3x)
2	22	49	29	30	28
3	14	14	18	9	16
4	21	20	17	19	18
5	4	4	9	7	8
Sum (exp. 2-5)	61	87	73	65	70

Table III

Plebejus argus. Intra- and interspecific male:male approaches. Dried and spanned butterflies. Latin square 3 x 3.

Exp. No.	1 Plebejus argus ♂	2 Plebejus idas ♂	3 Cyaniris semiargus ♂
1	10	23	19
2	20	42	27
	30	65	46

Table IV

Plebejus argus and Lycaeides idas. Male approaches to brown and blue females respectively. A. experiments with a mixed population of *P. argus* and *Lycaeides idas.* Males of both species respond to the dummies. B. Only *P. argus* occurred in the locality. Dried and spanned butterflies. Latin square 3 x 3.

A.	1 Lycaeides idas brown female	2 Lycaeides idas blue female	3 Lycaeides idas male
	17	81	96

B. Exp. No.	Plebejus argus brown female	Lycaeides idas blue female	Plebejus argus male
1	0	10	6
2	7	48	18

Table V
Comparison between the territorial behaviour in *Inachios io*, *Aglais urticae*, and *Heodes virgaureae*.

Behaviour characteristics	I. io (Baker, 1972)	A. urticae (Baker, 1972)	H. virgaureae (Douwes, 1975 b)
site of the territories	en route to oviposition sites	at the oviposition sites	at some distance from feeding and oviposition sites
territory: male ratio	high	low	low
number of males per territory	1	4	1 - 2
mating place	at roosting place to which the female is followed	at the territory	at feeding places
time for holding a territory	240 min	90 min	1 - 2 days
time for setting up a territory	midday earlier than A.u.	midday	morning
number of territories per male and day	1	2	1
voluntary displacement	before midday until settling down in a territory	before and between the territorial periods	after the territorial period
types of male:male interactions	deterring through presence, chasing (leading) away, contest of manoeuverability	chasing or leading away	chasing or leading away
territorial: nonterritorial male ratio	high	high	low
suggested selective advantages	increased female quota, proximity of roosting sites	increased female quota, containing roosting sites	spacing out the males, increased chances for the females to be fertilized, decreased female quota for territorial males

Table VI
Variations in behaviour as a function of population density.

Increasing population density	
Increasing	Decreasing
male:male interactions	territorialism
disturbances of egglaying females	territority:male ratio
physiological stress	undisturbed courtship persistence
net emigration	fecundity

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