

Sex-linkage of host plant use in butterflies

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INTRODUCTION: SEX-LINKAGE IN BUTTERFLIES

Plant-feeding insects account for much of the diversity of life, and this great diversity appears to some extent to have been caused by radiation onto an equally manifold food resource, the seed plants (Ehrlich and Raven 1964; Jermy 1984; Mitter et al. 1988; 1991; Janz and Nylin 1998). Recent hybridization studies on butterflies have offered new insight into the genetic mechanisms behind this relatively rapid diversification, suggesting an intriguing role of the X-chromosome in speciation in the Lepidoptera (Thompson 1988b; Jaenike 1989; Thompson et al. 1990; Sperling 1992; Scriber 1994; Sperling and Harrison 1994; Scriber et al. 1995; Scriber et al. 1996). Even taking into account the possibility of a sampling bias in the available data, it appears clear that species differences are disproportionately affected by genes on the X-chromosome (e.g. Charlesworth et al. 1987; Sperling 1994). The traits involved include diapause control, mimetic coloration, host plant ranking, pheromone composition, mate selection and female fecundity (Sperling, 1994, and references therein). These are all also important life history traits. What is the reason for this bias towards the X-chromosome?

Charlesworth et al. (1987) have shown theoretically that major genes on the X-chromosome will evolve faster than on the autosomes if mutations are fully or partially recessive. The reason for this is that recessive genes on the X-chromosome will be more exposed to selection in the heterogametic sex. As a contrast, there was no comparable difference in rate of evolution between the chromosomes for traits controlled by a number of loci with additive effects (Charlesworth et al. 1987). The increased rate of evolution would allow faster spread and fixation of favorable mutations in the population, especially in traits that are only expressed by the heterogametic sex. As females are heterogametic in the Lepidoptera, this phenomenon is especially suggestive as an explanation for X-linkage of

traits expressed only by females, such as host plant selection. On the other hand, X-linked characters in the Lepidoptera that are restricted to males, such as male-limited wing coloration, cannot be explained by this mechanism as males will have two X-chromosomes. However, as dosage compensation does not appear to occur in butterflies, males will have twice the dose of an X-linked enzyme than females, making it possible for a male-limited trait to be turned on or off by a large or small dose of a certain enzyme (Johnson and Turner 1979).

The accumulation of genes on the X-chromosome is further facilitated by the reduced rate of recombination for genes on the X-chromosome. Eventually this can result in the build-up of “co-adapted-gene complexes”, that would simplify fast and major changes in whole suits of traits, co-adapted to for example local climatic conditions (Scriber 1994). With time, these changes could then lead to population differentiation and speciation. Furthermore, the empirical finding that heterogametic hybrids often suffer from reduced viability and/or fertility, known as Haldane’s rule (Haldane 1922; Coyne 1992), would further reinforce this differentiation and help keep these gene complexes intact (e.g. Charlesworth et al. 1987; Sperling 1992; Scriber 1994).

Among the traits that make up these proposed co-adapted complexes of traits with X-linked inheritance is host plant preference. Several studies comparing interspecific hybrids between pairs of closely related *Papilio* butterflies have demonstrated a strong effect of the X-chromosome on host plant ranking (Thompson 1988b; Scriber et al. 1991; Scriber 1994), a suggestive finding in light of the ongoing discussion of sympatric speciation via host plant races (e.g. Bush 1975; Futuyma and Peterson 1985; Butlin 1987; Bush 1994). However, any host plant-mediated diversification also requires understanding of the evolution and maintenance of local adaptations on an ecological scale (e.g. Singer and Thomas 1996). We need to know more about the genetic control of *intraspecific* differences in host plant preference (Jaenike 1989).

A NEW PIECE IN THE PUZZLE

Evidence is accumulating on X-linkage in butterflies of important life-history traits, but some important gaps remain. I have conducted an interspecific hybridization experiment on the comma butterfly, *Polygonia c-album*, in an attempt to fill two of those gaps (Janz 1998). The first is the more general: if interspecific differences tend to be X-linked, is *within*-species variation similarly X-linked? The second concerns the difference between host plant ranking and specialization. In all studies on host plant preference mentioned above the investigators performed hybridizations of closely related species that differed in ranking, i.e. they preferred different plants. The question is, will the degree of specialization on one preferred plant be inherited in a similar way (i.e. be X-linked), or will it show autosomal inheritance, as could be expected from the more quantitative nature of this trait?

The comma butterfly is unusually well suited to address these questions, and I will briefly outline some important characteristics of this species. It is the only representative in northern Europe of the Holarctic genus *Polygonia* (tribe Nymphalini, family Nymphalidae). It has a wide distribution, ranging from Western Europe to Japan, and in Europe from Scandinavia to the Mediterranean. The host range is unusually wide for a butterfly, including host plants from seven families in four orders (Urticaceae, Ulmaceae and Cannabidaceae in Urticales, Salicaceae in Salicales, Grossulariaceae in Rosales, and Betulaceae and Corylaceae in Fagales). Of these plants, females usually prefer and larvae perform best on the plants in Urticales (Nylin 1988; Janz et al. 1994). There is a relatively high correspondence on the population level between female preference and larval performance in this species (Nylin 1988; Nylin and Janz 1993; Janz et al. 1994; Nylin et al. 1996), indicating that females base their choices largely on intrinsic qualities of the plants, and that external factors such as predators play a limited role in the establishment of the preference hierarchy.

Like most of its relatives in Nymphalini, the comma hibernates in the adult stage. Under favorable conditions it can produce a brighter colored directly developing form that

cannot normally survive the winter but must mate and give rise to a second summer generation (Nylin 1989). As the length of the favorable season changes with latitude, southern populations will regularly produce the direct developing form, while populations closer to the northern limit of the species' distribution will be strictly univoltine. At the latitude where there is barely enough time for a second summer generation there is increased selection for oviposition on plants that can support the shortest development times, leading to an increased specialization on these plants (Nylin 1988; see also Scriber and Lederhouse 1992). On the other hand, a bit further north there is never enough time for the second generation but still plenty of time for one, and consequently there is a lower selection pressure for specialization on plants that can support the fastest growth.

This phenomenon has provided us with the opportunity to find and compare populations of *P. c-album* that differ in degree of specialization, while retaining the same ranking (Nylin 1988; Janz and Nylin 1997). The populations used in these experiments came from southern England (a partially bivoltine population) and Stockholm, Sweden (a univoltine population). These populations were also used in the hybridization experiment to investigate the inheritance of oviposition specificity in *P. c-album* (Janz 1998). Butterflies from the two populations were cross-mated in all possible combinations, and females were tested in simultaneous choice trials with *Urtica dioica* as the preferred plant and *Salix caprea* as the less preferred plant. Offspring were all reared on *U. dioica* and females of all F1 crosses were then given the same oviposition choice trial. Larvae were reared in a photoperiod and temperature regime known to cause direct development in both populations (Nylin 1989). See Janz (1998) for a more comprehensive method description.

COMPONENTS OF HOST PLANT USE

Host plant use in butterflies can conveniently be divided into the two complex traits female oviposition preference and larval performance (Thompson 1988a). Oviposition

preference refers to the sequence of behavioral traits involved in locating and evaluating a potential host plant that ultimately leads to the decision to oviposit or not. Most butterfly species are relatively specialized, restricting oviposition to a few related plant species or genera. Even so, host plant species in the repertoire will usually vary in quality and preference is generally expressed as a hierarchical ranking of these plants. Singer (1971) and Wiklund (1975; 1981) provided some of the first empirical evidence for the hierarchical nature of host plant range in butterflies and other plant feeding insects. Females are more likely to oviposit on a high-ranked plant, but will accept lower ranked plants to a lesser degree, especially if the higher-ranked plants are not available.

There is a good deal of confusion surrounding the terms used to describe different types of oviposition behavior and strategies. To not add to this confusion I will briefly define my use of these terms, while trying to follow and combine existing definitions as much as possible (c.f. Thompson 1988b; Singer et al. 1992; this volume). All terms refer to oviposition behavior under controlled conditions, while actual host use may differ depending on abundance and availability of potential host plants in nature.

Host plant ranking is the order of host plants ranked by number of eggs oviposited on them (in simultaneous choice trials) or, the order of plants as they become acceptable (in sequential choice trials). Host plant range is the number of plants actually oviposited on in any type of choice trial. Specificity is used as a relative measure of how many eggs a female lays on a preferred plant in relation to other plants in the trial (in simultaneous choice trials) or of the length of the discrimination time on a preferred plant in relation to other plants (in sequential choice trials). Oviposition preference is perhaps the most vague of these terms, often just referring to the fact that a female shows a higher willingness to oviposit on certain plants than on others (see Singer (this volume) for a more thorough definition).

Larval performance refers to a measurable trait or set of traits that adequately approximate, or correlate well with, offspring fitness on a given host plant (Thompson

1988a; Nylin et al. 1996). Popular traits to investigate are development time, survival, pupal or adult weight, and growth rate. In some circumstances it might be necessary to further include female fecundity as well as the quantity and quality of the male contribution to fitness, i.e. spermatophore size and protein content (Wiklund and Kaitala 1995; Nylin et al. 1996; Wedell 1996).

HOST PLANT RANKING VS. SPECIALIZATION

A couple of studies on *Papilio* butterflies have demonstrated that host plant preferences in these butterflies are strongly influenced by genes on the X-chromosome (Thompson 1988b; Scriber et al. 1991). In both these studies, the species that were hybridized preferred different host plant species, i.e. they showed differences in ranking; no comparable studies have been made on differences in oviposition specificity. The relationship between ranking and specificity is not at all clear, but traditionally the traits have been treated as two rather different phenomena, caused by different mechanisms. This view dates back to the seventies and was formally described by Courtney et al. as “the hierarchy-threshold model” (1989). According to this model, host plant ranking is largely determined by external, plant-specific factors, such as plant chemistry, while specificity is determined by a threshold value that is depending on the insect’s internal motivational state (Fig. 1). Thus in the hierarchy threshold model specificity is not directly determined by plant characteristics, but is a property of the ovipositing female. There are several interesting predictions from this distinction. First, the genetic basis of a threshold trait is most likely to have polygenic determination, and thus best understood in terms of quantitative genetics (Courtney et al. 1989). As the X-linked genes discussed above are selected for essentially as major genes (Charlesworth et al. 1987), there is no reason to expect a disproportionate effect of the X-chromosome under the threshold model. Second, motivation to oviposit can vary, even over a single female’s life span, and thus specialization should be a relatively labile

trait. Ranking, on the other hand, will not change as readily, and should be much more evolutionarily stable (Courtney et al. 1989; Scriber 1994).

The results from my crossing experiment on *P. c-album* showed very clearly that specificity is strongly influenced by genes on the X-chromosome (Fig. 2, see also Janz 1998), showing a mode of inheritance very similar to host plant ranking in *Papilio* butterflies. The exact genetic mechanisms remain unknown, but at the very least this suggests that factors other than a threshold mechanism have a significant influence on what is expressed as specificity in *P. c-album*. One possibility is one or more modifier genes on the X-chromosome that influence the threshold value, but the simplest explanation would perhaps be that ranking and specificity are both different expressions of the same genes. This requires that acceptability of the different host plant species can vary independently from each other.

There is some evidence in support of the prediction that specialization should be more evolutionarily labile than ranking: while several studies have demonstrated individual variation in specificity, few have been able to demonstrate such variation in ranking (e.g. Jaenike 1990). However, this evidence is compatible with the view that both ranking and specificity are determined by the same genes. Typically, small changes in ranking would be expressed as changes in specificity, while only larger changes will result in reversals in ranking, and small changes will undoubtedly be more common than large ones. Furthermore, there are indications of reversals in ranking within the Swedish population of *P. c-album* (Janz et al. 1994). While that particular experiment did not clearly distinguish between genetic and environmental effects, recent experiments on the same population indicate a strong genetic component in the variation of host plant preference (Nylin, S., Windig, J. and Nygren, G., unpublished).

OVIPOSITION PREFERENCE VS. LARVAL PERFORMANCE

As most butterfly larvae are relatively immobile and lack the specific adaptations for dispersal and host plant selection sometimes found in other Lepidoptera (e.g. Tammaru et al. 1995), most of the host plant selection is exerted by the ovipositing female. For this reason one should expect a relatively high correspondence between the plants that are selected by females for oviposition and the plants on which the offspring fitness is highest, and it has been hypothesized that oviposition preference and larval performance should be genetically linked, or even be pleiotropic effects of the same genes (Bush 1975; Rausher 1984; Futuyma and Peterson 1985; Via 1986). Many studies have investigated this correlation between female oviposition preference and larval performance, and results are mixed (reviewed by Thompson 1988a). There could be several reasons why the correspondence between these traits is not always perfect (Thompson 1988a; Thompson and Pellmyr 1991). There could for example have been insufficient time to adapt to a novel host plant, or the preferred host may be so rare that it does not pay to search for it. Other factors that can influence the preference hierarchy are not easily quantified in a controlled choice trial in the lab; a favorable plant may grow in unfavorable habitats or be more exposed to enemies. Moreover, oviposition preference should really be expected to correlate with total offspring fitness, not with any single measure of performance (Thompson 1988a; Reavey and Lawton 1991; Janz et al. 1994; Nylin et al. 1996). Choosing an adequate performance measure is as important as it may be difficult, and requires good knowledge of the system under study.

Still, on average, we should expect, and often find, a good correlation between oviposition preference and traits that contribute to offspring performance, and some form of physical linkage between the traits would seem to make sense. Curiously, several studies, on as diverse organisms as papilionid butterflies (Thompson 1988b; Thompson et al. 1990), chrysomelid beetles (Keese 1996), and aphids (Guldmond 1990), have demonstrated that oviposition preference showed a different type of inheritance than larval performance.

Similarly, in my intraspecific cross of *P. c-album*, there was no evidence of an X-linked inheritance of growth rate on the preferred host plant *Urtica dioica*. This trait appeared to be largely determined by genes on the autosomes (Fig. 3). Consequently, there was no indication of X-linkage of larval performance. Hence, in none of these species was there any evidence for either pleiotropy or physical linkage between the genes that influenced preference and performance.

As it must be very important for the female to oviposit on plants that the larvae can feed most efficiently on, why is not a good correlation assured by linkage or pleiotropy? To put it differently, why are not the genes that influence larval performance included in the “co-adapted gene complexes” described in the Introduction? Part of the answer may lie in the asymmetrical relationship between the traits. While ovipositions on plants that the larvae can not survive on are very costly for the female, there is not necessarily a high cost associated with the capacity to feed on a wider range of plants than the female normally oviposits on. On the contrary, this would probably be adaptive, as females sometimes make oviposition mistakes (Chew 1977; Larsson and Ekbohm 1995) and the original food plant can be depleted. Several authors have also shown empirically that the larvae are able to grow and survive on a wider range of plants than the females actually oviposit on (Wiklund 1975; Smiley 1978; Roininen and Tahvanainen 1989). Furthermore, the often proposed physiological trade-off between larval feeding efficiency on different plant species has received relatively weak support (see Janz and Nylin 1997), making it less costly to retain presently unused plants in the larval host plant range. Thus, opportunistic oviposition strategies and conservative larval performance can both be seen as adaptations to a constantly changing environment, making a close linkage between the two traits non-adaptive.

SPECIES, POPULATIONS AND INDIVIDUALS

In his review of the genetic basis for species differences in the Lepidoptera, Sperling (1994) found that more than half of all reported differences between species were controlled by X-linked genes, a striking result considering that Lepidoptera have about 30 pairs of chromosomes. This indicates a strong bias for X-linkage of genes that account for species differences. Many species of Lepidoptera vary geographically in host plant use, in terms of both specificity and host plant ranking (Nylin 1988; Singer et al. 1989; Scriber 1992; Thompson 1993; Singer and Thomas 1996; Janz and Nylin 1997; Thompson 1997). Are the genetic determinants for intraspecific variation in host plant preference of the same sort as the interspecific variation studied by Thompson (1988b) and Scriber et al. (1991)?

Based on the theories of Charlesworth et al. (1987) and Jaenike (1989), Scriber (1994) hypothesized that while interspecific differences should be controlled by X-linked, recessive genes, intraspecific differences should be controlled by autosomal, dominant, or quantitative factors. However, my study of *P. c-album* showed a very strong influence of the X-chromosome on intraspecific differences in host plant specificity (Janz 1998). The two populations used in my study are widely separated geographically, and gene flow is probably minimal. If X-linkage is to play a role in diversification, genes on the X-chromosome should also account for much of the variation between populations on a geographical scale. An interesting and unexplored field of research would be to investigate the role of the X-chromosome in maintaining local adaptations in conspecific populations. Many of the traits that have been suggested to be involved in the co-adapted gene complexes on the X-chromosome (see Scriber 1994) are also traits that can be expected to vary locally, for example with latitude in temperate regions. It is also extremely important that local covariation of traits like photoperiod sensitivity, host plant specialization, diapause control, etc. is not broken by gene flow from other populations.

Variation *within* populations deserves more attention too. A few studies have demonstrated a significant heritability of oviposition preference, indicating that variation on this level is significantly influenced by genes with additive effects (Tabashnik et al. 1981; Singer et al. 1988; Carriere and Roitberg 1995). Preliminary results from a recent experiment on the Swedish population of *P. c-album* show that at least some of the within-population variation is determined by autosomal genes, although X-linked genes could also contribute to the variation (Nylin, S., Windig, J. and Nygren, G., unpublished). The relationship between the genetic determination of variation between individuals of the same population, between conspecific populations, and between closely related species, remains a puzzle that needs attention.

SUMMARY

X-linkage of co-adapted suites of life history traits has been hypothesized to play an important role in speciation in the Lepidoptera. Among the traits that have been shown to be strongly influenced by the X chromosome are species differences in host plant ranking. I have shown that even intraspecific differences in the degree of specialization were X-linked, suggesting a common genetic background for host plant ranking and specialization. In contrast, larval performance seems to be differently inherited than oviposition preference, which should make host race formation more difficult. The studies done thus far raise several suggestive hypotheses about population differentiation and maintenance of local adaptations. To answer these questions more attention must be directed towards understanding the relationship between genetic variation within and between populations and species.

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Figure legends:

Fig. 1. Schematic description of host plant ranking and specialization, according to the hierarchy-threshold model (Courtney et al. 1989). While ranking is determined by external factors, such as host plant chemistry, specificity is a result of the current motivational state of the ovipositing female. Changes in motivational state will cause the motivational threshold to move up or down, making the female accept or reject plants further down in the hierarchy.

Fig. 2. Degree of preference for the higher-ranked *Urtica dioica* over the lower-ranked *Salix caprea* by ovipositing females of *Polygonia c-album*. (a) Parental generation (hibernated), Swedish and English populations. (b) F1 crosses (summer generation). E= English, S= Swedish, mother's origin given first. Means \pm SE. Data from Janz (1998).

Fig. 3. Larval growth rate on *U. dioica*, for F1 crosses of Swedish and English *Polygonia c-album*, measured as the percent daily weight gain. E= English, S= Swedish, mother's origin given first. Means \pm SE.

Fig. 1

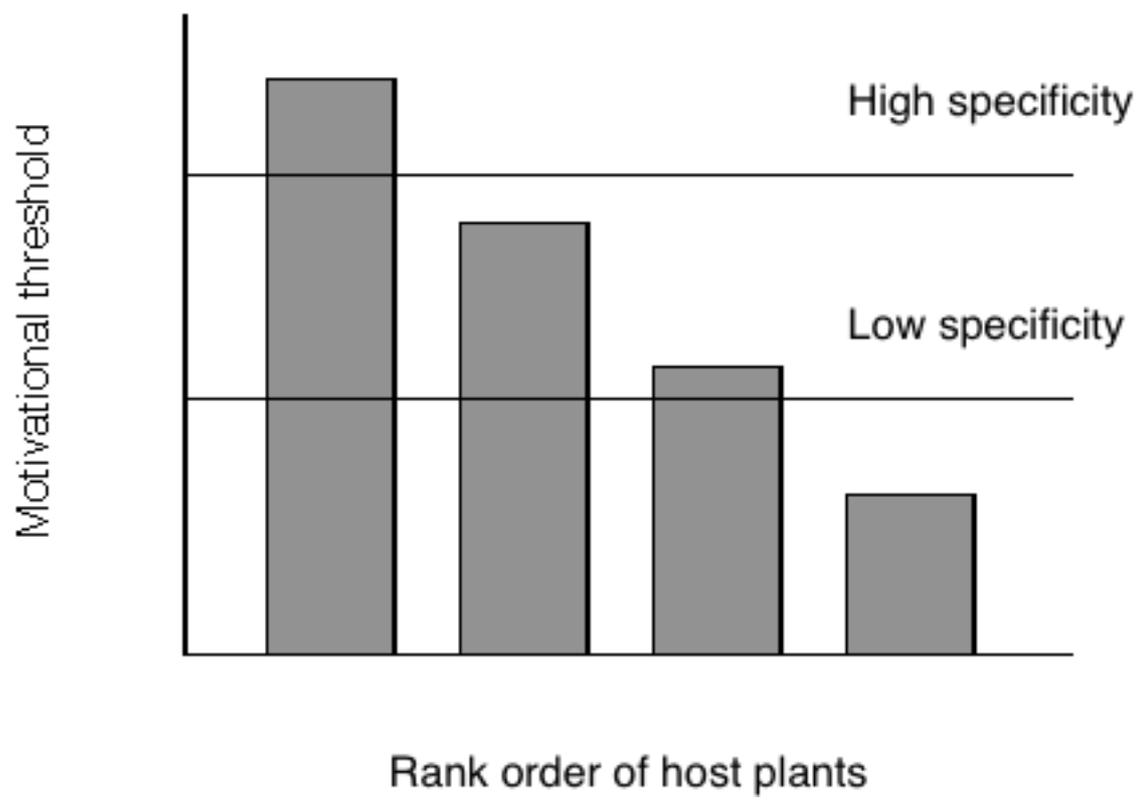


Fig. 2.

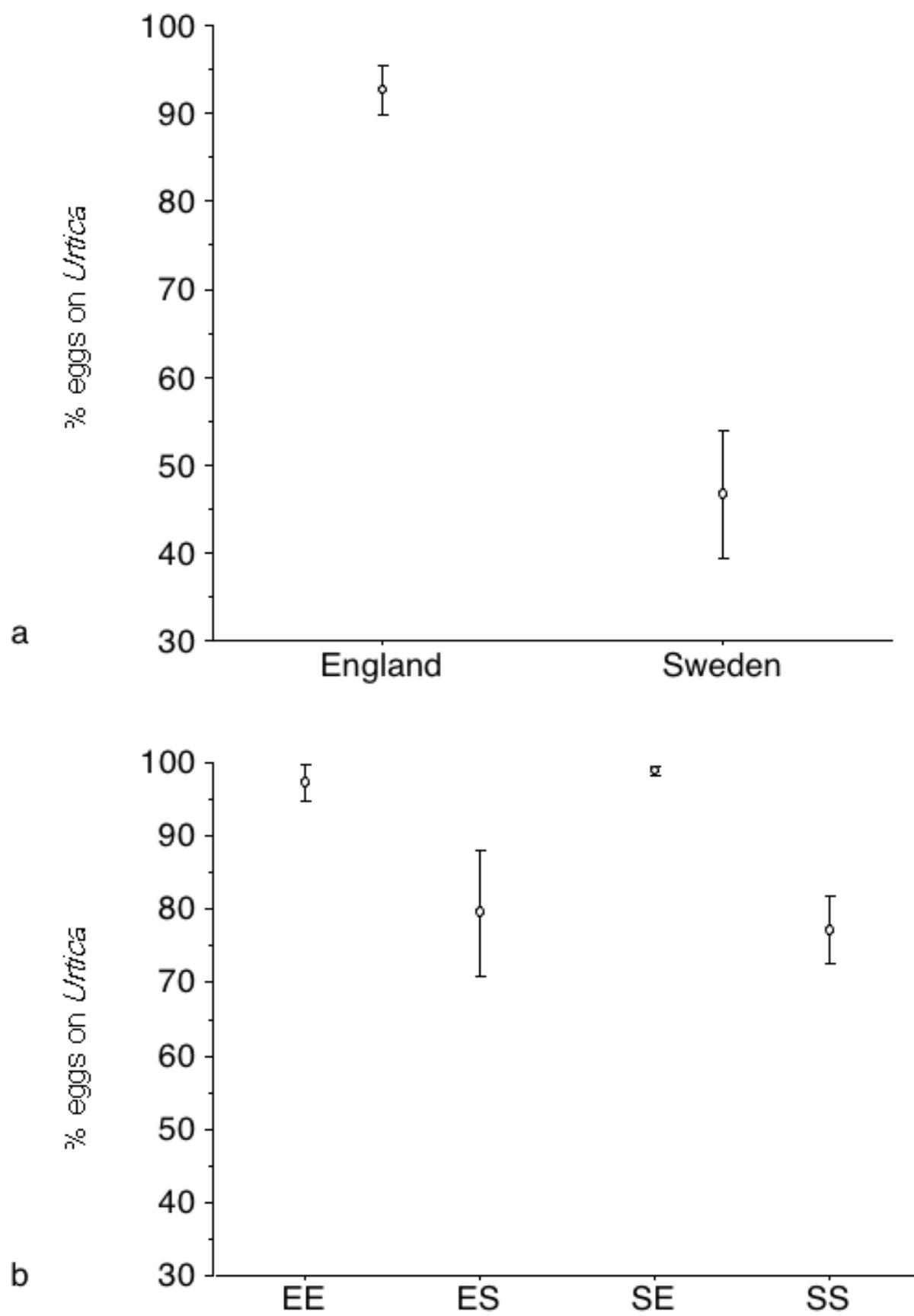


Fig. 3.

