

# Evolutionarily stable dispersal of a waterstrider in a temporally and spatially heterogeneous environment

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## Summary

Evolutionary stable dispersal and wing muscle histolysis strategies are studied in the waterstrider *Gerris thoracicus*. These strategies relate to spreading reproductive risk. Overwintering individuals have the choice of dispersing to either a brackish sea bay or a rock pool habitat. The former is reproductively more favorable than the latter during warm dry years and less favorable during cool wet years. After spring migration, individuals may histolyse their flight muscles and lay all their eggs in one pool or they may retain their flight ability and lay fewer eggs in total but spread them in several pools. We use a simple two-habitat model to examine the question of habitat dispersal. Our results indicate that, although the value of the evolutionary stable dispersal depends on the degree of variability in the environment and on the probability of local extinctions in either habitat, the population always disperses to both habitats as a consequence of density dependent growth. We use a more detailed multiple-rockpool habitat model to examine the question of wing muscle histolysis as a response to density dependence. Our results indicate that a wing muscle histolysis response to population density is an evolutionarily stable strategy when compared with the two alternatives of females always histolysing or never histolysing their flight muscles. The application of evolutionarily stable theory to stochastic problems presents a number of difficulties. We discuss these difficulties in the context of computing evolutionarily stable strategies for the problems at hand.

*Keywords:* Evolutionarily stable strategy; risk-spreading; dispersal behavior; flight muscle histolysis; waterstrider.

## Introduction

Fluctuating and uncertain environments may favor the reproductive strategy of spreading eggs or offspring with respect to space and time (Cohen, 1967; den Boer, 1968; Strathmann, 1974; Stearns, 1976; Root and Kareiva, 1984, 1986). Generally, this kind of reproductive behavior is called bet-hedging or risk-spreading (for a review, see Seger and Brockmann, 1987).

Egg spreading has also been reported in the waterstrider *Gerris thoracicus* Schummel (Vepsäläinen, 1978; Kaitala, 1989). Accordingly, risk-spreading has been used to explain the reproductive behavior of *G. thoracicus*: the waterstrider females spread eggs in different

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localities to avoid 'local extinctions', i.e. loss of all the offspring of a female, in a risky environment (Vepsäläinen, 1978).

Two assumptions often made in the risk-spreading literature are that, first, patches utilized by the organisms are similar and, second, the life histories of these organisms are similar. The reproductive behavior of the waterstrider *G. thoracicus*, however, departs in two aspects from these risk-spreading related assumptions. First, *G. thoracicus* is able to use two different types of unpredictable habitats. One of the habitats is a large sheltered brackish sea bay capable of hosting hundreds of insects, and the other consists of a number of relatively small rock pools, the smallest of which are capable of hosting only a few insects. Second, the reproductive capacity of a female depends on whether she retains her ability to fly during the reproductive period (Kaitala, 1988). Colonization of the two habitats takes place after post-wintering spring dispersal, when all the adults are able to fly (Kaitala, 1988). A female's egg-laying capacity increases if she histolyses her indirect flight muscles early in the reproductive season. Thus, if strategies of waterstriders living in uncertain environments involve retention of flight ability then fecundity is reduced. Field observations (Kaitala, 1989) show that retention of flight ability mainly occurs among those waterstriders inhabiting rock pools. Vepsäläinen *et al.* (1985) proposed that when the reproductive success in one habitat is low, then it is probable that the reproductive success in the other habitat is high (see below). Hence, the conditions for reproduction in each habitat seem to be negatively correlated.

We consider the evolutionarily stable dispersal strategies of the waterstrider *G. thoracicus* Schummel in an environment consisting of two distinct post-overwintering habitats. We compare evolutionarily stable dispersal strategies with those obtained using the theory of risk-spreading. We are interested in how different solution concepts relate to each other and how different uncertainty patterns affect the dispersal rates, rather than in finding a single strategy related to a particular environment.

The spread of offspring into different habitats can be realized in different ways. A single female can distribute her eggs into different habitats by flying between the habitats throughout the reproductive period (Vepsäläinen, 1978). In that case the female maintains her flight ability throughout the reproductive season. Another risk-spreading mechanism, which is of equal importance, takes into account the reproductive success of the offspring: after overwintering the sibling offspring distribute their reproductive effort among the two different habitats. The study of this problem needs a strategic formulation, and hence, we are mainly interested in evolutionarily stable strategies.

An evolutionarily stable dispersal strategy has the property that when it is common no other mutant strategy can increase (ESS, Maynard Smith, 1976). This characterization is, however, somewhat ambiguous in the context of fluctuating populations inhabiting a finite number of patches. In a randomly varying environment there will not be, in general, any strategy which is protected against invasion of any other strategy: 'there is always the chance of a run of years which will favor an inferior strategy' (Levin *et al.*, 1984). In this paper we apply an approach developed recently by Ellner (1985a, b) which is based on computing the expected growth rates of invading strategies.

The paper is organized as follows. First we review the life history of the waterstrider *G. thoracicus*. Then we develop a two-habitat model to study the post-overwintering distribution between the two habitats. In the following section we review the theory of evolutionarily stable strategies in populations inhabiting uncertain environments and we also shortly review the concepts of risk-spreading. We then present the results of various simulation studies relating to evolutionarily stable dispersal strategies in *G. thoracicus*. In the next section we present a more detailed model for the rock pool habitat to study the interaction between evolutionarily stable dispersal strategies

and the life history trade-off related to the egg-laying capacity and flight ability of *G. thoracicus* females.

### ***Gerris thoracicus* life history**

The ecology and the life history of the waterstrider, *G. thoracicus* is well documented (Vepsäläinen, 1973; Kaitala, 1987, 1988, 1989). Here we shall review life history traits which serve as a background for building the model and interpreting the results.

*G. thoracicus* occupies two different types of unpredictably changing habitats in the Finnish Baltic region, rock pools and protected brackish sea bays. During exceptionally warm and dry summers the small, temporary, and partially isolated rock-pools often dry out causing egg and larval mortality. By partially isolated we mean that waterstriders are able to fly, but seldom are able to walk or swim, between the rock pools. Hence, the rock pools are isolated for larvae and for waterstriders not able to fly. During warm summers the sea bay habitats offer a stable site for reproduction, and the temperature of the brackish water is relatively high facilitating rapid development of larvae. On the other hand, during cold summers the rock pools do not dry out. They offer a suitable habitat for reproduction while, especially at the start of reproduction, sea bays provide cool habitats in which waterstrider larval development is slow (Vepsäläinen and Patama, 1983).

*G. thoracicus* is a generalized predator on insects which they capture, dead or alive, on the water surface. Food availability depends on the abundance of airborne insects falling onto the water surface and on the abundance of the aquatic insects. Food conditions seem to vary with summer weather conditions, affecting both the larval development as well as the reproductive capacity of the females (Kaitala, 1987). Cannibalism has been demonstrated under laboratory conditions (Salemaa, 1984).

The species is mainly univoltine and long-winged. The adult waterstriders overwinter on land. The overwintered adults disperse during the spring after which reproduction starts. During the reproductive period, flights between the rock pools are frequent and females disperse their eggs among many sites. The rock pools may dry out during summer (Kaitala, 1989), and females seem not to have any environmental cues to predict the future environment quality of larval development. Hence, the habitat is considered unpredictable.

Kaitala (1988) has shown that long-winged *G. thoracicus* has two morphs with respect to maintaining flight ability, namely, flyers and non-flyers. These two morphs represent two different reproductive strategies. First, the flyers are able to fly throughout the reproductive period. Thus, they can lay their eggs in many pools and also in the two different habitats. Hence, the flyers avoid putting their eggs in one basket. Second, the non-flyers histolyse their indirect flight muscles after reproduction has started. Further, Kaitala (1988) showed that the number of eggs laid under abundant and varying food conditions is higher among non-flyers than flyers. She also found that during food deprivation non-flyers were able to survive better than the flyers. Hence, it is expected that there is a trade-off between the egg-laying capacity and flying ability of the waterstriders in an uncertain environmental system, and that risk is spread by distributing siblings between different habitats.

The observed distribution of the two morphs is related to habitat instability. Flyers are the dominant morph in rock pools and non-flyers are the dominant morph in sea bays, but both morphs are found in both habitats (Kaitala, 1988). The distribution of waterstriders between the two habitats in spring is not related to the distribution of individuals in the previous autumn (Kaitala, 1989). Thus, individuals born in a particular habitat may return to the same habitat

after overwintering, but they may also choose a different type of habitat than the one in which they matured.

### A two-habitat model of dispersal

#### *Dispersal and habitat selection*

The strategy is defined as the fraction  $\gamma$  of the offspring of an individual (i.e., siblings) which occupy the sea bay habitat during the reproductive season. Hence, the fraction  $1 - \gamma$  of the siblings occupy the rock pool habitat. We assume here that an individual reproduces either in the sea bay habitat or in the rock pool habitat, but not in both habitats. Since it is individuals and not the population that play a strategy, we interpret this strategy  $\gamma$  as the probability  $\gamma$  than any given individual selects the sea bay habitat.

The subscripts  $l$  and  $r$  will be used to denote individuals in the sea bay and rock pool habitats, respectively (for a summary of the model variables and parameters, see page 287). Further, let  $k$  denote a time index updating the generations, and let  $X_l(k)$  and  $X_r(k)$  denote the female parent population respectively reproducing in the sea bay and rock pool habitats. Assume that, in the previous generation, the female parent populations  $X_l(k - 1)$  and  $X_r(k - 1)$  produce a total of  $x_l(k)$  and  $x_r(k)$  female offspring in each of these habitats. Hence, the number of the female offspring entering the overwintering phase prior to reproduction by the  $k$ th generation is given by  $x_l(k) + x_r(k)$ . Assume, for simplicity, that a fixed fraction  $\mu$  of overwintering individuals survive to disperse the following spring. Then the number of females successfully overwintering is given by

$$X(k) = \mu(x_l(k) + x_r(k)) . \quad (1)$$

Finally, let the stochastic parameters  $\alpha_{lk}$  and  $\alpha_{rk}$  respectively describe the environmental conditions in year  $k$  in the sea bay and rock pool habitats and, for  $s = l, r$ , let  $Y_s(X_s, \alpha_{sk})$  denote the number of female offspring produced per female in season  $k$  as a function of population density  $X_s$  and environmental condition  $\alpha_{sk}$ . Noting that  $X_l(k) = \gamma X(k)$  and  $X_r(k) = (1 - \gamma)X(k)$  it follows that the population dynamics model has the form

$$x_s(k + 1) = X_s(k)Y_s(X_s(k), \alpha_{sk}), s = l, r \quad (2)$$

where  $k = 0, 1, 2, \dots$

#### *Growth functions*

Although a number of different functional forms can be selected for  $Y_s$ , in this study we select the following form (Maynard Smith, 1976) because it is relatively simple and captures the essence of the density-dependent response (see Getz and Kaitala, 1989): that is,

$$Y_s(X_s, \alpha_s) = \frac{\sigma_s \alpha_s}{1 + 2X_s/\beta_s} , s = l, r \quad (3)$$

where  $2X_s$  is the total population size in the habitat (assuming an equal sex ratio), the environmental parameters satisfy  $0 \leq \alpha_s \leq 1$ , the parameter  $\sigma_s > 0$ ,  $s = l, r$  is the density-independent growth under ideal conditions (that is, when  $\alpha_s = 1$ ), and  $\beta_s$ ,  $s = l, r$  is a niche capacity parameter that represents the population density at which the density-independent growth is reduced by one half. Note from (3) that the same relative variation in production of new individuals due to environmental fluctuations is observed at each level of population density.

The density dependence introduced in Function (3) could be due to a reduction in the egg laying capacity and/or larval survival rates as a consequence of competition between individuals

for food and space. We later present a model where it is important to distinguish between density-dependence arising from the competition between adults and between larvae.

We also studied the following version of the model

$$Y_s(X_s, \alpha_s) = \frac{\sigma_s}{1 + 2X_s/(\beta_s\alpha_s)}, \quad s = l, r \quad (4)$$

which is equivalent to assuming that environmental fluctuations only impact production indirectly by decreasing the value of the niche capacity parameter  $\beta_s$ . The results we obtain using model (4) are qualitatively similar but not as dramatic as those obtained using (3). Hence, here we only report the results obtained using model (3).

### Parameter estimates

The environmental fluctuations of the two habitats,  $\{\alpha_{lk}\}_{k=0}^{\infty}$  and  $\{\alpha_{rk}\}_{k=0}^{\infty}$ , are assumed to be independent and identically distributed random variables. We also assume that they are independent of the population densities  $x_s(k)$  or  $X_s(k)$ ,  $s = l, r$ , for any  $k$ . Later we will study two different cases where the fluctuations in the two habitats are independent or negatively correlated.

In the first of our simulation studies, which we conducted to explore the trade-off represented by different values of the dispersal parameter  $\gamma$ , the following parameter values were used:  $\mu = 1$ ,  $\sigma_r = 100$ ,  $\beta_l = 5$ , and  $\beta_r = 2.5$ . The parameters  $\sigma_s$  describe the egg-laying capacities of the females. It was found by Kaitala (1988), under laboratory conditions when food is not a limiting factor, that the average capacity of the *G. thoracicus* females to lay eggs is 212 ( $\pm 102$ ) in the non-flyer females and 108 ( $\pm 60$ ) in flyer females. Under varying food conditions both morphs tend to increase their longevity and decrease the number of eggs laid daily (Kaitala, 1988), resulting in a decrease in total number of eggs laid by both morphs to  $163 \pm 68$  and  $67 \pm 52$ , respectively. Half of the eggs are assumed to produce females. There are reasons to expect that the dispersal behavior of the females and males differ from each others (Kaitala, 1988). In this paper, however, we shall study the dispersal behavior of the females only and assume that males dispersal does not affect the reproduction of females.

The parameter values for  $\beta_l$  and  $\beta_r$  in our model are chosen to reflect the conditions in a real population studied by Kaitala (1989). In the absence of fluctuations the equilibrium (female) population sizes computed from the model are between 250 and 740 depending on the dispersal fraction. These values are of the same order as the particular local population studied by Kaitala (1989). With these parameters, we are essentially evaluating the trade-off between the sea bay habitat and one rock pool habitat that has a maximum capacity that is one half the maximum sea bay capacity. A more realistic model would divide the rock pool habitat into several smaller rock pools, as is done below. This simpler model, however, is adequate to analyze the qualitative aspects of the dispersal strategy  $\gamma$ .

### Evolutionary stability

#### *Viable dispersal strategies*

Consider model (1)–(3). In general, this model permits any of the following population growth patterns under fluctuating conditions. First, the population can be driven to extinction. Second, the population may increase without limit. The second case can only occur if  $Y_l$  and  $Y_r$  are non-saturating functions of population size. Third, the population may fluctuate between an upper and a non-zero lower limit. The latter implies that the population does not become extinct. Note

that the fluctuations may not be due entirely to the environmental uncertainty: the density-dependence itself can contribute to such fluctuations by producing periodic and chaotic oscillations in the absence of environmental fluctuations (May and Oster, 1976; Getz and Kaitala, 1989).

Ellner (1985a, b) derived an evolutionarily stable strategy (ESS, see Maynard Smith, 1976) for seed dispersal in plants using a model that is equivalent to our model if we assume that one of the functions  $Y_l^i$  or  $Y_r^i$  is constant. In Ellner's model, density-dependence and environmental uncertainty affect only the growth of germinating seeds and not the survival of nongerminating seeds which remain dormant until the next year's growing season (that is, independent of the environmental fluctuations and the number of germinating and dormant seeds). Ellner (1984) identified conditions under which the stochastic process defined by equations such as (1) and (2) converge to a unique stationary distribution concentrated on  $(0, \infty)$ . Following Ellner (1985a) we say that a strategy is viable if it converges to a stationary distribution. A stationary distribution is a distribution which is independent of time and the initial conditions. It should be noted that Ellner (1985a) uses the term morph where we use the term strategy. We have reserved, however, the term morph to be used in the context of dimorphism describing the different flying capacities of the waterstriders.

Following Ellner's (1985a, b) approach, insight into the dynamics of our model can be obtained by considering the sign of the quantity

$$v(\gamma) = \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{k=0}^{t-1} \ln \{ \mu [ \gamma Y_l(0, \alpha_{lk}) + (1 - \gamma) Y_r(0, \alpha_{rk}) ] \}.$$

Thus,  $v(\gamma)$  is the expected value of the logarithm of the per capita growth rate for the strategy  $\gamma$  when the population is rare. As in Ellner, if  $v(\gamma) > 0$ , then the strategy  $\gamma$ , when the population is rare, ensures the population will grow. On the other hand, if  $v(\gamma) < 0$  then the strategy  $\gamma$  will ultimately result in extinction of the population. If  $v(\gamma) > 0$  for a range of dispersal strategy values  $\gamma$  then one of them may be best in some sense. Next we discuss finding on evolutionarily stable dispersal based on the notion of a stochastic process converging to a unique stationary distribution under conditions where both  $v(\gamma) > 0$  and the growth of the population is also bounded above by the fact that  $Y_s(X_s, \alpha_{sk})$ ,  $s = l, r$ , are bounded for all  $X_s > 0$  and  $0 \leq \alpha_{sk} \leq 1$ .

### *ESS dispersal strategies*

Our approach to the problem of deriving an ESS strategy follows Hastings (1983), Brown and Vincent (1987), and Ellner (1985a, b), who assumed that populations playing different strategies are non-interbreeding. Hence, we consider the case in which the habitats can be invaded by another related species differing only in the dispersal rate. In this case the different populations interact with each other through the density dependence of the reproductive dynamics (cf. Equations (2)–(4)).

An evolutionarily stable dispersal strategy has the property that when it is common no other mutant strategy<sup>1</sup> can increase. This characterization is somewhat ambiguous in the context of fluctuating populations: an evolutionarily stable dispersal strategy should be able to resist an invasion of a rare strategy at different population levels (i.e., including when the population playing ESS dispersal is itself rare) and during rare environmental conditions favoring the mutant strategy. Hence, if we commit ourselves exclusively to the non-invasion criterion, then evolu-

<sup>1</sup> From here on we follow the convention of using the term mutant to denote the strategy of an invading population.

tionary stability approach would be difficult, if not impossible, to apply in most problems dealing with fluctuating populations.

Ellner (1985a) proposed that we deal with the difficulties of defining an ESS strategy in the context of fluctuating populations by considering the stationary distribution of populations playing various strategies. He also proposed that we analyze the dynamics of the system using a model linearized about a point corresponding to zero for the level of the invading population, and identity conditions under which a mutant strategy can invade. Although this approach may lead to the identification of an ESS strategy which is invadable under a highly unusual run of environmental conditions, we follow it because it appears to provide the most direct extension of deterministic ESS theory.

Let  $\gamma^1$  and  $\gamma^2$  respectively denote the resident and mutant strategies, and let  $X^1$  and  $X^2$  respectively denote the overwintered populations sizes of resident and invading populations. Then we consider the expected growth rate of a rare population  $X^2$  invading a resident population  $X^1$  in its stationary distribution, using the following set of equations

$$X^1(k + 1) = \mu X^1(k)[\gamma^1 Y_l(X_l(k), \alpha_{lk}) + (1 - \gamma^1) Y_r^1(X_r(k), \alpha_{rk})], \tag{5}$$

$$X^2(k + 1) = \mu X^2(k)[\gamma^2 Y_l^2(X_l(k), \alpha_{lk}) + (1 - \gamma^2) Y_r^2(X_r(k), \alpha_{rk})], \tag{6}$$

for  $k = 0, 1, 2, \dots$ . Here  $X_l(k) = X^1(k) + X^2(k)$  is the total number of the insects occupying the sea habitat and  $X_r(k) = X_r^1(k) + X_r^2(k)$  the total number of the insects occupying the rock pool habitat, where  $X_l^i(k) = \gamma^i X(k)$  and  $X_r^i(k) = (1 - \gamma^i) X(k)$ ,  $i = 1, 2$ . Both the resident and mutant strategies are assumed to be viable in the sense of Ellner (1985a).

When the invading strategy is rare, its contribution to the total density is neglected. Since, we are interested in the expected growth rate of the invading population the following equations are applicable (cf. Ellner, 1985a):

$$X^1(k + 1) = \bar{X}^1(k) \tag{7}$$

$$X^2(k + 1) = \mu X^2(k)[\gamma^2 Y_l^2(\gamma^1 \bar{X}^1, \alpha_{lk}) + (1 - \gamma^2) Y_r^2((1 - \gamma^1) \bar{X}^1, \alpha_{rk})], \tag{8}$$

where  $k = 0, 1, 2, \dots$ , and  $\bar{X}^1$  denotes the resident strategy in its stationary distribution.

The mean logarithmic growth rate of the invading strategy is

$$\rho(\gamma^1, \gamma^2) = \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{k=0}^t \ln \{ \mu [\gamma^2 Y_l^2(\gamma^1 \bar{X}^1, \alpha_{lk}) + (1 - \gamma^2) Y_r^2((1 - \gamma^1) \bar{X}^1, \alpha_{rk})] \}. \tag{9}$$

If the resident strategy is evolutionarily stable, the mean logarithmic growth rate of any invading strategy is negative by definition. Thus, if the mean logarithmic growth rate of some invading strategy is positive, then the resident strategy is not an evolutionarily stable strategy.

In deterministic cases, the stationary distribution of a single strategy model usually reduces to an equilibrium state (although periodic and chaotic dynamics are possible). Hence, when we consider the possibility that a mutant strategy attempts to invade the population, we assume that the population size of the resident strategy is at its equilibrium level (assumed here to be unique).

To find an ESS we need consider only viable strategies: that is, strategies for which  $v(\gamma) > 0$ . First we select a candidate ESS strategy for the resident population. Then simulations are carried out such that the distribution for the resident strategy is generated and the mean logarithmic growth rate of all candidates for the invading strategy are calculated using (9). If the candidate ESS strategy cannot resist the invasion of one or more of the mutant strategies then another candidate for the ESS strategy is selected. The only numerical method that can locate all the ESS solutions is to search through all the different values of  $\gamma$ .

### *Risk-spreading strategies*

Basically, risk-spreading means that a female avoids putting all her eggs in one basket in an uncertain environment. In a review of the concepts of risk-spreading, Seger and Brockmann (1987) identify five classes of strategies or contexts, which have been used in the literature to discuss risk-spreading. They settle on two different definitions of risk-spreading or bet-hedging, both of which require temporal environmental variation. First, risk-spreading refers to strategies which reduce both the arithmetic mean and associated variance of an individual's fitness: that is, the expected number of offspring that reach maturity. In this case, the best risk-spreading strategies often maximize the corresponding geometric mean, which is more sensitive to variance than the arithmetic mean<sup>2</sup>. This concept of risk-spreading has been used by Cohen (1967), Root and Kareiva (1984) and Strathmann (1974). Second, risk-spreading refers to strategies in which members of a genotype adopt different phenotypes, where the proportion adopting each phenotype is expressed in a probabilistic way. In this case, the geometric mean fitness also may be maximized at the expense of arithmetic mean fitness; although, as Seger and Brockmann (1987) point out, the variance of realized individual fitnesses may be increased.

A strategic model like ours is applicable when modelling the fitness of an individual female by taking into account not only the juvenile mortality determining the expected number of offspring that reach maturity but also their reproductive capacity. In our model the waterstrider females do not spread risk during egg laying. Rather risk-spreading is realized at the strategy level since sibling offspring distribute between the two habitats, thereby spreading their mother's risk. The problem will be more complicated when the reproductive value of the females, and hence of the offspring, depends on their dispersal behavior (see below).

### **Analyses and simulation results**

#### *Mutually independent fluctuations*

Here we consider two habitats with independent fluctuations. We assume that the uncertainty parameters  $\alpha_l$  and  $\alpha_r$  are either constant and equal to 0.5, or one or both fluctuate such that they have a uniform distribution with mean value equal to 0.5. The calculations of ESS solutions represents averages of three independent results calculated over 5000 generations.

We first consider the deterministic version of the model (1)–(3), where all the fluctuations are replaced by their expected values. The evolutionarily stable dispersal strategy is 0.67 (see Table 1). Hence, no temporal variation is needed to explain dispersal of waterstriders between different

Table 1. The evolutionarily stable dispersal strategies ( $\gamma$ ) in constant and fluctuating habitats with no correlation and with negative correlation ( $\alpha_l = 1 - \alpha_r$ ). In all cases  $\sigma_l = \sigma_r = 100$ . In 'Local extinction' the probabilities that  $\alpha_l = 1$  or 0 are both 0.25.

No correlation	Constant	Both fluctuate	Only sea bay fluctuates	Only pools fluctuate
ESS	0.67	0.63	0.60	0.70
Negative correlation	Constant	Small variation $\alpha_l \in [0.25, 0.75]$	Large variation $\alpha_l \in [0.0, 1.0]$	Local extinction $\alpha_l \in [0.0, 1.0]$
ESS	0.67	0.65	0.61	0.56

<sup>2</sup> The arithmetic mean of  $x$  and  $y$  is  $(x + y)/2$  while the geometric mean is  $(xy)^{1/2}$ .

habitats. It is due purely to the density-dependent growth response that results from a finite environment. It can be shown that the higher the contribution made by one habitat to the equilibrium total population size, the higher the proportion of the overwintered insects that should occupy the habitat.

In general, the evolutionarily stable dispersal rate does not maximize the total population size in a deterministic habitat system (Hastings, 1983). Here, however, we have a special case, where the strategy which maximizes the total population sizes at the equilibrium is the ESS. In general, as discussed by Hastings (1983), the ESS maximizes the average per capita reproduction rate in both habitats.

Where there is variation in both habitats, the evolutionarily stable dispersal strategies are decreased as compared with the constant environment (Table 1). Further insight can be obtained by letting only one of the habitats vary at a time. If the sea bay fluctuates, then the fraction of the offspring occupying it decreases as compared with the constant environment. And if the rock pool habitat fluctuates, then the fraction of the offspring occupying the sea bay increases. Hence, the offspring of a female realizing the evolutionarily stable strategy tend to avoid fluctuating habitats. This result of avoiding fluctuation could be explained as an attempt by the waterstriders to minimize variations in the reproductive success. The behavior of minimizing variation is a form of risk-spreading.

Consider a population that lives in a constant rock pool habitat, but has the opportunity to disperse into a fluctuating sea bay habitat which is presently unoccupied. Computer simulations show that any strategy in which a proportion of siblings disperse into the empty sea bay habitat will take over rapidly in the population. One of these strategies is the ESS dispersal strategy (Table 1). This is the case despite the fact that occupying the new habitat, or distributing the reproductive effort between two different habitats, which is usually understood as the basic idea of the risk-spreading strategy, also increases the variance in the number of the offspring and in the population size.

We also studied the evolutionarily stable strategies in a two-habitat environment in which one of the habitats is risky in the sense that local extinctions are possible there. No qualitative difference was observed while keeping fluctuation patterns of one of the habitats unchanged and gradually making the other fluctuating habitat more risky. A fraction of females reproduce in the risky habitat despite the threat of individual extinction. This result contradicts the predictions obtained from risk-spreading models stating that females should avoid individual local extinction, i.e., loss of all of her offspring (e.g. Vepsäläinen, 1978). The fraction of females reproducing in a risky habitat, however, decreases with increasing risk of local extinction.

### *Negatively correlated fluctuations*

Assume next that environmental conditions in the sea bay and rock pool habitats are correlated negatively (Vepsäläinen *et al.*, 1985). In particular, let  $\alpha_l = 1 - \alpha_r$ , and consider the cases where  $\alpha_l = 0.5$  and  $\alpha_l$  is uniformly distributed on  $[0.25, 0.75]$  ('small fluctuations') and on  $[0, 1]$  ('large fluctuations'). Hence, we calculated the evolutionarily stable dispersal strategies for increasing fluctuations. As the fluctuations increase the value of  $\gamma$  decreases (that is, the proportion of the insects going to the sea bay decreases, see Table 1) even more than the environments are uncorrelated.

Suppose fluctuations increase beyond the large variation case so that there is a positive probability that the population will be wiped out during the season in one of the local habitats (e.g., rock pools dry up or sea bay does not warm up sufficiently to permit completion of development). In the simplest model we assume that when the production in one of the habitats fails, then the other habitat produces the maximum number of the progeny (that is, if  $\alpha_r = 0$

then  $\alpha_l = 1$ ). In this case only local extinctions are possible. Strategies  $\gamma = 0$  or  $1$  are not persistent. All other  $\gamma \in (0, 1)$  are viable. Here we consider the relatively extreme case, where  $\alpha_r = 1 - \alpha_l$  are uniformly distributed on  $(0, 1)$  and the probabilities that  $\alpha_l = 0$  or  $1$  are both  $0.25$ . Since  $\alpha_l = 0$  or  $\alpha_r = 0$  occurs  $50\%$  of the time, the probability that the populations become locally extinct in one of the habitats is on average once every other year. Now, the ESS dispersal strategy is  $0.56$ , which is considerably lower than any other ESS strategy found so far. Altogether, we see that the more severe the fluctuations are, the more evenly the distribution is carried out between the two habitats.

We next compare the ESS strategy with the bet-hedging strategy that corresponds to minimizing the total population geometric mean level with respect to time. The strategies maximizing the arithmetic and geometric means are respectively  $0.66$  and  $0.62$ , and the standard deviations of the population sizes are respectively  $100.2$  and  $99.7$ . Hence, the geometric mean strategy yields a slightly lower variance in the population size than the strategy maximizing the arithmetic mean but the evolutionarily stable strategy yields the lowest variance of these three strategies. However, there are other strategies yielding even smaller variances (e.g.  $\gamma = 0.4$  yields the population standard deviation equal to  $96.5$ ) and hence the ESS strategy is not determined by the properties of the population variance.

We next turn to study the possible reasons for wing muscle dimorphism. Simulations show that in a two habitat system a wing muscle histolysis strategy, which corresponds to  $\sigma_r = \sigma_l$  in our model, always wins in the ESS sense over a strategy in which the flight muscles are maintained throughout the reproductive period. Hence, a two habitat model as such, cannot be used to explain why some individuals in the rock pool habitat maintain their flight muscles.

Facultative flight muscle histolysis is an additional strategy which permits individuals to escape from a habitat when its favorability for reproduction dramatically declines. In the next section, we shall add one more property to the model: the trade-off between the possibility of migrating between habitats during reproduction.

### Wing muscle trade-off

The two habitat model proposed thus far is too simple to explain why some individuals migrating to the rock pool habitat fail to histolyse their wing muscles. In this section we consider one of several possible evolutionary forces which may favor some individuals maintaining flight ability. Specifically, we show that maintaining flight ability provides a strategic advantage when the population level is low and the environment is patchy. In this case, when there are unoccupied rock pools and when density-dependence acts more strongly between larvae than adults, individuals may do better by distributing a smaller number of eggs in many pools rather than reducing their flight muscles and laying all their eggs in one small rock pool. This seems to be the case when a single female can produce lots of eggs compared to the carrying capacity of a single rock pool. On the other hand, when the population level is high, all the rock pools are occupied anyway. In this case it is of little value to distribute a smaller number of eggs into several different rock pools, each close to its carrying capacity in eggs.

### Model

Here we develop a more detailed model for a system containing a sea bay and a large number of rock pools. The model covers both situations in which a single female lays eggs only in one rock pool, and situations where females visit several different rock pools, laying a small number of eggs in each of them.

The model assumptions are now modified as follows:

- (i) density-dependence is modelled in the terms of the number of larvae;
- (ii) an invasion by a 'mutant' strategy is attempted by a single female, and unlike above, her contribution to the density-dependence of the growth rates is explicitly included in the model;
- (iii) the number of the small rock pools,  $n$ , is large but finite. Rock pools are identical; that is, they are characterized by the same density-dependence parameter  $\beta_r$ , which is small compared with that of the sea bay habitat;
- (iv) the habitat distribution parameter  $\gamma$  is the same for each population type  $i$ ;
- (v) a strategy is given by  $\eta$  which defines the proportion of the females in the rock pool habitat that maintain their flight ability. The proportion of the females maintaining their flight ability is assumed to depend on the population density.

The production function for the sea bay is now given by

$$Y_i(X_{i\sigma}, \alpha_i) = \frac{\sigma_i \alpha_i}{1 + X_{i\sigma} / \beta_i}, \tag{10}$$

where we have modelled the density-dependence in the terms of the number of eggs of larvae  $X_{i\sigma}$ , where

$$X_{i\sigma} = 2X_i \sigma_i$$

For the rock pool habitat, we construct a more detailed behavioral model related to the patchiness of the habitat. Adults which maintain their flight ability can easily visit many pools per day; hence, all the pools are accessible to them. For non-flying adults and larvae, the rock pools are isolated since the ability of the waterstriders to disperse on land is poor and hardly ever observed to occur.

The dispersal in the rock pool habitat takes place as follows. Fraction  $\eta$ , which is a strategy parameter, is the proportion of the females that reduce their flight muscles in the rock pool habitat. Hence, the number of females reducing the flight muscles (non-flyers) is given by

$$X_r^n(k) = \eta X_r(k) \tag{11}$$

and the number of females maintaining their flight muscles (flyers) is

$$X_r^f(k) = X_r(k) - X_r^n(k). \tag{12}$$

A female maintaining her flight ability distributes her eggs evenly in each of the small rock pools. We assume that her contribution to the population density of a single pool is  $1/n$ . It should be noted that a variety of assumptions can be introduced here. For example, instead of distributing her eggs in each rock pool, a female may visit only those pools that are not occupied by non-flyers. This latter behavior would be observed, for example, if non-flyer females established and defended territories.

A female reducing her flight muscles occupies only one pool where she lays all of her eggs. The females reducing their flight muscles distribute themselves uniformly in the rock pool habitat such that when a female arrives, she chooses a rock pool that has the smallest number of females.

The number of non-flyer and flyer females that lay eggs in pool  $j$  is denoted respectively by  $X_{rj}^n(k)$  and  $X_{rj}^f(k)$ . Hence, the total number of eggs laid in pool  $j$  is

$$X_{j\sigma} = X_{rj}^n(k) \sigma_n + X_{rj}^f(k) \sigma_f / n,$$

where  $\sigma_n$  and  $\sigma_f$  denote the egg laying capacity of the non-flyers and flyers.

The number of female offspring produced in rock pool  $j$  is given by

$$x_{rj}(k + 1) = X_{rj}^n(k) Y_{rj}^n(X_{j\sigma}, \alpha_{rjk}) + X_{rj}^f(k) Y_{rj}^f(X_{j\sigma}, \alpha_{rjk})/n,$$

where

$$Y_{rj}^s(X_{j\sigma}, \alpha_{rjk}) = \frac{\sigma_s \alpha_{rjk}}{1 + 2X_{j\sigma}/\beta_{rj}}, \quad s = n, f, \quad j = 1, 2, \dots, n.$$

*Expected growth rate*

The stationary distribution of the eggs laid by the resident strategy can be obtained assuming that only one strategy is present. We denote the stationary distribution of the number of the eggs laid by the resident strategy 1 in the lagoon by  $\bar{X}_{l\sigma}^1$  and in rock pool  $j$  by  $\bar{X}_{rj\sigma}^1$ .

The mean logarithmic growth rate is now different from (9) depending on the interpretation of the ‘rareness’ of the invading strategy. Here we take the view that an invasion by a rare type applying the mutant strategy 2 is always attempted at the beginning by one female. Let  $\gamma$  denote the probability that the invading female chooses the lagoon for reproduction, and let  $p$  denote the probability that, if she chooses the rock pool habitat, she lays eggs in one rock pool, i.e., reduces her flight muscles. Then the mean logarithmic growth rate of the invading strategy is

$$\begin{aligned} \rho = & \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{k=0}^t \ln \{ \mu [ \gamma Y_{l\sigma}^2(\bar{X}_{l\sigma}^1 + \sigma_l, \alpha_{lk}) + (1 - \gamma) [ p E_j ( Y_{rj}^2(\bar{X}_{rj\sigma}^1 + \sigma_n, \alpha_{rjk}) ) \\ & + (1 - p) \sum_{j=1}^n Y_{rj}^2(\bar{X}_{rj\sigma}^1 + \sigma_f/n, \alpha_{rjk}) ] ] \} \}, \end{aligned} \tag{13}$$

where  $\mu$  denotes the rate of winter survival, and  $E_j(\cdot)$  denotes the expectation over all rock pools.

Our simulation experiments with competing types, e.g. simulation equations comparable to (5) and (6), show that the growth rate (13) gives a more reliable prediction of the invasion than a prediction based on the expected growth rate through either of the habitats alone. However, this observation cannot be verified using Ellner’s (1985a, b) theory since the problem treated in this section cannot be formulated in a way which would be mathematically compatible with the approach developed by Ellner (1985a, b).

An intuitive explanation for our observation is as follows. Assume that the expected growth rate through the rock pool habitat is positive. Then the invading strategy will experience some growth in the first year. However, during the second year some individuals playing the mutant strategy disperse to the lagoon. It can happen that despite the positive expected growth rate through the rock pool habitat, the expected growth rate through the lagoon is negative which, together with the fluctuating success in the rock pool habitat, can prevent the invasions by the mutant strategy. Hence, a good estimate of the invasion abilities can be obtained by combining both habitats in the estimate to get a mean logarithmic growth rate.

*Dispersal strategies in rock pools*

In general, there is a possibility that the fraction  $\eta$  of females which maintain flight ability in the rock pool habitat depends on the population density in such a way that the proportion of flyers increases as the population density decreases. It is premature at this stage, however, to compute an ESS strategy involving different behavior at different population densities. The

simpler case of investigating whether there exist conditions under which maintenance of flight ability is selected for needs to be examined first.

We confine our attention to examining the evolutionary stability of three strategies. (i) In the ‘dynamic’ strategy, the decision to maintain flight ability depends on the population density. Specifically, all females maintain their flight ability if the number of the females in the rock pool habitat is less than  $m$ , otherwise they all reduce their wing muscles: i.e.,  $\eta = 1$  if the number of the females in the rock pool habitat is less than  $m$ , otherwise  $\eta = 0$ . We contrast this strategy with two other strategies: (ii) In the ‘non-flying’ strategy all females histolyse their flight muscles ( $\eta = 0$ ), and (iii) in the ‘flying’ strategy no females histolyse their flight muscles ( $\eta = 1$ ). Below the ‘dynamic’ strategy is considered as the candidate for an ESS solution.

*Simulation example*

Consider a simulation example, in which we used the following parameter values:  $n = 50$ ,  $m = 50$ ,  $\beta_l = 2000$ ,  $\beta_r = 20$ , and  $\gamma = 0.5$  for each strategy. Each rock pool is similar so that  $\alpha_{rjk} = \alpha_{rk}$  for each  $k$ . We also assume that the environmental conditions in the sea bay and in the rock pool habitats are negatively correlated so that  $\alpha_{rk} = 1 - \alpha_{lk}$  for each  $k$ . Two patterns for  $\alpha_{lk}$  were studied. First,  $\alpha_{lk}$  is a random variable distributed uniformly in  $[0.25, 0.75]$  and second,  $\alpha_{lk} = 0.5$  for each  $k$ . Winter survival  $\mu$  is a random variable with a uniform distribution on  $[0.15, 0.65]$ .

The expected logarithmic growth rates of the invading strategies (three runs each lasting 2000 generations) are given in Table 2 for the fluctuating environment. The only strategy that can resist invasions by the two other strategies is the dynamic strategy (i.e., the strategy in which wing muscles are histolysed only when there are more females than rock pools). Moreover, the dynamic strategy is able to invade populations playing any of the two other strategies. Hence, it is a unique ESS for the three-strategy game described above.

The difference between the non-flying and flying strategies can be seen when the population size fluctuates due, for example, to fluctuating winter survival. At low population densities the flying strategy is able to utilize the rock pool habitat more efficiently. For example, when only one flyer female occupies the rock pool habitat, she is able to produce on the average 22.7 female offspring, whereas a nonflyer is able to produce only 4.5 female offspring. When the number of the females occupying the rock pool habitat is greater, then advantage of flying decreases (e.g., 30 flyers and non-flyers respectively produce 187.5 and 136.3 females) and is finally lost. The dynamic strategy is able to respond to population fluctuations, and hence, it is expected to overcome both the non-flying and flying strategies.

We also studied the same game by assuming that both the sea bay and rock pool habitats provide

Table 2. The expected logarithmic growth rates of the invading strategies in negatively correlated fluctuating habitats ( $\alpha_l = 1 - \alpha_r$ ).

		Resident strategy		
		Dynamic	Flyer	Non-flyer
Invading strategy	Dynamic	×	0.010 ± 0.001	0.014 ± 0.002
	Flyer	- 0.246 ± 0.010	×	- 0.230 ± 0.002
	Non-flyer	- 0.021 ± 0.002	- 0.011 ± 0.003	×

a constant environment for the waterstriders. Specifically, we assumed that  $\alpha_i = \alpha_{rj} = 0.5$  for all  $j = 1, \dots, n$ ; that is, the reproductive success is constant in each habitat. The winter survival was, however, uncertain. The qualitative results did not differ from those obtained in fluctuating environments: the dynamic strategy is an ESS.

We conclude from the results in this section that an uncertain patchy, environment can favor density-dependent wing muscle dimorphism when the population densities fluctuate. However, it is not the uncertainty of the habitats alone that contributes to the flying ability of the waterstrider females. Patchiness of the environment can also affect flying ability by reducing the advantage of wing muscle histolysis when the environment (e.g. winter mortality) fluctuates sufficiently to reduce the population to unusually low densities.

Distribution of eggs or offspring so far has been connected almost exclusively in the literature with the uncertainty of the environment. We have shown that environmental patchiness can favor density-dependent wing muscle dimorphism when the population densities fluctuate. When population densities are low, and the sites for reproduction are small and many, there are unoccupied sites which are worth exploiting at the cost of reduced numbers of eggs. When the population density is high, the advantage of on-site dispersal between rock pools is crucially decreased since all the sites are occupied.

## Conclusions

Risk-spreading theory has received attention in many studies of organisms reproducing in uncertain environments due to its association with fluctuating reproductive success. The theory of evolutionarily stable strategies may not have been applied in these studies because of the problems with the definition of an evolutionarily stable solution in an uncertain environment. The recent extension by Ellner (1985a, b) of evolutionarily stable strategy theory to uncertain conditions has facilitated its application to problems including dispersal and reproduction in uncertain and heterogeneous environments.

We have studied evolutionarily stable dispersal strategies of waterstrider *G. thoracicus* in a system consisting of two different habitats (sea bays and rock pools) each of which may be stochastic and unpredictably favorable during different years. First, under deterministic, density-dependent conditions we found that uncertainty is not needed to explain distribution of waterstriders between different habitats: in a constant environment all the available habitats will be occupied. Second, contrary to the predictions that females avoid local extinction (i.e., loss of all of her offspring, see Vepsäläinen, 1978), we observed that under an ESS strategy females continue to reproduce in two habitats when only one of them is associated with local extinctions. Hence, no qualitative difference was observed in our strategic models between less fluctuating and risky habitats: only the fractions of females occupying the habitats change with environmental uncertainty. We also noted that (i) strategies maximizing arithmetic mean or geometric mean fitnesses (that is, strategies maximizing the respective average population levels) are not evolutionarily stable strategies, and that (ii) the evolutionarily stable fraction dispersing to the different habitats does not maximize the total population size but maximizes the average per capita reproduction rate in both habitats.

Finally, our analysis of whether females have the option of either maintaining their ability to fly throughout the reproductive season (i.e., distributing their eggs between different small rock pools) or histolysing their flight muscles (i.e., using this additional energy in producing more eggs in one rock pool) led to the conclusion that habitat uncertainty is not needed to explain this type of 'risk-spreading'. When rock pools are so small that competition between the siblings of a female becomes significant if the female lays all of her eggs in one pool, then it is beneficial

to maintain flight ability and lay fewer eggs in many rock pools when there are fewer females than rock pools. When the population level is high, competition between larvae cannot be excluded by dispersal behavior, since all the pools are occupied anyway. This conclusion was observed to be valid both in a constant and in a stochastic environment.

We emphasize that we have considered only a restricted class of uncertainty patterns. Conclusions in this respect may be sensitive to the underlying assumptions and further work is needed to obtain a better understanding of the connections among density-dependence, environmental fluctuations and dispersal polymorphism.

### Glossary: model variables and parameters

#### *Two-habitat model*

$\gamma$ , strategy variable, fraction of the sibling offspring that occupies the sea habitat;  $k$ , the time index;  $X_l(k)$ ,  $X_r(k)$ , female populations reproducing in the sea and rock pool habitats;  $x_l(k)$ ,  $x_r(k)$ , female populations produced in the sea and rock pool habitats;  $\mu$ , overwintering survival;  $\alpha_{lk}$ ,  $\alpha_{rk}$ , environmental fluctuations;  $Y_l$ ,  $Y_r$ , number of female offspring produced per female in the sea and rock pool habitats;  $\sigma_l$ ,  $\sigma_r$ , density-independent growth;  $\beta_l$ ,  $\beta_r$ , niche capacity parameters.

#### *Wing muscle trade-off model*

$\eta$ , strategy variable, fraction of the females maintaining their flight ability in the rock pool habitat;  $\gamma$ , constant, fraction of the offspring of an individual that occupies the sea habitat;  $n$ , number of the rock pools.

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