Res. Popul. Ecol. 37(1), 1995, pp. 111-118.

Special issue:
Dispersal Polymorphism of Insects:
Its Adaptation and Evolution
Papers from a symposium in Okayama, 1994

Factors and Consequences of a Non-Functional Alary Polymorphism in *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae)

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Abstract. Functional alary polymorphisms have been studied rather extensively in several insect species. This review article deals with factors controlling wing polymorphism in a flightless species, *Pyrrhocoris apterus* (L.), and discusses its adaptive significance and mechanisms for their persistence under natural conditions. The macropterous morph is determined by a recessive allele whose penetrance depends on photoperiod and temperature. Natural populations of this species contain a small fraction of flightless macropters. The disadvantages of being a macropter (increase of development time, decrease of fecundity) are minimal, while the benefit may consist in the tendency to pre-reproductive arrest of ovarian development in teneral females. It prevents establishing a second generation which would mostly die during the next winter. The mechanism of alary morph regulation may be an ancestral trait linking *P. apterus* with other polymorphic Heteroptera, while its decreased penetrance may be a derivative character. Variation in fitness due to alary morphs is small compared to the one associated with differences in body size. The latter is environmentally determined, and not linked to the genetic basis of wing polymorphism. In the "mosaic" of phenotypes of various size the significance of the genetic macroptery may be close to neutral.

Key words: genetic determinants, environmental factors, body size, life strategies, adaptivity, phylogenetic constraints, neutrality.

Introduction

Causes and consequences of the evolution of brachyptery and wing polymorphism in insects have been recently reviewed by Roff (1986, 1990) and Roff and Fairbairn (1991). Brachyptery, a secondary trait, may confer an adaptive advantage under specific environmental conditions including habitat stability and its low complexity. Brachyptery (or flightlessness) is usually connected with properties that may increase fitness under favourable conditions, like increased fecundity and shorter development. The contrary conditions of patchy distribution and temporary availability of resources will favour macropterism (or flight ability), i.e. individuals whose agility helps them to escape the extinction of a local population. Polymorphic species may share the advantage of both wing morphs. Winged morphs are produced under specific environmental conditions which signalize the onset of an unfavourable period when flight becomes a prerequisite for survival of the species. While this explains alary polymorphism in species where the macropterous or winged morph is capable of flight, species where both morphs are unable to fly pose the question why their polymorphism persists and what its significance is.

Heteropteran species have been a frequent subject of the study of wing dimorphism (Vepsäläinen 1974; Braune 1983; Heliövaara 1984; Tanaka and Wolda 1987; Muraji and Nakasuji 1988; Fujisaki 1989, 1992, 1993a,b; Solbreck and Anderson 1989; Harada and Taneda 1989; Zera and Tiebel 1991; Harada and Numata 1993; Socha et al. 1993). The only case of a non-functional polymorphism is *Gerris remigis* Say (Fairbairn 1986, 1988) where macropters are prone to pre-diapause reproduction in warm habitats. Non-functional macropterism in this species persists due to its coupling with another adaptive trait. *Pyrrhocoris apterus* (L.) is another example of a non-functional wing polymorphism.

Pyrrhocoris apterus is a Palearctic species with core distribution in the Mediterranean area and eastern and central Asia. Its biology has been reviewed by Socha (1993). Isolated populations are present as far as southern Sweden, northern Russia and central Siberia. The adults are about 1 cm long, black with an aposematic red design. The larval development lasts about 40 days at 26°C and long-day photoperiod. In the Czech Republic, central Europe, *P. apterus* has one generation per year. The overwintered adults lay eggs in late March to June, and in batches of 30–60, with the egg depositions being separated by about 1 week intervals. As the threshold temperature for egg and larval development is above 12°C (Honěk and Kocourek 1990; Numata et al. 1993), the species is thermophilic. The larvae have a conspicuous thermoregulatory behaviour. They increase the body temperature by basking at low ambient temperatures, but actively escape warm places and shelter at high temperatures. This behaviour prevents rapid development and early adult moulting, and sets the development length in the open to about 3 months (Honěk and Šrámková 1976). Adults of the new generation appear from June but most adult moultings occur in August and September. Diapause is induced and maintained by short day photoperiod of less than 16L: 8D (Hodek 1968). At 50°N latitude, this day length (including the civil twilight) is attained on August 11. Some of the early moulted adults may reproduce in the same year. This is fatal for their offspring most of which do not mature before the onset of the winter and then die. There is no precise study of voltinism in mediterranean and subtropic regions where *P. apterus* may have two generations per year. In southern regions the bugs feed on seeds of different Malvaceae. In central Europe, the essential food are seeds of linden (*Tilia cordata* Miller).

Pyrrhocoris apterus has a conspicuous wing polymorphism. In brachypters (*br*), the fore-wing membranes are absent and the hind wings are reduced to small scales or completely missing. In macropters (*ma*), the fore-wing membranes match or exceed the last abdominal tergite, and the hind wings are partly or fully developed. The thoraces of *br* and *ma* are also differently shaped. The fore-wing membranes persist from adult moulting until starting oviposition, then they break down. The ma of *P. apterus* cannot fly.

The flightlessness of the *ma* morph raises the question of its function and adaptive significance: why does this morph persist in a population? In the discussion I will consider two alternatives: (1) the *ma* morph confers an advantage other than dispersal or migration, or (2) the trait is selectively neutral and persists in populations as a relic of functional polymorphism. The fitness variation due to presence of a "gene" for a wing morph may become unimportant if there exist a source of fitness variation which is not linked with genetic basis of the alary polymorphism. Such important source of fitness variation is individual differences in body size. In the second part of this review I consider the causes of body size variation and their influence on fitness.

Review of experimental results

Factors of wing polymorphism and its consequences

The factors influencing alary polymorphism of central European populations were investigated under laboratory conditions. The development of wing morphs is under genetic control. F_1 offspring of strains derived from wild populations of the Czech Republic and reared at 26°C and long day photoperiod (17L: 7D) yielded 0–11% of *ma* males and 1–14% of ma females (Honěk 1976a). Nine generations of selection under long day conditions increased the average proportion of *ma* to 70%. An alternative method of increasing the selective pressure against *br* morph (larval development at short day, oviposition of ensuing ma at long day) increased the proportion of *ma* to >90% under long day and to 60% under short day conditions (Honěk 1979). The plateau was maintained, under intermittent selection, for 65 generations. Crossing experiments with a *br* wild material revealed that macropterism is controlled by a recessive allele whose penetrance is influenced by a series of modifiers. The selection involves increasing the frequency of the recessive allele, and decreasing the control of the modifier complex over the penetrance of the homozygotes (Honěk 1986c).

The penetrance of the *ma* allele depends largely on photoperiod and temperature (Honěk 1976a). In the wild material maximum penetrance of *ma* was achieved under long-day photoperiod and temperatures between 24–27°C (Fig. 1). Selection for macropterism decreased the development response to short-day photoperiod but did not alter photoperiodic sensitivity (Honěk 1979). A short

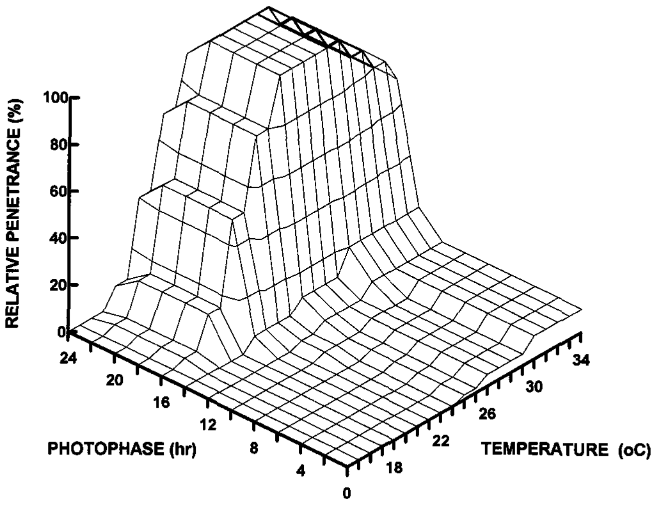

Fig. 1. The effect of photoperiod and temperature on the relative penetrance of the macropterous trait (maximum = 100%) in wild material.

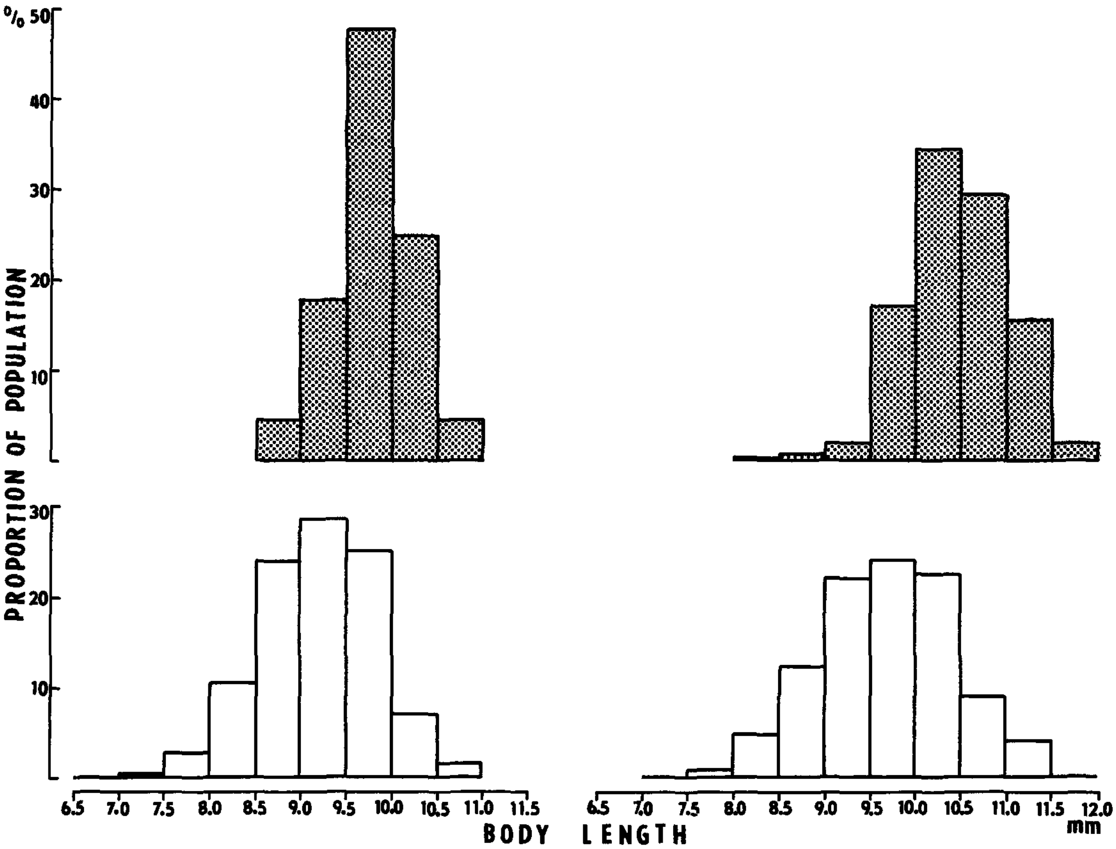

Fig. 2. Distribution of adult body length of macropterous (above, shaded bars) and brachypterous (below, open bars) males (left) and females (right) in natural populations of the Czech Republic (Honěk 1981).

(2 day) exposure to cold had a strong brachypterizing effect, particularly when applied in the 4th and early 5th instars (Honěk 1981). Population density also affected wing development; maximum production of *ma* occurred at medium population densities while, severe crowding as well as rearing of larvae in isolation had a brachypterizing effect (Honěk 1976a).

Both wing morphs differed in a number of physiological and morphological traits. Average body size is greater and the range of its variation smaller in *ma* than in *br* (Fig. 2). Development time of *ma* and *br* is nearly identical in the wild material, but in the selected strain development of *ma* took longer than that of *br*. The difference was 42.5 day degrees (9.1% of the total development time) in males and 30.7 dd (6.7%) in females (Honěk 1985). The most important difference was the tendency in *ma* to arrest the ovariole development immediately following adult ecdysis, even under diapause preventing long-day conditions (Fig. 3). Long preoviposition is associated with a decrease in overall fecundity but this difference was compensated by prolonged exposure to cold (Honěk 1985). The effect of chilling during hibernation makes the fecundity of both morphs in the following season similar. Diapausing *br* that were transferred from the open to favourable laboratory conditions also started laying eggs earlier than *ma*. However, in post-diapause (quiescent) individuals (transferred to the laboratory in March) there was no difference in preoviposition.

The occurrence and relative fitness of wing morphs in the open

In the Czech Republic I have investigated 13 wild populations systematically for 10 years, and 114 further populations I have visited occasionally. The proportion of *ma* was low, typically between 0–14% (Fig. 4) and higher in males than females (Honěk 1976a, 1981). Annual variation in the percentage of *ma* was significant. This data concerns the overwintering populations where the larvae had either finished their development or died. The proportion of *ma* was determined by the proportion of adults which moulted before August, i.e. in the period favourable for *ma* production. Among adults which moulted in July in warm years (e.g. 1992), up to 75% of the males and 77% of the females was *ma*. In the open, an unspecified combination of environmental conditions

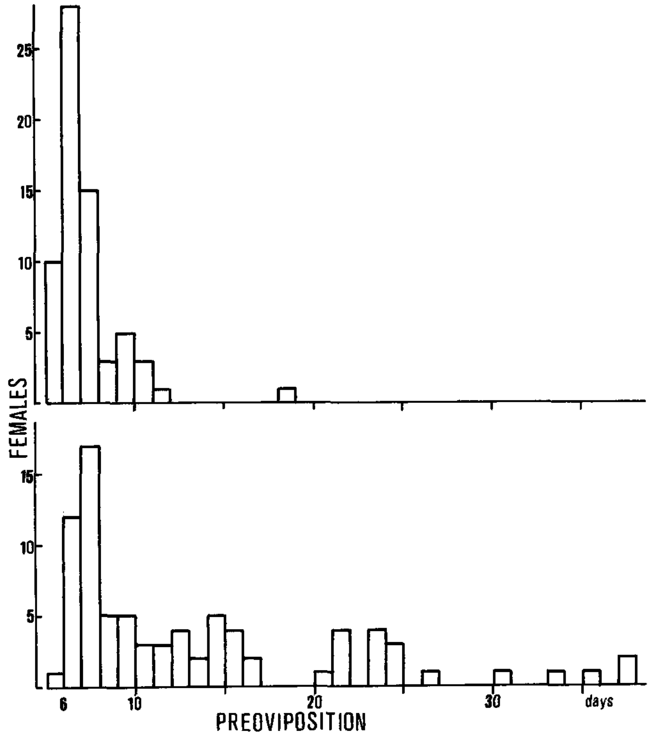

Fig. 3. The frequency of the length of the teneral preoviposition period at 18L: 6D photoperiod and 26°C in brachypterous (above) and macropterous (below) females (Honěk 1985).

(probably temperature fluctuations and changing daylength) promoted *ma* production more than the "optimum" laboratory conditions. The role of temperature in the open could be demonstrated from a positive correlation between percentage of *ma* in different years and sunshine hours in June-August (Honěk 1976b), and from a negative correlation between percentage of *ma* and the length of the larval development (Honěk 1981). From mid-August on the larvae experience short day photoperiods and occasionally also cold spells, and moult to *br*. The small June-July population of adults with a high proportion of *ma* is then "diluted" by the great number of *br* moulting in August-September.

The differences between the fitness of *br* and *ma* morphs in the open appear small. The energy used for development is probably greater in *ma* than in *br*, but the difference may hardly become important as food is usually in surplus. There was no difference in winter survival, and post-hibernation mating was not assortative (Honěk 1976b). The differences in fecundity and longevity could not be traced due to erosion of fore-wing membranes and hind wings in ma which makes the morphs undistinguishable during the reproduction period. The de-alation probably increases similarity in the reproductive output of both forms.

Macropters may benefit from the tendency for arrest of ovariole maturation at the teneral period which prevents immediate oviposition in early moulted adults. The photoperiod in late June and July is sufficiently long to promote reproduction in *br*. A fraction of newly moulted *br* females start to lay eggs. These females die during the winter together with their offspring which largely cannot complete larval development before the onset of the winter. Macropters appear to be protected from this untimely reproduction.

The correlation between the penetrance of the *ma* morph and development length may be among the causes of the presumed north-south gradient of the increasing frequency of *ma* (Honěk 1987b). Brachypters of a strain with low penetrance of recessive macropterous trait had a larval development that was 10% shorter than br of a high penetrance strain. The difference could be due to the reversal of the macropter development pathway into a brachypter one during late ontogeny. The cryptomacropters, i.e. brachypters which start to develop along the macropterous development pathway and turn to a brachypterous one at the 4th or early 5th larval instars, have longer development than individuals which develop along the br pathway from the egg stage. This prolongation of the development may be fatal near the northern edge of distribution of the species.

Variation in body size and its consequences

The difference between wing morphs is only one source of variation that may affect individual fitness of adults. A very important source of variation of fitness parameters is variation in body size. I have investigated the origin and consequences of individual size variation.

Body length (from the tip of the rostrum to the hind margin of the last abdominal tergite) varies between 6.0–11.5 mm in males and 6.5–12.5 mm in females (Fig. 2). Experimental studies revealed some causes of this variation. A part of it is determined already by egg size; rearing groups of individuals established from eggs of uniform weight (0.34–0.46 mg) showed that regression of egg weight explained 45 and 51% of the variation of male and female adult weight, respectively (Honěk 1987a). The average weight of eggs decreases with the age of the mother. However, the significance of this type of variation in natural populations appears small. Larvae born of small eggs have a low survival rate, succumb to competition with larger larvae, and contribute little to the total number of adults in the open (Honěk 1992).

A more important factor of adult size is food availability, particularly during the last larval instar. The minimum body weight required for adult moulting (16 mg) is attained typically 2 days after moulting to the last (5th) larval instar. The more mass is then gained during the last

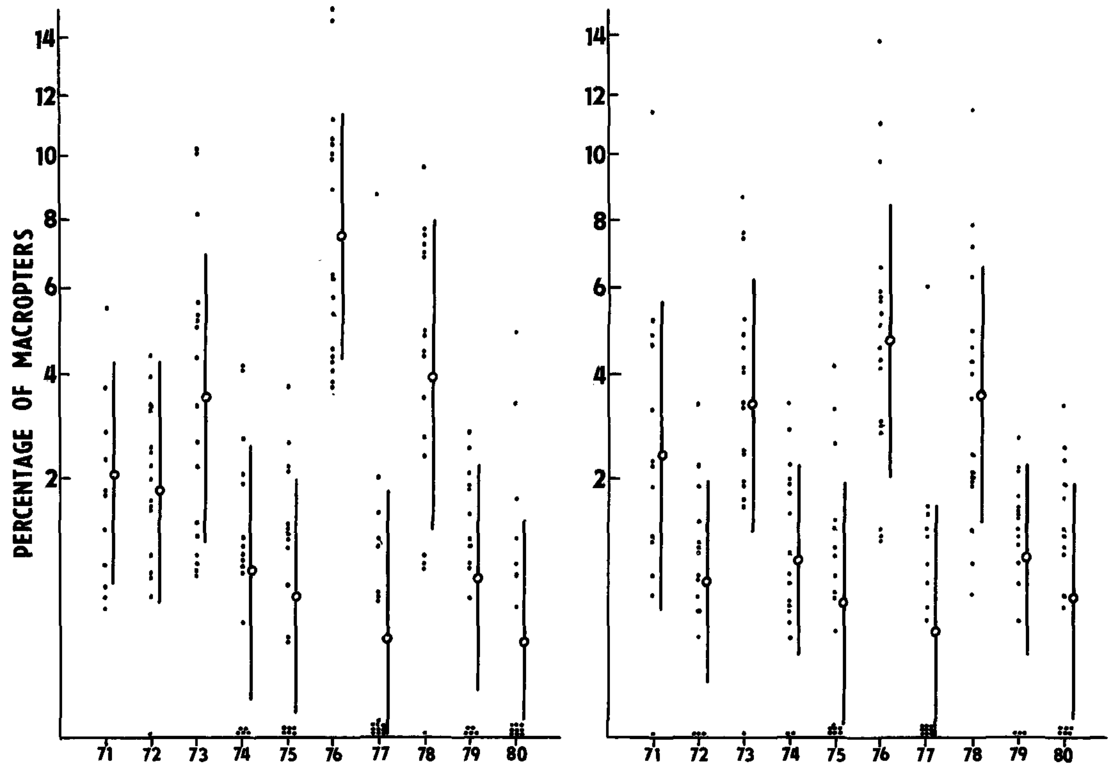

Fig. 4. The frequency of macropters in several local populations of the Czech Republic (points), in males (left) and females (right), 1971–1980. Open circles and bars represent annual means and standard deviations (Honěk 1981).

larval instar (whose duration is fixed at 8 days under 26°C) the greater the adults. Low temperature (15–19°C) decreases adult size by ca. 10% compared with an optimum one, probably due to a reduced feeding activity (Honěk 1987a).

In the open, average body size varies between local populations and annually (Fig. 5). The variation is caused by local availability of food and annual variation in temperature. The size of new adults decreases towards autumn. In consequence, the greater the fraction of individuals moulting in the late season is, the smaller is average body length and the greater its variation. Particularly small are the adults of the partial second generation which moult very late (Honěk 1986a). Generally, the size of adults in natural populations is mostly below the one attained at optimum trophic and temperature laboratory conditions (Fig. 5).

The consequences of being small are multiple, but their importance under field conditions is not yet fully understood. Body size may influence sexual selection. In a small arena, single males or single females that were presented with a pair of small and large individuals of the opposite sex preferred the larger mate. However, in natural populations body size did not significantly affect mating preferences (Honěk in prep.). Winter mortality of small individuals was greater than of large ones. Reproduction output of young females (mg eggs produced per unit of time) also increased with body size (Fig. 6). There was also a positive relationship between average body length and average lifetime fecundity of local populations, but the significance of this relationship varied between years (Honěk 1986a, 1992).

Annual differences in fecundity appeared in parallel at many localities. They were largely due to variation in longevity and total number of batches laid by a female. The number of eggs in particular batches varied little. An important determinant of longevity and number of batches was the incidence of diseases (Honěk 1986a, b).

Discussion

In the context of the above results I will discuss two topics: (1) The place of non-functional wing polymorphism in the evolution of insect life strategies, and (2) the question of its adaptive significance.

The factors of wing polymorphism were studied in nine insect orders: Homoptera—aphids and leafhoppers—(Mori and Nakasuji 1990), Orthoptera (Arai 1978; Masaki and Sugihara 1992), Coleoptera (Aukema 1990), Hymenoptera (Salt 1952), Thysanoptera (Nakao 1993), Psocoptera (Lee 1987), Dermaptera (Briceño and

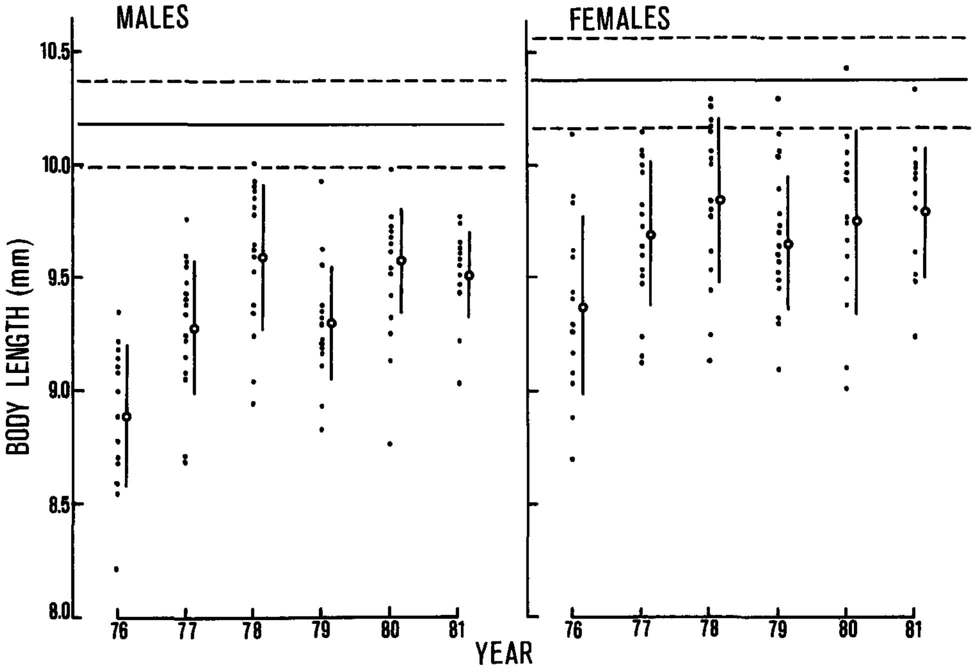

Fig. 5. Average body length in males (left) and females (right) of several local populations of the Czech Republic (points), 1976–1981. Open circles and bars represent annual means and standard deviations. Above: Average body length of adults from laboratory populations reared at optimum trophic conditions, 26°C and long day (solid line) and its standard deviation (hatched lines) (Honěk 1986a).

Eberhard 1987), Plecoptera (Saltveit and Brittain 1986) and Heteroptera. The factors controlling expression of wing morphs include genetic and maternal factors as well as environmental determinants-photoperiod, temperature, food and crowding. They are common for the studied species, but their relative importance varies between the taxa.

The differences may be due to (a) adaptive changes in the relative importance of the factors controlling morph production which reflect the diversity of life strategies of the groups or to (b) phylogenetic constraints which determine a particular taxonomic group to have a similar mechanism of regulation of wing polymorphism. In fact, the modes of control of the expression of alary morphs are correlated with life cycle strategies of the particular groups. Genetic control is typical for univoltine species and species that live several years. In such species the adaptation consists in selecting the allele frequencies that match local requirements for production of sedentary wingless or *br* breeders and winged or *ma* migrants. The proportion of macropters then reflects the balance between the risk of migration and risk of extinction of the local population. By contrast, in polyvoltine species the wing morph tends to be determined by environmental factors since adaptation to temporal phenomena is a crucial factor of survival of the short-lived adults. Periodical seasonal fluctuations of environmental conditions are correlated with changes of photoperiod. The latter may be used as a precise "token" stimulus in species where production of the *ma* morph is in response to periodical change of habitat, obligatory host alteration, etc. Temperature modifies photoperiodic effects and adjust the production of *ma* to the particular conditions. At last, non-periodical short term changes such as deterioration of food quality or overpopulation require an instantaneous response in terms of production of a winged morph that may escape the local crisis. This task is well matched with polymorphisms controlled by trophic and/or crowding stimuli. The mode of control

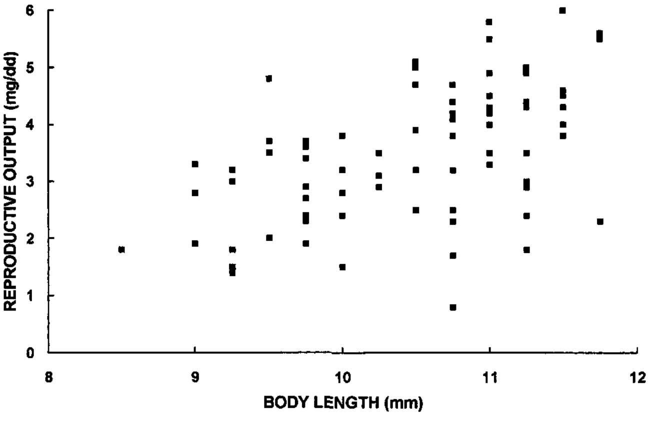

Fig. 6. The reproduction output (mg fresh egg weight/ female/ day degree) in young females (at the time of deposition of the batch 2 to 4) in relation to their body length (mm) (Honěk 1992).

(genetic—periodical environmental stimuli—non-periodical environmental stimuli) varies in parallel with life cycle strategy of the species, from long living *K*-strategists (carabids with genetic adaptation) to short living *r*-strategists (aphid exules produced in response to ephemeral trophic/crowding stimuli). Adoption of a particular type of regulation of the alary polymorphism may be limited by mechanisms inherited from the ancestral taxa.

The loss of function of the alary polymorphism in *P. apterus* provides an opportunity to consider the relative importance of adaptation and phylogenetic constraints. Non-functional polymorphism in *P. apterus* has been viewed as a temporary stage in the process of evolution of brachyptery (Seidenstuecker 1953). In fact, the factors controlling the morph penetrance (photoperiod and temperature) are similar to factors controlling alary polymorphism in other heteropteran species. This may indicate the role of a phylogenetic constraint in determining the mechanism of wing morph production. Decreasing the penetrance of the *ma* morph may be viewed as a derivative adaptation to conditions when *ma* morph has only an occasional and indirect significance. The control of alary polymorphism in *P. apterus* thus probably includes a plesiomorphic mechanism of wing morph determination and an apomorphic control of its penetrance.

We established that phenotypic manifestation of macroptery in *P. apterus* may have a positive effect on increasing individual fitness. This is due to a correlated trait, the arrest of ovarian development of teneral females. On the other hand, the difference in fitness due to being a genetic macropter or brachypter is probably small compared to the fitness differences due to other types of individual variation. In the open, phenotypic *ma* are in the average slightly larger than phenotypic *br*, because *ma* individuals are produced early in the season. However, the majority of genotypic *ma* is among the phenotypic *br* since the moulting of phenotypic *br* continues until the autumn. The expression of macroptery in these individuals has been prevented by environmental conditions. A majority of genotypic *ma* and br thus both share similar consequences of being small. The small fitness difference between ma and br morphs thus will be damped by large fitness differences caused by body size and/or other factors not correlated with alary polymorphism. This variation is a kind of fitness "mosaic", which makes the contribution from being a genetic *ma* or *br* unimportant. Under such circumstances alary polymorphism in *P. apterus* appears to be close to selective neutrality.

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Received 1 November 1994; Accepted 17 April 1995