

The role of sink to source re-colonisation in the population dynamics of insects living in unstable habitats: an example of terrestrial chironomids

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Certain species of terrestrial chironomids (Diptera) are specialised on open patches in initial stages of primary or secondary succession (early fallow, lichens and mosses on rocks, etc.). These “source” habitats provide good quality food for their larvae and most offspring are produced here, but they are sensitive to summer desiccation. This often results in extinction of the summer larval population, followed in winter by re-colonisation from less suitable, but more stable “sink” habitats in the surrounding landscape.

Soil dwelling and long-lived larvae are poor migrants; short-lived, winged adult females select patches for their development. Proper choice of oviposition sites and consequent distribution of eggs among individual habitats is thus critical for the success of these species.

A mathematical model was developed in order to find out whether this re-colonisation strategy could ensure population persistence at the landscape level. The model was verified using long-term data on *Smittia atterima* abundance in old fields. The results indicate that even a small proportion of eggs laid in a sink habitat can ensure a successful re-colonisation of the source habitat. Thus, re-colonisation of source habitats from sink habitats is concluded to be one of the reasons for persistence of the latter. The model indicates that this re-colonisation may ensure population persistence even in conditions when exclusive use of only one habitat leads to population extinction either due to environmental stress or to a negative growth rate.

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Many animal species occur in the landscape in a set of habitats of various qualities. This habitat heterogeneity can conveniently be described by the concept of source and sink habitats: In the source habitats, local conditions can ensure population growth, while in the sink habitats local production does not compensate for local mortality (Pulliam 1988, Pulliam and Danielson 1991). In source habitats, emigration exceeds immigration and vice versa. The species may survive in sink habitats for

some time, but long-term persistence is enabled only by immigration from the source habitats. Pulliam (1988) and Pulliam and Danielson (1991) have shown that utilisation of sink habitats can maximise the total number of offspring produced in the landscape. Migration to sink habitats can reduce competition pressure in source habitats and at the same time produce some additional offspring. Even if in a sink habitat immigration exceeds emigration, some individuals may certainly

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emigrate from here. Morris (1991) has shown that a source to sink equilibrium can be maintained as an evolutionarily stable strategy of habitat selection only when reverse sink to source migration also occurs. Holt (1997) predicts that using a sub-optimal but more stable sink habitat may be advantageous when the population in the source habitat displays unstable local dynamics. These sink habitat emigrants may become ecologically important, for example, when populations in the source habitats are depleted for some reason. Then the source habitat may be recovered by the emigrants from the sink habitat. Whereas the role of source-sink habitats in various biotic interactions has been subject to many studies and critical comments (e.g. Pulliam and Danielson 1991, Doncaster et al. 1997, Loreau and DeAgnes 1997), little attention has been paid to the re-colonisation from sink to source habitat (Boughton 1999).

In many insect species, offspring care is limited to selection of suitable habitats for larval development. Larvae are frequently poor migrants, and their opportunities to find new habitats are very limited. Conversely, adults migrate easily between patches and select oviposition sites for the next larval generation based on various aspects of habitat quality, such as its suitability, carrying capacity, persistence in time, or stability (Southwood 1977, Thompson 1988, Kouki 1993, Sowig 1995, Doncaster et al. 1997, Tyler and Rose 1997). Many species of insects utilise habitats of a high, but strongly fluctuating quality. Persistence on the meta-population level can be maintained here by colonisation of newly appearing suitable habitats from older local populations, which ultimately go extinct (McLachlan 1983, Hanski 1991, Eber and Brandl 1996, Hill et al. 1996). Another possibility is re-colonisation of source habitats from sink habitats. This strategy is particularly effective when occurrence of source habitats is seasonal and suitable habitats are thus seasonally absent in the landscape and when sink habitats are more resistant to environmental stress (McLachlan 1988).

Here, we use a mathematical model of source-sink dynamics and field data on terrestrial chironomids to describe the situation where the source-sink population dynamics is affected by environmental stress and to show that survival of the population can be safeguarded even by low rates of oviposition in the lower quality sink habitat, which ensures subsequent re-colonisation of the source habitat that has been depleted.

Biological background

Terrestrial chironomids are frequently abundant in initial stages of secondary succession, while later on their abundance decreases (Strüve-Kusenbergl 1981, Frouz 1994a, 1997a, b). The reason for this decrease is proba-

bly the reduction of patches covered by sparse vegetation, which are preferred for oviposition (Frouz 1994a, 1997b). This seems to correspond with abundance of their food source: soil algae and mosses (Frouz and Lukešová 1995).

Smittia atterima has been frequently recorded in high numbers (up to 12000 individuals/m² [Delettre and Lagerlöf 1992]) in open, disturbed areas, such as arable land and in initial stages of succession. Its abundance decreases during succession with the development of a dense plant cover (Delettre and Lagerlöf 1992, Frouz 1994a, 1997a, b). Larvae live in the surface soil horizon where they feed on plant litter, fungi, soil algae, and mosses (Frouz and Lukešová 1995). The larvae are also found in low densities in surrounding habitats covered by a denser vegetation. When the population in the open habitat decreased, larval density in the dense vegetation also decreased (Frouz 1997b). Thus the majority of the population develops in the open, disturbed "source" habitats and the surrounding dense vegetation can be considered as a sink, which is mainly saturated from the source habitats.

Similarly to other chironomids, adult males form swarms, attract females here and mate. After mating females disperse and search for oviposition sites (Armitage 1995). In soil-dwelling chironomids, females lay eggs individually or in small groups, the precise selection of oviposition site being very important because migration abilities of soil-dwelling larvae are very limited (Pinder 1995). *S. atterima* has two generations per year. The overwintering larvae mature in spring (April–May) and produce a summer larval generation in late summer or early autumn (Delettre and Lagerlöf 1992, Frouz 1994b, 1997b). In both generations, females prefer patches with early successional vegetation for oviposition, but previous studies indicated that success of their offspring here differs markedly (Frouz 1997b). Whereas during winter an abundant larval generation develops, the summer larval generation is strongly reduced or even locally disappears due to summer drought (Frouz 1997b). Nevertheless, in autumn an abundant larval generation reappears, probably established by females emerging from neighbouring habitats overgrown by dense vegetation, which are less sensitive to desiccation during the summer (Frouz 1997b). Thus *S. atterima* is a nice model species for the situations studied by Holt (1997) and Morris (1991). Similar patterns were also observed in other chironomid species, like *Bryophaenocladus cf. illimatus*, abundant in pioneer successional stages (Frouz 1997b) and in *Limnophyes minimus* (Delettre 1986). The latter is living in shallow soil formed by raw humus, lichens and mosses on rock surfaces in Brittany (France). The summer generation completely disappears here due to desiccation, and these habitats are re-colonised in autumn by adults emerging from neighbouring sites.

Material and methods

Life cycle

The life cycle of *S. atterima* was studied in a suburban fallow field near České Budějovice (see Frouz 1997b, Frouz and Olejníček 1999 for more details). Open patches, covered by sparse vegetation, were used for study of larval development. These patches were preferred for oviposition by chironomid females (Frouz 1997b). Five soil samples (area 125 cm², depth 7 cm) were taken during each sampling occasion from October 1993 to October 1994. The larvae were extracted from samples using a modified Tullgren apparatus (Meyer 1980). *S. atterima* has four larval instars (Frouz 1994b). To assess the frequency distribution of individual larval instars, width of head capsule was measured. From each sampling either all larvae (if less than 25) or a sample of at least 25 larvae were mounted on temporary slides in glycerine and the maximum distance between the lateral points on the head (from a dorsal view) was measured. The development of the first three instars is very fast and larva spend the majority of their development time in the last, fourth instar (Frouz 1994b). To determine the degree of last instar larvae development more finely (Wülker and Götz 1968) the phase of the last instar was evaluated using imaginal disc development. The fourth instar larvae were then cleaned in ethylene-glycol glycerine mixture (1:1) and the development of imaginal discs on their second thoracic segment was observed. The phases in development of imaginal discs distinguished were roughly equivalent to phases 2–5 used by Wülker and Götz (1968).

Five yellow water pan traps (16 cm in diameter), located in the same habitat as above were used to record adult flight (see Frouz 1997b, Frouz and Olejníček 1999 for more details). To assess egg load, 25 females trapped in spring 1994 were dissected and egg loads were counted. Because of potential egg-load reduction during oviposition the five largest egg loads were used for calculation of the average potential egg load.

Soil samples were taken in March, June, and November 1995 to compare summer survival rates in open and dense vegetation. Five samples (area 625 cm², depth 7 cm) were taken from open patches. Two types of tall and dense vegetation were distinguished, five samples were taken from each and their weighted average (with respect to the area covered by these habitats) was used to assess the average larval population in the dense vegetation.

The model

We assume that the number of females and their fertility determines the total number of eggs produced by one generation. Eggs produced can be laid in two habitats, A and B, which differ in larval survival rate. Habitat A

represents a source and habitat B a sink habitat. Thus, the survival rate in habitat B is assumed to be constant and density independent throughout the whole year, while the survival rate in habitat A is assumed to be density independent, constant within a season, but fluctuating between seasons: it is higher in winter and lower (close or equal to zero) in summer, compared with that in habitat B (Fig. 1a). The proportion of eggs laid in a particular habitat depends on the relative proportion of its total cover and on habitat preference. The latter is

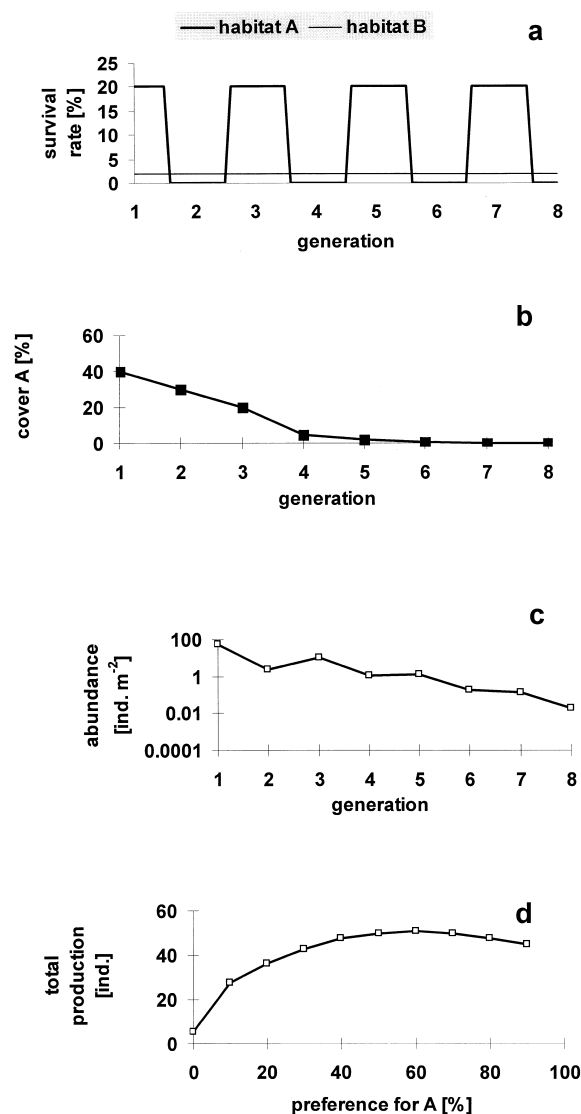


Fig. 1. Scheme of individual steps of the model: a) changes in survival rates (i.e., percentage of eggs laid that survived to the adult stage) in habitats A and B; b) changes in cover of habitat A; c) number of individuals produced in individual generations after autumnal and spring colonisation during one simulation run; d) total number of individuals in both habitats produced during particular simulation runs as a function of preference for habitat A. The optimal preference is the abscissa value, for which the highest value of total production is reached.

Table 1. Comparison of model parameters fitted to the data by Frouz (1994a) and to those by Frouz (1997b), with parameter values observed in the field (mean \pm SD or range given).

Parameter	Data fitted		Observed parameter values	Source
	Frouz 1994a	Frouz 1997b		
Initial number of colonisers	62	20		
Eggs per female ¹	75	72	66.7 \pm 16.7 (0–114)	This study
Survival in A, s_{aw} [%] ($s_{as} = 0$)	50	71	ca 50	This study
Survival in B $s_{bs} = s_{bw}$ [%]	0.5	0.5	close to zero	Frouz 1994b
Preference for A [%]	62	98	75–95	Frouz 1997b

¹ average and standard deviation of top five values from 25 measurements, range of all measurements in parentheses.

assumed to be constant during the few generations simulated. The number of adult females (assuming a 1:1 sex ratio) produced in a particular habitat is calculated as the number of eggs laid in this habitat times their survival rate. The number of adults in the next generation is the sum of adults produced in both habitats. Formally:

$$N_{n,2} = \frac{1}{2} N_{n,1} f \left(\frac{c_{n,1} p}{c_{n,1} p + (1 - c_{n,1})(1 - p)} s_{as} + \frac{(1 - c_{n,1})(1 - p)}{c_{n,1} p + (1 - c_{n,1})(1 - p)} s_{bs} \right) \quad (1a)$$

$$N_{n+1,1} = \frac{1}{2} N_{n,2} f \left(\frac{c_{n,2} p}{c_{n,2} p + (1 - c_{n,2})(1 - p)} s_{aw} + \frac{(1 - c_{n,2})(1 - p)}{c_{n,2} p + (1 - c_{n,2})(1 - p)} s_{bw} \right) \quad (1b)$$

where $N_{n,t}$ is the number of adults in year n and season t ($t = 1, 2$ means spring and autumn generations, respectively), f is female fertility (number of eggs per female), $c_{n,t}$ is the proportional amount of habitat A, which can be time dependent, p is preference for habitat A (proportion of eggs laid in habitat A, provided relative covers of both habitats are equal), s_{as} and s_{bs} are summer survival rates in habitats A and B, and s_{aw} and s_{bw} are winter survival rates in habitats A and B, $s_{as} = 0$, $s_{bs} = s_{bw}$ for the reasons described above.

For model verification, two data sets on chironomid abundance and vegetation changes were used (Frouz 1994a, 1997b). Changes in chironomid abundance were based on changes of cover of the suitable habitat (Matějka 1990, Frouz 1997b, Fig. 1b). Because only larval abundance data were available, adult abundance was assessed as the number of larvae before pupation.

For fitting the module Solver in MS Excel was used. The parameters (habitat preference and survival rates) were compared with the values independently observed in the field (Table 1).

To assess the optimal habitat preference that maximises population fitness (defined as the sum of individuals produced during the existence of suitable habitat), we have simulated the population dynamics in eight consecutive generations during four years. Changes in cover of habitat A (Fig. 1b) were again based on

long-term data on secondary succession in abandoned fields (Matějka 1990, Frouz 1994a). For each cohort, the sum of individuals produced in both habitats during each of eight consecutive generations was calculated. This was done for habitat preferences from 0 to 100% in order to find the preference for habitat A that maximises the sum of individuals produced (see Fig. 1d for an example). Not considered were those preferences which resulted in extinction of the population during the first two generations. Summer survival rate in B was always set equal to the winter survival.

Results

Life cycle

Larval abundance was the highest after oviposition, decreased slightly during winter and steeply so during early spring (Fig. 2a). The steep decrease apparently corresponds to pupation and adult emergence. Comparison of larval abundance after oviposition in autumn and before pupation in spring indicates that the winter survival rate in the open habitat is about 50%. After the adult flight in the spring, larval abundance increased again (Fig. 2a). In the end of May, larval abundance decreased and no larvae were observed during the summer. The larvae reappeared during autumn after the autumnal adult flight. Four larval instars were clearly distinguished. During the spring, the fourth instar larvae dominated among the larvae found. After the adult flight in the spring, the larvae of younger instars appeared massively in the samples (Fig. 2b). The development of the first instars was fast and most larvae reached the last instar within 15 d. Younger larvae dominated again in autumnal samples. Nevertheless, both in spring and autumnal samples some fourth instar larvae were found. A detailed comparison of the phase of development of the last instar larvae indicated that larvae found in autumn were less developed than those found in spring (Fig. 2c).

This suggests that the larvae that appear in the soil samples during the autumn are a new larval generation and not spring larvae that survive summer in diapause. Because no larvae were observed during the summer in

this habitat, adults that establish this new larval generation probably originated from some other habitat in the surrounding landscape. Comparison of summer larval abundance in 1995 indicates that summer survival in dense vegetation is higher than in open patches (Fig. 3).

Model

When the model was fitted to the empirical data sets of *S. atterima* population change, no significant differences between simulation and empirical data were found using the χ^2 test ($\chi^2 = 11.6$, d.f. = 7 for Fig. 4a and $\chi^2 = 0.487$, d.f. = 3 for Fig. 4b), which illustrates the model's ability to simulate chironomid population dynamics. In addition, the parameters obtained by this model fitting exercise, i.e., fertility, survival rates, and preferences for habitat A, were close to those directly measured in the field (Frouz 1994b, 1997b; Table 1), which independently verifies the model.

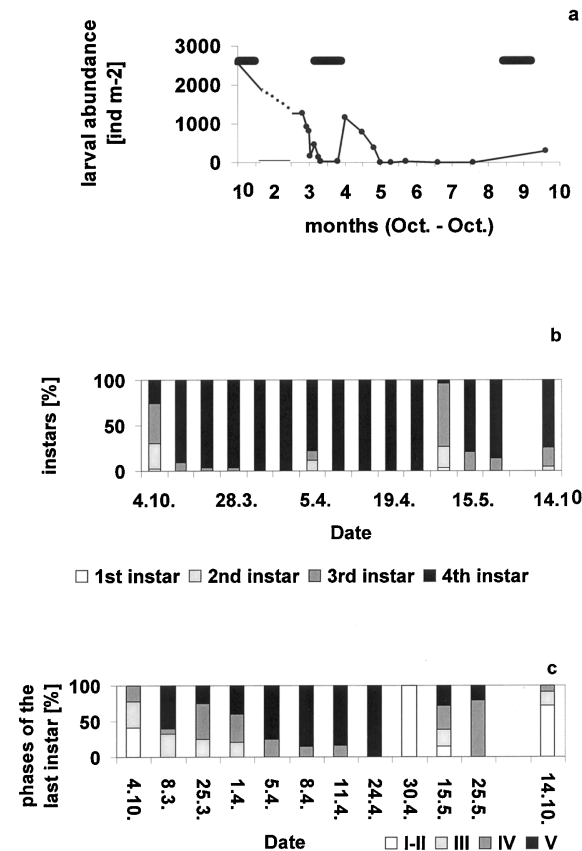


Fig. 2. Development of *Smittia atterima* from October 1993 to October 1994: a) changes of larval abundance – the thick horizontal lines in the upper part of the figure represent adult flight period; b) proportion of each instar in individual samples; c) proportions of stages of the last instar in individual samples.

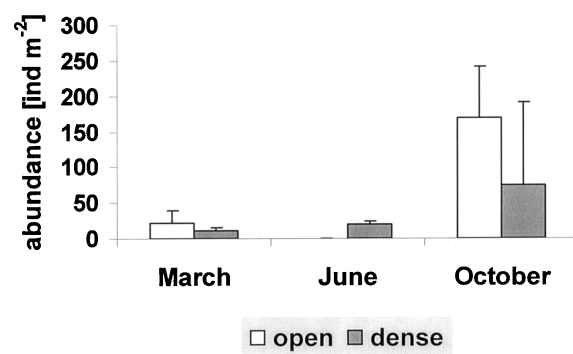


Fig. 3. Abundances of *Smittia atterima* larvae in spring, summer and autumn samples during 1995 in open and dense vegetation (bars represent standard errors of mean).

Exclusive oviposition into the sink habitat B resulted in permanently low densities. Exclusive oviposition into the habitat A necessarily resulted in population extinction the next summer, as $s_{as} = 0$. A large preference for habitat A typically resulted in population fluctuations, as the population density was high following the suitable season due to adults produced in habitat A and low following the unsuitable season – as it was consisting exclusively of adults produced in B (Fig. 5a). The total population produced by reproduction in both habitats was, however, larger than by exclusive preference for only one of them. This was evidently true when exclusive preference for only one habitat resulted in population extinction due to either a negative growth rate here or due to periodical catastrophes. Proper distribution of eggs between stable and suitable habitats, determined by oviposition preference, is therefore critical for overcoming unsuitable periods (e.g., summer drought) and consequently for population fitness.

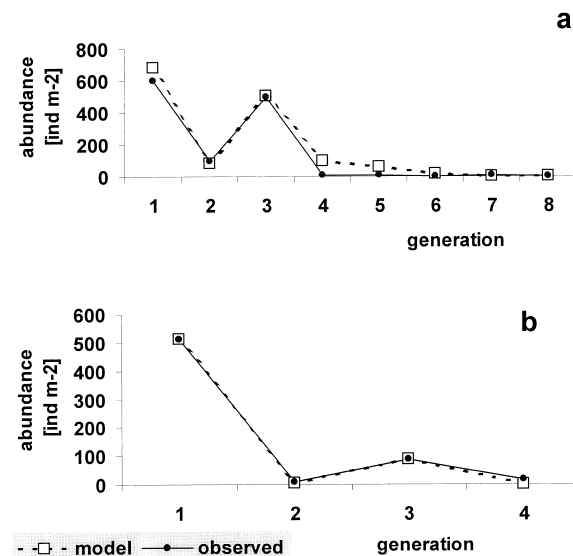


Fig. 4. Comparison of simulation results with empirical data: a) by Frouz (1994a); b) by Frouz (1997b).

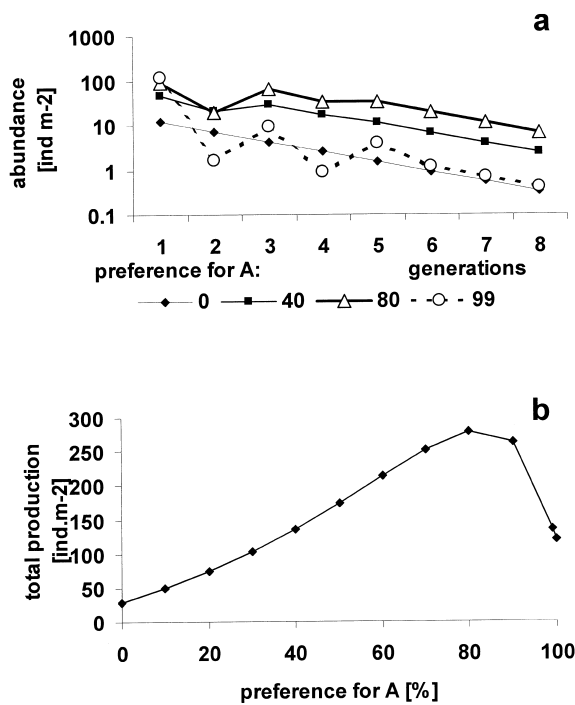


Fig. 5. Changes in population density during eight successive generations predicted by the model (1) for $f=60$, $s_{aw}=0.2$, $s_{as}=0$, $s_{bs}=s_{bw}=0.02$, $N_{1,1}=20$, cover of A as in Fig. 1b: a) for various preferences for habitat A; b) sum of individuals produced during eight consecutive generations for various preferences for habitat A.

As stated in the Model section, to evaluate the role of survival rates during one colonisation event, we determined the optimal preferences for various combinations of fertilities and survival rates (Figs 5b, 6). According to the model, the optimal preference for habitat A decreased as the survival rate in the sub-optimal stable habitat increased. Nevertheless, even if the survival rate in the sub-optimal habitat ensured a self-sustainable population, habitat A was still preferred. Habitat B became more preferred only when the survival rate in B reached one half or more of the survival rate in the optimal, periodically disturbed habitat A (Fig. 6a). Preference for habitat A decreased as the fertility of females increased (Fig 6b). This is because both high survival rates in habitat B and high fertility increase the growth rate in habitat B, and thus it becomes advantageous to produce a higher proportion of the offspring in the sub-optimal habitat B.

Discussion

Detailed observations of larval development are consistent with previous findings about *S. atterima* biology (Delettre and Lagerlöf 1992, Frouz 1994a, b, 1997a, b, Frouz and Lukešová 1995) and support the hypothesis

that the larvae are strongly reduced during summer in the preferred open habitat and a complete extinction of summer larval population in this habitat is probably frequent. This agrees with some earlier observations of terrestrial chironomids dwelling in moss cover on rocks where the summer larval generation may completely disappear due to summer drought (Ducrotoy 1980, Delettre 1986).

The larvae exist in low densities also in other habitats, e.g., in tall and dense vegetation (Frouz 1997b). The populations in these habitats are not self-sustainable and disappear after some time (Frouz 1994a). Because these habitats are more resistant to summer drought, individuals which survive here may re-colonise open habitats when the drought is over. Re-colonisation of the optimal (source) habitat from sub-optimal (sink) habitat was also found in several other studies on chironomids in rain pools (McLachlan 1988) or in initial stages of succession in burned peatlands (Delettre 1994) and it was shown to be the necessary condition for maintenance of the source to sink equilibrium (Morris 1991). This situation may be relatively frequent in nature, because many species use sub-optimal habitats for survival, if the source habitats are sensitive to

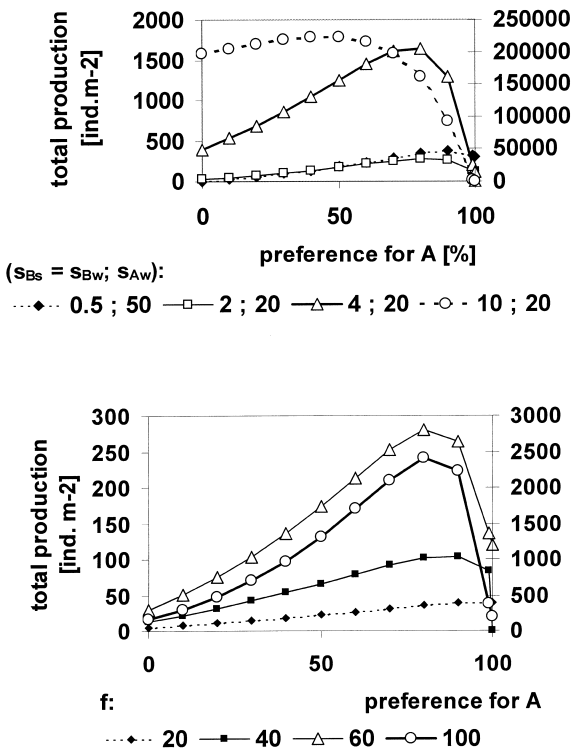


Fig. 6. Total amount of individuals produced during eight consecutive generations as a function of preference for habitat A: a) for various combinations of $s_{Bs}=s_{Bw}$ and s_{Aw} ($f=60$, scale on the right hand side is for $(s_{Bs}=s_{Bw}; s_{Aw})=(10; 20)$); b) for various fertilities ($s_{aw}=0.2$, $s_{Bs}=s_{Bw}=0.02$, scale on the right hand side is for $f=100$). Other parameter values as in Fig. 5.

some catastrophic environmental stress: drought (Ducrottoy 1980, Delettre 1986, McLachlan 1988) or frost (Thomas et al. 1996).

Direct observation of this re-colonisation process is difficult because of low abundances in the sub-optimal habitats, and thus empirical evidence about some sink to source re-colonisation is sparse (Boughton 1999). We have, therefore, used a mathematical simulation to check, whether the source-sink re-colonisation may produce a pattern similar to empirical data.

The model parameters can be split into two groups: those describing environmental factors (survival rates) and those characterising the population (fertility and oviposition preference). Sharing of rich, unstable, source habitats and poor, stable, sink habitats appears to be a suitable strategy for a wide range of both population and environmental parameters. This sharing can be useful for overcoming of seasonal fluctuations in source habitat occurrence or suitability.

The source habitats may occur each season at the same place, as in the cases of terrestrial chironomids in shallow soils on rocks, or in African rain pool dwellers (Delettre 1988, McLachlan 1988). Alternatively, their occurrence may be variable in space as a result of random appearance and disappearance of suitable patches, as in the initial stages of secondary succession (Frouz 1994a, 1997b). In the latter case the newly appearing source-sink systems must be colonised from residual populations in the neighbouring sink habitats or from other source-sink systems in a similar way as described for grasshoppers specialised on open areas in riverbanks formed by catastrophic floods (Stelter et al. 1997).

Reinforcement of sink habitats from source habitats can maintain a resident population in sink habitat persistent for several generations. This low density sink population can be widespread in the landscape and, thus, quickly colonise even very small source habitats, e.g., initial succession stages formed by disturbances which are small and have a very short duration (Delettre 1994, Thomas et al. 1996). This situation is different from the classical metapopulation approach, where re-colonisation between "islands" of source habitats is assumed and where the process is limited by the size and age of the new suitable island and its distance from the source (Bascompte and Sole 1996, Hill et al. 1996). Periodical occurrence of small source habitats may increase population persistence in sink habitats. Another frequently mentioned reason for oviposition in a sub-optimal habitat is insurance against random, catastrophic disappearance of source habitat, which may occur from time to time (Pulliam 1988, Pulliam and Danielson 1991, Förare and Engqvist 1996, Holt 1997). From the evolutionary point of view, the critical parameters for success of this strategy are high fertility (population growth rate) and proper distribution of eggs between source and sink habitats on the population level.

On the individual level, oviposition is a very complex process consisting of several steps such as dispersal, searching for oviposition site, sampling and selection of a site and egg deposition (Browne 1993). Each of these steps can be affected by a set of internal cues such as energetic and mating status of females, number of eggs carried, previous oviposition history as well as a set of external cues such as vegetation pattern, allelochemicals, moisture and temperature of substrate, presence of predators or competitors, etc. (Millar et al. 1992, Minkenberg et al. 1992, Blaustein and Kotler 1993, Kouki 1993, Isoe and Millar 1995). Variation in response to these cues in each of these steps may result in variation of oviposition preferences on the population level. Insect populations typically harbour at least a moderate phenotypic variability for preference of novel food or substrates that are often not optimal for larval development (Sheeba et al. 1999).

Several reports indicated that females exert an increased acceptance of less preferred oviposition sites following periods during which they have been denied the opportunity to oviposit (Browne 1993). Females first search for the optimal habitat. If these habitats are rare and the female has not found any of them for some time, or after it has spent most of her energetic reserves, she lays eggs in the sub-optimal habitat. Suitability of source and sink habitats may vary temporally (Boughton 1999). In our model situation the oviposition attractiveness of sub-optimal patches with tall vegetation may be higher early in the spring before the period of intensive plant growth begins.

Hatched females search first for a male for mating and only after mating they start to search for oviposition sites (Browne 1993). Oviposition site must be within a certain distance from the mating site. Therefore, the position of the mating site can affect the selection of the oviposition site. This can be important in situations where mating sites are selected by males, e.g., males mating swarms of Chironomidae and Ceratopogonidae (Armitage 1995).

Females better supported by nutrients during their larval development have longer wings, carry more eggs, and are better migrants (McLachlan 1983, Delettre 1988). Nutritional status of females, particularly the amount of energetic reserves can also affect their behaviour (Browne 1993). Females that carry more eggs have relatively less time for searching of oviposition site and therefore a higher sensitivity for lower ranked oviposition sites (Minkenberg et al. 1992). Thus, females having a different nutritional status may vary in acceptance of oviposition sites of various quality.

Insect females select oviposition sites on a short-term scale – in comparison with larvae, which utilise them for a longer time. Females of terrestrial chironomids try to maximise the success of the next generation by selection of the best oviposition site. The criteria include mainly nutritional status of the selected habitat,

but also absence of possible competitors or predators (Millar et al. 1992, Blaustein and Kotler 1993). Little information exists about the role of characteristics which determine habitat stability for decision about oviposition site (Sowig 1995). Oviposition in sub-optimal patches is assumed to be an insurance of the population against catastrophic events in the optimal habitat (Förare and Engqvist 1996). The question remains, whether the sub-optimal patches are selected at random or with respect to their potential stability.

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