

# Evolutionarily stable versus fitness maximizing life histories under frequency-dependent selection

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## SUMMARY

There has been recent interest in using the techniques of quantitative genetics to study optimal life histories under frequency-dependent selection, but a search of the literature has revealed no clear quantitative genetics recursion that incorporates both frequency dependence and overlapping generations. This may be due in part to the historical tendency of life-history theory to ignore frequency dependence. Here we provide such a recursion, and use it to explore the general question of how frequency-dependent selection on life-history traits can cause the evolutionarily stable strategies to differ from the point of maximum mean fitness.

## 1. INTRODUCTION

The concept of evolutionary stability has proven to be a useful tool for modelling in evolutionary biology (Maynard Smith & Price 1973; Maynard Smith 1982; Vincent & Brown 1988). Intuitively, if a stable strategy is possible, evolutionary change through natural selection will continue until such a strategy is reached. Therefore, to predict the outcome of evolution, one simply needs to characterize such stable phenotypes. An alternative to this philosophy is to determine the phenotype that maximizes population mean fitness. Traditionally, models of life-history evolution have employed this latter approach, which we term the *r*-max approach below (Roff 1992; Stearns 1992). It is well known, however, that strategies which maximize mean fitness are not always evolutionarily stable (Haldane 1932; Wright 1942; Huxley 1938, as cited in Lande (1976)). For example, under frequency-dependent selection, a population at its fitness maximum may continue to evolve until a different, stable phenotypic distribution is reached. Our purpose here is to produce a quantitative genetic recursion for the evolution of a character mean under frequency dependence and overlapping generations. We then use this equation to explore how evolutionarily stable life histories differ from those that maximize mean fitness.

To avoid confusion we define how the term 'evolutionary stability' will be used. Typically, the so-called 'ESS approach' assumes an effectively monomorphic population and characterizes strategies that are uninvadable by rare mutants. The concept of evolutionary stability, however, can be applied to any model that specifies an evolutionary dynamic, including a quantitative genetic model. Here we term a population mean strategy evolutionarily stable (an ESS) if evolutionary change ceases at this mean and it tends to restore this mean after small perturbations.

Traditionally, models of life-history evolution have employed the *r*-max philosophy and this field has developed largely untouched by the concepts of frequency dependence and evolutionary stability (Stearns 1976, 1977, 1992; Roff 1992). There has been sporadic interest in incorporating these ideas, and this has resulted in a few specific models but no general framework. Kawecki (1993) provides a recent example and summarizes much of the previous work. Here, we present a general quantitative genetic procedure which can be used for investigating the qualitative difference between such evolutionarily stable and fitness maximizing life histories. The procedure allows considerable flexibility in model assumptions and provides a simple and general framework for the studies mentioned above. It also makes many further such investigations somewhat routine.

Below are two main sections. In the first we derive a quantitative genetic recursion for the mean of a trait under frequency dependence and overlapping generations, and describe a general method for addressing the above mentioned life-history questions. The second section considers some specific examples to illustrate this method.

## 2. EVOLUTIONARY STABILITY VERSUS FITNESS MAXIMA

We begin by assuming a normal phenotypic distribution. Under normality, an ESS can be defined as an equilibrium mean and variance at which small perturbations are damped by selection (Taylor & Day 1996). Here we assume the variance is fixed and focus on the mean only. Thus evolutionary equilibria are values of the mean where the selection differential vanishes. Below we assume such equilibria are evolutionarily stable. Fitness maxima are defined as points where the population mean fitness function is station-

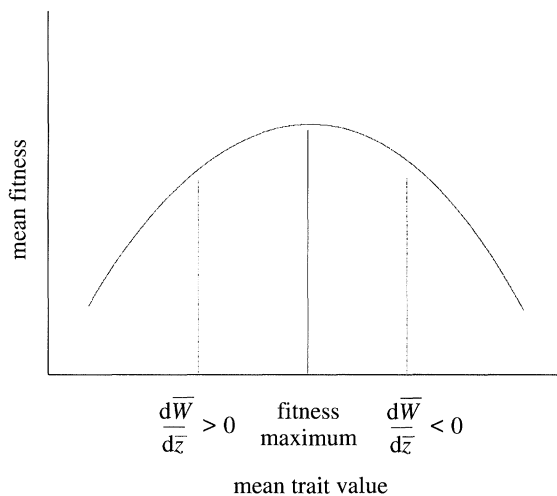


Figure 1. The sign of  $d\bar{W}/d\bar{z}$  allows prediction of whether the ESS mean trait value will be larger or smaller than that which maximizes mean fitness.

ary (i.e.  $\bar{W}' = 0$ ). We begin with the quantitative genetic recursion for the mean value of a trait,  $z$  (Falconer 1989);

$$\Delta\bar{z} = h^2 S, \quad (1)$$

where  $h^2$  is the narrow sense heritability (i.e. additive genetic variance divided by total phenotypic variance;  $\sigma_g^2/\sigma_p^2$ ), and  $S$  is the selection differential. Lande (1976; equation (9)) has shown that under frequency dependence and non-overlapping generations the selection differential can be written as,

$$S = (\sigma_p^2/\bar{W}) [(d\bar{W}/d\bar{z}) - E(\partial W/\partial \bar{z})], \quad (2)$$

where

$$E[f(z)] = \int f(z)p(z)dz$$

and  $p(z)$  is the phenotype density, assumed normal. The first term in parentheses is the derivative of mean fitness with respect to the mean trait value and the second term is the average partial derivative of individual fitness with respect to the mean trait value. This has been used to construct frequency-dependent quantitative genetic models by several authors (Lande 1976; Taper & Case 1992; Charlesworth 1993). When  $W$  is not frequency dependent, the second term of equation (2) vanishes giving the familiar quantitative genetic equation (Lande 1976),

$$S = (\sigma_p^2/\bar{W})(d\bar{W}/d\bar{z}). \quad (3)$$

We note, (Lande & Arnold 1983; Taylor 1996) that both equations (2) and (3) can be expressed as  $S = \sigma_p^2 E(\partial W/\partial z)/\bar{W}$  which involves the derivative of individual fitness with respect to individual trait value. Equation (2) provides an elegant procedure for determining whether the fitness maximizing phenotype is bigger or smaller than the evolutionarily stable phenotype. At the fitness maximum,  $\bar{W}$  is maximized in  $\bar{z}$  and therefore,  $d\bar{W}/d\bar{z} = 0$ . When  $W$  is not frequency dependent, equation (2) reduces to (3) and thus  $S = 0$  at the fitness maximum (i.e. the fitness

maximum is evolutionarily stable as well). Under frequency-dependent selection, however, equation (2) reveals that if the expected value of  $\partial W/\partial \bar{z}$  is positive, then  $S < 0$  at the fitness maximum and natural selection will result in evolution towards a smaller  $\bar{z}$ . The reverse holds if this average is negative. For evolutionary stability we require that  $S = 0$  and from equation (2) this gives

$$d\bar{W}/d\bar{z} = E(\partial W/\partial \bar{z}). \quad (4)$$

Therefore, evolutionary equilibrium will occur at a value of  $\bar{z}$  for which the sign of the slope of the  $\bar{W}$  versus  $\bar{z}$  graph is the same as the sign of the expected value of  $\partial W/\partial \bar{z}$ . By definition this graph has a maximum at the fitness maximizing  $\bar{z}$ , and therefore if the right-hand side of equation (4) is positive, the evolutionarily stable phenotype will be smaller than the fitness maximizing phenotype and vice versa (figure 1). This argument is local and assumes that the difference between the solutions will be small.

To use a similar argument for life-history phenotypes we require a version of equation (2) that holds for overlapping generations. Under *frequency-independent* selection, Lande (1982) has derived an analogue of equation (3) for weak selection and overlapping generations;

$$S = \sigma_p^2 (d\bar{r}/d\bar{z}). \quad (5)$$

Here,  $\bar{r}$  is defined implicitly by the characteristic equation,

$$1 = \sum_i e^{-\bar{r}i} \bar{k}_i, \quad (6)$$

where  $\bar{k}_i$  is the expected value of  $k_i$ , the age  $i$  reproductive function, i.e.

$$k_i(z) = l_i(z)m_i(z), \quad (7)$$

such that  $l_i(z)$  is the probability of survival from birth to age  $i$ , and  $m_i(z)$  and the expected number of offspring at age  $i$  for an individual with phenotype  $z$ . Under frequency dependence the reproductive functions in (7) will also depend on some population parameter(s). For simplicity we assume that the only relevant parameter is the population mean,  $\bar{z}$ . Therefore the age-specific reproductive functions (7), depend on  $z$  and  $\bar{z}$  only. Charlesworth (1993) has suggested extending equation (5) to a frequency-dependent setting using a form analogous to equation (2); i.e.

$$S = \sigma_p^2 [(d\bar{r}/d\bar{z}) - E(\partial r/\partial \bar{z})], \quad (8)$$

where  $r$  is now a function of  $z$  and  $\bar{z}$  defined implicitly by

$$1 = \sum_i e^{-ri} k_i(z, \bar{z}). \quad (9)$$

Note that  $\bar{r}$  is not the expectation of  $r(z, \bar{z})$  but it can be shown that they differ by  $O(\epsilon^2)$  where  $\epsilon$  is defined in the Appendix. Charlesworth has cautioned however, that this form no longer provides an accurate recursion relation, even when selection is weak (i.e. it is not accurate to first order in  $\epsilon$ ). Consequently, we seek an alternate formulation.

To begin we define the relative fitness of an individual with phenotype  $z$  in a population with overlapping generations and an approximate stable age distribution. We write this as lifetime reproductive output discounting future offspring by the growth factor  $e^{\bar{r}}$  (Kozłowski 1993), i.e.

$$w(\bar{r}, z, \bar{z}) = \sum_i e^{-\bar{r}i} k_i(z, \bar{z}). \quad (10)$$

Using definition (10), the Appendix shows that, for frequency dependence and overlapping generations, the following selection differential holds under weak selection:

$$S = \sigma_p^2 [(d\bar{r}/d\bar{z}) - \bar{T}^{-1} E(\partial w/\partial \bar{z})]. \quad (11)$$

The differentiation of  $w$  in equation (11) is with respect to  $\bar{z}$ , holding  $\bar{r}$  and  $z$  fixed and therefore we display all three arguments of  $w$  in equation (10). Although  $\bar{r}$  is determined by  $\bar{z}$ , varying  $\bar{z}$  will in general have two effects on  $w$ ; it changes both  $\bar{r}$  and  $k_i(z, \bar{z})$ . The partial derivative in equation (11) takes account only of the change in fitness through changes in  $k_i(z, \bar{z})$ . In addition,

$$\bar{T} = \sum_i i e^{-\bar{r}i} \bar{k}_i \quad (12)$$

is the mean age of parents of a new generation of zygotes in a population where all individuals are using the reproductive function,  $\bar{k}_i$ , and is often termed the generation time.

Equation (11) is useful for our purposes here, and it also provides a quantitative genetic expression for modelling the dynamics of frequency-dependent selection in an age-structured population (see also equation (21)). Note that under frequency-independent selection, the second term in equation (11) vanishes reducing it to equation (5); the  $r$ -max and the ESS approaches then yield the same prediction.

We are now in a position to investigate how ESS and fitness maximizing life histories differ. Because  $d\bar{r}/d\bar{z} = 0$  at the fitness maximum, we need only determine the sign of the second term in the parentheses of equation (11) and employ the argument outlined earlier (figure 1). Noting that  $\bar{T}^{-1}$  is a positive constant, we have the following: if the second term of equation (11) is positive, the fitness maximizing phenotype is greater than the evolutionarily stable phenotype. If the second term of equation (11) is negative, the reverse holds. Below we provide some worked examples to illustrate this idea.

### 3. EXAMPLES

We restrict attention to univariate life-history problems and summarize the approach in three steps: (i) identify the independent variable of interest; (ii) state which life-history components are affected by this variable; and (iii) state explicitly how frequency dependence affects life-history components. This frequency dependence will typically arise as a result of competitive interactions. In all examples we assume a deterministic relation between the independent variables and other life-history attributes.

The first two examples assume that the life history of interest is composed of a juvenile stage and an adult stage, each with constant mortality rates,  $j$  and  $a$ , and that there is determinate growth. With these assumptions we take  $m$  to be zero prior to maturity and a constant thereafter. Therefore equation (10) becomes

$$w(\bar{r}, z, \bar{z}) = \frac{e^{-(\bar{r}+j)\alpha} m}{1 - e^{-(\bar{r}+a)}}, \quad (13)$$

where  $m$  is fecundity per unit time and  $\alpha$  is age at maturity. Therefore, for the first two examples, we can evaluate the derivative of  $w$  with respect to  $\bar{z}$  using the closed form (13) and then take its expectation.

#### (a) Example 1. $\alpha$ versus $m$ : age at maturity / fecundity

It is postulated that postponing age at maturity allows an individual to increase its fecundity. Thus we use the following: (i)  $z = \alpha$  is the independent variable; (ii) increasing  $\alpha$  increases fecundity,  $m$ ; and (iii) an increase in the population-wide age at maturity,  $\bar{\alpha}$  (holding  $\alpha$  constant) results in competitors of greater size and hence competitive ability. This decreases fecundity for any given individual age at maturity. Therefore equation (13) becomes

$$w(\bar{r}, \alpha, \bar{\alpha}) = \frac{e^{-(\bar{r}+j)\alpha} m(\alpha, \bar{\alpha})}{1 - e^{-(\bar{r}+a)}}, \quad (14)$$

where  $m$  is increasing in  $\alpha$  and decreasing in  $\bar{\alpha}$ . Taking the derivative of equation (14) with respect to  $\bar{\alpha}$  holding  $\bar{r}$  and  $\alpha$  fixed gives

$$\partial w/\partial \bar{\alpha} = w[(\partial m/\partial \bar{\alpha})/m]. \quad (15)$$

From step (iii) above, equation (15) is negative and its expected value is negative as well because all individual ages at maturity are affected similarly. Thus under frequency dependence, the evolutionarily stable age at maturity is later than that of the  $r$ -max approach.

Kawecki (1993) has derived this result previously for a patch-structured model and he discusses similar such results involving competition for light in plants. The power of the above approach is its simplicity and generality. For many arguments, the details of the model do not have to be made mathematically explicit. All that is needed is a basis for unambiguously determining the sign of the second term in equation (11). This generality also allows the immediate conclusion that, for the life history specified, all forms of frequency dependence that cause decreasing individual fecundity with increasing  $\bar{\alpha}$  regardless of individual age at maturity, will predict a later age at maturity. This result is independent of how an individual's age at maturity,  $\alpha$ , affects its fecundity.

Also, it is not necessary to confine the effects of frequency dependence to a single life-history component. For example, in the above life history it may be that a size increase from postponing maturity results not only in increased fecundity, but in decreased adult mortality as well. Additionally, increasing the population-wide age at maturity,  $\bar{\alpha}$ , may result in

competitors of greater size and ability and this may depress fecundity and increase mortality rate for any given  $\alpha$ . Under this hypothesis, both  $m$  and  $a$  in equation (14) are functions of  $\alpha$  and  $\bar{\alpha}$ . This gives

$$w(\bar{r}, \alpha, \bar{\alpha}) = \frac{e^{-(\bar{r}+j)\alpha} m(\alpha, \bar{\alpha})}{1 - \exp[-(\bar{r} + a(\alpha, \bar{\alpha}))]} \quad (16)$$

Taking the derivative of equation (16) with respect to  $\bar{\alpha}$  holding  $\bar{r}$  and  $\alpha$  fixed gives

$$\frac{\partial w}{\partial \bar{\alpha}} = w \left[ \frac{\partial m / \partial \bar{\alpha}}{m} - \frac{e^{-(\bar{r}+a)} \frac{\partial a}{\partial \bar{\alpha}}}{1 - e^{-(\bar{r}+a)}} \right] \quad (17)$$

The first term of equation (17) is negative, as is its expected value, and the second term and its expected value will be positive. Again the evolutionarily stable age at maturity is greater than the  $r$ -max age at maturity.

**(b) Example 2.  $j$  versus  $\alpha$ : juvenile mortality / age at maturity**

It is postulated that individuals must reach a fixed size to mature and foraging in productive habitats decreases the expected time to this size at the expense of an increased juvenile mortality rate. Thus we use the following: (i)  $z = j$  is the independent variable; (ii) increasing  $j$  decreases time to maturity,  $\alpha$ ; and (iii) an increase in the population-wide mortality rate,  $\bar{j}$ , implies that there are more individuals foraging in the productive habitats and this increases time to maturity,  $\alpha$  for any given individual  $j$ . Therefore equation (13) becomes

$$w(\bar{r}, j, \bar{j}) = \frac{\exp(-(\bar{r}+j)\alpha(j, \bar{j}))m}{1 - e^{-(\bar{r}+a)}} \quad (18)$$

where  $\alpha$  is decreasing in  $j$  and increasing in  $\bar{j}$ . Taking the derivative of equation (18) with respect to  $\bar{j}$ , holding  $\bar{r}$  and  $j$  fixed gives

$$\partial w / \partial \bar{j} = -w(\bar{r}+j)(\partial \alpha / \partial \bar{j}). \quad (19)$$

Assuming  $\bar{r} \geq 0$ , step (iii) reveals that equation (19) will be negative as will its expected value. Therefore, the evolutionarily stable foraging strategy will be one with a higher mortality rate. It is interesting to note that if the population size is decreasing, equation (19) may be positive for some individuals. Therefore for some (negative) value of  $\bar{r}$ , it is possible that the expected value of equation (19) is zero; the evolutionarily stable and  $r$ -max predictions are then equal.

**(c) Example 3.  $a$  versus  $m$ : adult mortality / fecundity**

As a final example we no longer restrict ourselves to determinate growth and appeal directly to the second term of equation (11) for its sign. It is postulated that foraging in productive habitats increases an individual's fecundity at the expense of greater adult mortality and that an individual chooses a single foraging strategy for its entire adult life. We take: (i)  $z = a$  as the independent variable; (ii) increasing  $a$  increases fecundity at all adult ages; and (iii) an

increase in  $\bar{a}$  implies that more of the population is foraging in productive habitats and therefore fecundity should decline for any individual  $a$  at all adult ages.

Under these assumptions, the derivatives,  $\partial k_i / \partial \bar{a}$  will be negative for all  $i$ . Therefore, from equation (10) we find that  $E(\partial w / \partial \bar{a})$  will be negative as well. Thus the evolutionarily stable foraging strategy is one that is more risky than that which maximizes fitness.

#### 4. DISCUSSION

Even in the early work of Leslie (1948), it was understood that the dependence of fitness on population density can have an effect on optimal life-history traits (see Charlesworth 1994, p.54 for a discussion of the literature). Consideration of frequency dependence has come much later. Much of this development has been a result of the ESS formulation of Maynard Smith & Price (1973). While the body of literature spawned from these results has focused primarily on monomorphic models, a parallel body of literature in quantitative genetics has developed the implications of frequency dependence as well (Lande 1976; Slatkin 1979, 1980; Iwasa *et al.* 1991; Taper & Case 1992; Abrams *et al.* 1993; Charlesworth 1993). However, because many of these developments assume non-overlapping generations their utility in addressing life-history evolution has been limited.

The extension of Lande's (1982) results presented here allows frequency-dependent life-history evolution to be investigated using a quantitative genetic model. In particular, we have used equation (11) to formulate a general procedure through which one can examine the qualitative difference between evolutionarily stable and fitness maximizing life histories. Previous work in this area has been sporadic. For example, Abrams (1983) considered whether an evolutionarily stable reproductive effort should maximize population growth rate and also whether absolute fitness measures are maximized under competitive character displacement (Abrams 1989; see also Brown & Vincent 1987). Matsuda & Abrams (1994) have recently looked at how frequency-dependent selection can even lead to population extinction. A collection of other recent work is summarized by Kawecki (1993).

The general procedure presented here allows one to address a range of life-history questions with a minimum of assumptions and mathematical formalism. It can be used to look for general trends of ESS versus fitness-maximizing life histories across a range of tradeoffs. Even more useful perhaps, it allows one to focus on a particular life-history trade-off (e.g. example 1), and make generalizations about the types of frequency-dependent interactions that will lead to a stable phenotype being bigger or smaller than that which maximizes fitness.

Because frequency dependence may result from competitive interactions, it may often be accompanied by density dependence. Therefore it is useful to consider how our results are altered when the population size is constant ( $\bar{r} = 0$ ). From equation (A 5) of the appendix we see that equation (11) becomes

$$S = (\sigma_p^2 / \bar{T}) [(d\bar{R}_0 / d\bar{z}) - E(\partial R_0 / \partial \bar{z})], \quad (20)$$

where  $R_0$  is lifetime reproductive output and  $\bar{T}$  is given by equation (12) with  $\bar{r} = 0$ . Equation (20) can be employed in an analogous way to equation (11). Note that equilibria found by setting  $S = 0$  in equation (20) are subject to the condition  $\bar{R}_0 = 1$  just as they are in the frequency-independent case.

If one is primarily interested in using equation (11) to construct a frequency-dependent quantitative genetic model with overlapping generations, the procedure of Taylor (1996) allows equation (11) to be expressed in the more succinct form,

$$S = (\sigma_p^2/\bar{T})E(\partial w/\partial z), \quad (21)$$

where  $w$  is defined by equation (10) and the differentiation is with respect to individual trait value,  $z$ . This form is valid under both frequency-dependent and independent selection. Also, the density-dependent ( $\bar{r} = 0$ ) version of equation (21), is  $S = \sigma_p^2 E(\partial R_0/\partial z)/\bar{T}$ .

Finally, although the above procedure is a fairly simple approach for incorporating frequency dependence into many life-history questions, there are cases where its general arguments are not sufficient. For example, it is not always possible to unambiguously determine the sign of the second term in equation (11) without constructing a more formal model of frequency-dependent interactions. Consider a life history described by equation (13) in which the length of the juvenile stage is fixed (by season for example) and foraging in productive habitats allows a greater adult size and hence fecundity,  $m$  at the expense of higher juvenile mortality,  $j$ . It is difficult to determine the sign of  $\partial m/\partial \bar{j}$  because an increase in  $\bar{j}$  will correspond to larger competitors but fewer of them. Because these two factors work in opposite directions it is not possible to determine how fecundity will change without being more explicit about the nature of these interactions. Nevertheless, we hope this approach will provide a useful framework through which the importance of frequency-dependent selection in life-history evolution is given more consideration.

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## APPENDIX

The derivation here follows that of Lande (1982). We assume weak selection and posit that the nature of frequency dependence is such that an approximate stable age distribution is attained. We also assume that the distribution of breeding values in newly formed zygotes each generation is Gaussian. We define  $\bar{r}$  by equation (6) and the age specific response to selection as  $\delta_i = h^2 \text{Cov}(z, k_i)/\bar{k}_i$ .

To control the overall strength of selection we write

$$k_i(z, \bar{z}) = \bar{k}_i(1 + h_i(z, \bar{z})\epsilon), \quad (\text{A } 1)$$

where  $h_i$  is defined by equation (A1) with  $\epsilon = 1$ . Note that  $\epsilon = 0$  implies a monomorphic population and therefore evolutionary equilibrium as well (i.e.  $\delta_i = 0$  and therefore  $\Delta\bar{z} = 0$ ). For weak selection we 'turn up'  $\epsilon$  a small amount and ignore terms involving powers of  $\epsilon$  greater than one. We first seek an expression for  $\Delta\bar{z}$  that is valid to first order in  $\epsilon$ .

Assume that the population's mean phenotype changes by an amount  $\Delta\bar{z}$  each time step so that in  $i$  time steps it will change by an amount  $i\Delta\bar{z}$ . Now consider a group of newly formed zygotes. Their mean phenotype will equal the mean breeding value of parents across all ages. However, the mean breeding value of parents of a given age  $i$ , will in general differ from the overall mean of this new cohort for two reasons. First,  $i$ -year old parents were born into a cohort with a mean value  $i\Delta\bar{z}$  less than the present mean. Second, by definition the mean of that cohort will have changed by an amount  $\delta_i$  through selection over the past  $i$  years (when weighted by age- $i$  fecundity). Therefore the mean breeding value of age- $i$  parents (weighted by age- $i$  fecundity) differs from the present cohort's mean by an amount  $\delta_i - i\Delta\bar{z}$ . However, the mean of this difference across all parental ages must equal zero. Writing  $q_i$  for the probability that a parent of a random offspring is of age  $i$  gives,

$$0 = \sum_i q_i(\delta_i - i\Delta\bar{z}). \quad (\text{A } 2)$$

Here  $q_i$  is given by a weighted sum over the frequency distribution of different phenotypes, but because we only need  $\Delta\bar{z}$  to order  $\epsilon$ , and because  $\delta_i$  is

already of order  $\epsilon$ , we need only calculate these probabilities at  $\epsilon = 0$  (i.e. deviations from this will be of order  $\epsilon^2$ ). These probabilities are simply given by  $\bar{q}_i = e^{-ri}\bar{k}_i$ . This gives,

$$\bar{T}\Delta\bar{z} = \sum_i \bar{q}_i \delta_i + O(\epsilon^2) \quad (\text{A } 3)$$

where  $\bar{T}$  is defined by equation (12). Now for any differentiable function  $f(z, \bar{z})$ ,

$$\text{Cov}(z, f) = v^2[(\partial\bar{f}/\partial\bar{z}) - \text{E}(\partial f/\partial\bar{z})] \quad (\text{A } 4)$$

over a Gaussian density with variance  $v^2$ . Combining equations (A 3) and (A 4) with the definition of  $\delta_i$  gives;

$$\Delta\bar{z} = \frac{\sigma_g^2}{\bar{T}} [\sum_i e^{-ri} \partial\bar{k}_i/\partial\bar{z} - \sum_i e^{-ri} \text{E}(\partial k_i/\partial\bar{z})] + O(\epsilon^2). \quad (\text{A } 5)$$

By differentiating equation (6) with respect to  $\bar{z}$  we discover that the first term in parentheses of equation (A 5) can be written as

$$\bar{T}d\bar{r}/d\bar{z}. \quad (\text{A } 6)$$

Now after taking the expectation outside of the summation in the second term of equation (A5), it can be identified as the expectation of the partial derivative of equation (10) with respect to  $\bar{z}$ . Therefore (A5) can be re-written as,

$$\Delta\bar{z} = \sigma_g^2 [(d\bar{r}/d\bar{z}) - \bar{T}^{-1}\text{E}(\partial w/\partial\bar{z})] + O(\epsilon^2) \quad (\text{A } 7)$$

Reference to equation (1) then gives result (11) (to first order in  $\epsilon$ ).