



## The Selection Differential in Quantitative Genetics and Ess Models

Peter D. Taylor

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## COMMENTS

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### THE SELECTION DIFFERENTIAL IN QUANTITATIVE GENETICS AND ESS MODELS

PETER D. TAYLOR

*Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada*  
E-mail: taylorp@post.queensu.ca

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Some recent articles in this journal (Charlesworth 1990; Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993) have focused on the relationship between quantitative genetics (QG) and evolutionarily stable strategy (ESS) models of the evolution of continuous traits under conditions of frequency dependence, and an ESS approximation  $S\sim$  for the selection differential  $S$  has been proposed. Here I recall a formula of Lande and Arnold (1983) for  $S$  which holds in normally distributed population and which illuminates the relationship between the two models, and I extend it to the case in which fitness depends also on the average behavior of a local interaction group (equation 12). I calculate  $S$  and  $S\sim$  for a number of standard fitness functions, and verify the results of Wilson and Dugatkin (in press) on kin selection and assortative interactions.

Let  $x$  denote the value of the continuous trait, and assume it is distributed with mean  $\bar{x}$  and variance  $V$ . In what I will call the *non-structured model* of frequency-dependence, individual fitness is assumed to depend both on  $x$  and  $\bar{x}$ :

$$W = W(x, \bar{x}). \quad (1)$$

Alternatively, I will consider a *group-structured model*, in which individuals assort into interaction groups of equal size and individual fitness depends also on the average trait value  $y$  of the interaction group:

$$W = W(x, y, \bar{x}). \quad (2)$$

I suppose the group mean  $y$  is distributed with mean  $\bar{x}$  and variance  $G$ , and I denote the quotient of between group and total variance by  $R$ :

$$R = \frac{G}{V} = \frac{\text{cov}(y, y)}{\text{cov}(x, x)} = \frac{\text{cov}(x, y)}{\text{cov}(x, x)}. \quad (3)$$

The last equality follows by noting that  $\text{cov}(y, y) = \text{cov}(E(x), y) = \text{cov}(x, y)$  where the expectation is over the group, and it is understood in the last expression that  $x$  is a random individual in the  $y$ -group. In models of kin selection, with an assumption of additive dependence of phenotype on genotype,  $R$  measures the relatedness of an individual to a random member of his group (including himself), and it is most commonly written using the expression on the right (Michod and Hamilton, 1980).

When different phenotypes have different fitness, the action of selection will typically cause a shift in the population mean in each generation. The selection differential is given by the Robertson-Price equation:

$$S = \frac{E(xW)}{E(W)} - \bar{x} = \frac{\text{cov}(x, W)}{\bar{W}} \quad (4)$$

and measures the difference between the selected and unselected populations. This fundamental equation was discovered independently by Robertson (1966), Li (1967) and Price (1970); Frank (1995) gives a nice account of its significance. It is interesting for this paper that shortly after finding this formula, Price introduced Maynard Smith to the ESS (Maynard Smith and Price 1973).

The overall change in  $\bar{x}$  over a single generation incorporates the effects of reproduction by multiplying  $S$  by the heritability  $h^2$ .

$$\Delta\bar{x} = h^2S \quad (5)$$

(Falconer 1960). The equilibrium condition for this model is  $S = 0$ .

#### *The ESS Approach*

The standard ESS argument for a non-structured population (Maynard Smith and Price, 1973) considers a monomorphic population (fixed at  $\bar{x}$ ) and argues that if it is to be uninvadeable by a rare mutant strategy  $x$ , then  $W$  must be maximized in  $x$  at  $x = \bar{x}$  and the local necessary condition for that is the equilibrium condition

$$\left. \frac{\partial W}{\partial x} \right|_{x=\bar{x}} = 0. \quad (6)$$

This will be a local maximum if for  $x$  near  $\bar{x}$ ,  $\partial W/\partial x > 0$  when  $x < \bar{x}$  and  $\partial W/\partial x < 0$  when  $x > \bar{x}$ .

Behind this stability condition, there is the idea that the sign of the selection differential  $S$  will be the same as the sign of  $\partial W/\partial x$  at  $x = \bar{x}$ , that is, if the partial derivative is positive at  $\bar{x}$ , selection will tend to increase the population mean, at least when the action of local mutants is considered, and if the partial derivative is negative, selection will tend to decrease the population mean. But, further to this, one can ask for a candidate expression for  $S$  in an ESS model which would give some measure, not only of its sign, but of its magnitude. Such an expression could be used to provide a dynamic for the evolution of the phenotype, but it could only be heuristic, because the ESS model as such makes no explicit assumption on the population structure. A recent proposal of Iwasa et al. (1991) is

$$S\sim = \frac{V}{W(\bar{x}, \bar{x})} \left. \frac{\partial W}{\partial x} \right|_{x=\bar{x}} \quad (7)$$

where  $V$  is the population variance in  $x$ . Essentially the same formula appears in Taper and Case (1992) and Abrams et al. (1993), except in both cases, they have replaced the denominator by  $\bar{W}$ . For technical reasons (e.g., see equation 18 and compare equations 20 and 21) I prefer the version given in (7). All three of these cited papers have shown, without any assumptions on the population distribution, (by expanding  $W$  in a Taylor series) that (7) approximates (4) when selection is weak. The ornament ~ warns that (7) is not intended to be an exact measure of  $S$  for any actual population structure.

In the group-structured population, the ESS equilibrium condition is most easily obtained with an inclusive fitness argument (Hamilton 1964). The approach of Taylor and Frank (1996) calculates the inclusive fitness increment  $\Delta W_1$  of the behaviour by differentiating  $W(x, y, \bar{x})$  with respect to  $x$ , treating  $y$  as a function of  $x$  (which it is not—it only covaries with  $x$ ), and then replacing  $dy/dx$  by the relatedness  $R$ , thought of as the slope of the regression of  $y$  on  $x$ :

$$\Delta W_1 = \frac{dW}{dx} = \frac{\partial W}{\partial x} + \frac{\partial W}{\partial y} \frac{dy}{dx} = \frac{\partial W}{\partial x} + \frac{\partial W}{\partial y} R. \quad (8)$$

As an example, suppose  $x$  measures the tendency towards altruistic behavior, an altruist incurring a cost  $c$  and providing a benefit  $b$  distributed in some random way among the members of the group. Then an  $x$  individual in a  $y$  group will have fitness  $W(x, y) = -cx + by$  and the inclusive fitness increment is  $\Delta W_1 = -c + bR$  obtained by Hamilton (1964). The equilibrium condition is

$$\left. \frac{\partial W}{\partial x} + \frac{\partial W}{\partial y} R \right|_{x=y=\bar{x}} = 0 \quad (9)$$

and the group-structured analogue of (7) would appear to be

$$S \sim = \frac{V}{W(\bar{x}, \bar{x})} \left[ \frac{\partial W}{\partial x} + R \frac{\partial W}{\partial y} \right] \Bigg|_{x=y=\bar{x}} \quad (10)$$

### Quantitative Genetics Approach

The quantitative genetics (QG) approach assumes  $x$  is normally distributed with mean  $\bar{x}$  and variance  $V$ . In the non-structured model,  $S$  can be rewritten as:

$$S = \frac{V}{\bar{W}} E \left( \frac{\partial W}{\partial x} \right) \quad (11)$$

(Lande and Arnold 1983) and this expression provides an immediate heuristic argument that  $S \sim$  in (7) approximates  $S$  in a normal population when selection is weak. Indeed, under weak selection, neither  $W$  nor  $\partial W/\partial x$  should change much over the bulk of the population distribution, and their value at  $\bar{x}$  should approximate their average value.

In the group-structured model, I assume that the group mean  $y$  is normally distributed, and that the individuals within each group are also normally distributed with variance independent of  $y$ . This is equivalent to the assumption that  $x$  and  $y$  are jointly normally distributed. If we regress  $W$  on the phenotypic values  $x$  and  $y$ , we get:

$$W = \beta_{Wx,y}x + \beta_{Wy,x}y + \delta \quad (12)$$

where the  $\beta$  are the partial regression coefficients, and  $\delta$  is

uncorrelated with  $x$  and  $y$ . I am assuming that  $W$  is a function of  $y$  and  $z$  (and this a common assumption of ESS models), but (12) is valid when  $W$  is only correlated with these variables. Then the selection differential is obtained from (4):

$$\bar{W}S = \text{cov}(W, x) = \beta_{Wx,y}\text{cov}(x, x) + \beta_{Wy,x}\text{cov}(y, x). \quad (13)$$

This formulation is essentially Queller's (1992) equation (6), except he works with changes in mean genotype rather than phenotype. A standard calculation (Lande and Arnold 1983; see Appendix) shows that if  $x$  and  $y$  are jointly normally distributed, then

$$\beta_{Wx,y} = E \left( \frac{\partial W}{\partial x} \right) \quad (14)$$

and

$$\beta_{Wy,x} = E \left( \frac{\partial W}{\partial y} \right). \quad (15)$$

If we put these into (13), we get

$$S = \frac{V}{\bar{W}} E \left( \frac{\partial W}{\partial x} + R \frac{\partial W}{\partial y} \right) \quad (16)$$

and this reduces to (11) when  $W$  is independent of the group mean  $y$ . Comparison with (10) again shows that in a normally distributed group-structured population,  $S \sim$  approximates  $S$  when selection is weak.

I now calculate and compare  $S$ , in (11) and (16), with  $S \sim$ , in (7) and (10), for a number of commonly used fitness functions. In particular I notice when they have the same sign, for in this case, they will predict the same equilibria.

### Comparison of $S$ and $S \sim$

The most basic result, first noted by Charlesworth (1990), is that when  $W$  is linear in  $x$  and  $y$ , then  $S$  and  $S \sim$  are equal. It was further noted by Abrams et al. (1993) that if  $W$  is a quadratic polynomial in  $x$  and  $y$ , then  $S$  and  $S \sim$  are equal when  $\bar{W}$  is used instead of  $W(\bar{x}, \bar{x})$  in the denominator of (7) and (10). Indeed, in this case, both partial derivatives of  $W$  are linear in  $x$  and  $y$ , and their expected value will equal their value at  $\bar{x}$  and  $\bar{y}$ . Thus, if  $W$  is linear or quadratic in  $x$  and  $y$ , then  $S$  and  $S \sim$  differ by a constant multiple and will have the same sign, and the QG and the ESS equilibria are identical. Charlesworth (1993) has generalized the analysis of Abrams et al. (1993) to the case of a multivariate trait in an age-structured population.

In quantitative genetics models a common class of fitness functions are the exponential and gaussian  $W$  because these maintain normality in the population (Lande 1976b; Felsenstein 1977), and this allows the quantitative genetics analysis to remain valid generation after generation, provided we also track the change in variance. Though Turelli and Barton (1994) have showed that something very close to a normal distribution of breeding values will typically be obtained even under strong truncation selection, when offspring values are normally distributed around the parental mean.

If  $W$  is exponential:

$$W(x, y) = e^{ax+by} \quad (17)$$

where  $a$  and  $b$  might depend on  $\bar{x}$ , then a calculation with (10) and (16) shows that

$$S \sim = S = V(a + Rb) \tag{18}$$

and the common equilibrium condition is  $a + Rb = 0$ . The result in a non-structured population is obtained by setting  $b = 0$  in (17) and (18). Such a fitness function might arise in a continuous time model of altruism, in which the instantaneous relative rate of fitness change is  $W'/W = -cx + by$  (see the discussion after equation 8). Then, starting at  $W = 1$ , the fitness at  $t = 1$  would be given by (17), with  $a = -c$ .

A fitness function that is often used to model stabilizing selection is gaussian:

$$W(x, \bar{x}) = e^{-(x-\bar{x})^2/2Q} \tag{19}$$

where the mode  $\theta$  and the selection strength  $1/Q$  can depend on  $\bar{x}$ . For the non-structured case, (7) and (11) become:

$$S \sim = \frac{V}{Q}(\theta - \bar{x}) \tag{20}$$

and

$$S = \frac{V}{Q + V}(\theta - \bar{x}) \tag{21}$$

respectively (Lande, 1976b), and in both cases, the equilibrium condition is

$$\bar{x} = \theta \tag{22}$$

that is, at equilibrium, the population mean will coincide with the mode of the fitness function.

In the group-structured model, assume that  $W$  has a product form:

$$W(x, y) = W_1(x) W_2(y) \tag{23}$$

where  $W_1$  is gaussian with mode  $\theta_1$  and square width  $Q_1$  (Boyd and Richerson, 1980). In this case, the ESS and QG equilibria are not quite the same. Indeed, (10) and (16) become:

$$S \sim = V \left[ \left( \frac{\theta_1}{Q_1} + R \frac{\theta_2}{Q_2} \right) - \bar{x} \left( \frac{1}{Q_1} + R \frac{1}{Q_2} \right) \right] \tag{24}$$

and

$$S = \frac{VG^*Q_1}{G(Q_1 + K)} \left[ \frac{\theta_1}{Q_1} \left( 1 + R \frac{K}{Q_2} \right) + R \frac{\theta_2}{Q_2} - \bar{x} \left( \frac{1}{Q_1} \left( 1 + R \frac{K}{Q_2} \right) + R \frac{1}{Q_2} \right) \right] \tag{25}$$

where  $K$  is the within-group variance, which is assumed to be independent of  $y$ , and  $G^*$  is the variance of  $y$  after selection:

$$\frac{1}{G^*} = \frac{1}{G} + \frac{1}{Q_2} + \frac{1}{Q_1 + K}. \tag{26}$$

The equilibrium conditions, obtained by setting  $S \sim$  and  $S$  equal to 0, are

$$\text{ESS}(S \sim = 0): \quad \bar{x} = \frac{\frac{\theta_1}{Q_1} + R \frac{\theta_2}{Q_2}}{\frac{1}{Q_1} + R \frac{1}{Q_2}} \tag{27}$$

(Boyd and Richerson 1980, eq. 5), and

$$\text{QG}(S = 0): \quad \bar{x} = \frac{\frac{\theta_1}{Q_1} \left[ 1 + R \frac{K}{Q_2} \right] + R \frac{\theta_2}{Q_2}}{\frac{1}{Q_1} \left[ 1 + R \frac{K}{Q_2} \right] + R \frac{1}{Q_2}} \tag{28}$$

If  $K \ll Q_2$ , which will be the case if selection is weak or if the groups are nearly clonal, then (27) and (28) will give approximately the same equilibria. Both (27) and (28) display the population mean as a weighted average of the two fitness function modes. The weights in (27) appear to make sense—each  $\theta_1$  is weighted by the reciprocal of the square width  $Q_1$  of the fitness function (which measures the strength of selection) and  $\theta_2$  is additionally weighted by the within-group relatedness  $R$ . The QG formula (28) gives a slightly higher relative weight to the individual mode  $\theta_1$  than does the ESS formula (27).

*Example: Altruistic Interactions*

Wilson and Dugatkin (in press) have examined a model of a normal trait  $x$  in which groups of size  $N$  are formed, either by kin relationships or assortatively, and fitness depends on individual phenotype  $x$  and average group phenotype  $y$  according to equation (23). It is assumed that  $\theta_1 < \theta_2$  so that maximum individual benefit is obtained with a group value higher than the individual value; in this sense the trait can be regarded as promoting altruistic/cooperative behaviour. In fact Wilson and Dugatkin take  $\theta_1 = 75$ ,  $\theta_2 = 125$ ,  $Q_1 = Q_2 = 400$ , population variance  $V = 25$ , and group size,  $N = 10$ . Note that  $V \ll Q_1$  so that the assumption of weak selection is reasonable. In this case, the approximation (23) for  $\bar{x}$  gives

$$\bar{x} = \frac{75 + 125R}{1 + R} \tag{29}$$

The case  $R = 1$  of zero within-group variance gives  $\bar{x} = 100$ ; this is the phenotype that maximizes group fitness. In general, we expect  $\bar{x}$  to be between 75 and 100.

In their first scenario, groups are sib groups in an outbred population. In this case, the normality assumptions on the distribution of group means is satisfied, and the equilibrium value should be approximately given by (29) with  $R = 0.55$  (Table 1).

In the second scenario, groups are formed assortatively in the following manner. A random sample of  $10k$  individuals is drawn from the population, and under the assumption that phenotype is recognizable, the top 10 individuals form a group, then the next 10 form another group, and so forth. In this case, the normality assumptions on the distribution of group means is not satisfied, nor is the assumption of constant within-group variance. However, we might still expect (29) to give a reasonable approximation.

Wilson and Dugatkin simulated this process, and found that the case  $k = 2$  gave roughly the same value of  $\bar{x}$  as the

TABLE 1. Simulated values for  $\bar{x}$  are taken from Wilson and Dugatkin (in press, figure 2). For the case of sib groups, the within-group relatedness is  $R = 0.9(0.5) + 0.1(1.0) = 0.55$ . The  $R$  value for  $k = 1$  is obtained by noting that a sample of 10 drawn randomly from a standard normal distribution has within-group variance 0.9, giving a between-group variance of 0.1. The  $R$  calculation for  $k = 2$  is approximate, and is in fact a slight overestimate, making (29) also an overestimate for  $\bar{x}$ . I underestimated the within-group variance by supposing that the top 10 individuals (of the 20) were drawn at random from the right half of the standard normal distribution. This distribution has variance  $1 - (2/\pi) \approx 0.363$  so that the group of 10 will have within-group variance  $(0.9)(0.363) \approx 0.327$ , giving an overestimate of 0.673 for the between-group variance  $G$ . The  $R$  calculation for  $k = 4$  was done approximately from standard normal tables.

	$\bar{x}$ simulated	$R$	$\bar{x}$ calculated from (25)
sib groups:	93.0	0.55	92.7
assortative:			
$k = 1$	79.5	0.1	79.5
$k = 2$	93.5	0.67	95.0
$k = 4$	99.0	0.86	98.2

case of sib groups. In Table 1, I present their simulation results together with the results provided by (29). In all cases, the approximation from (29) is seen to be close.

DISCUSSION

In the QG literature, when fitness is frequency dependent, a standard formula of Lande (1976a) is often used:

$$S = \frac{V}{\bar{W}} \left[ \frac{d\bar{W}}{d\bar{x}} - E \left( \frac{\partial W}{\partial \bar{x}} \right) \right] \quad (30)$$

and when fitness is not frequency dependent, the second term vanishes. For our purpose, which is to make a comparison with ESS dynamics, formula (11) is more useful, and ought to be better known, and the group-structured generalization (16) is particularly elegant. I have not found a nice generalization of (30) for the group-structured case.

When  $S$  and  $S\sim$  have the same sign, then the QG and the ESS models have the same equilibrium points, but are these equilibria simultaneously stable? The answer is yes if we assume selection is weak and if we use the notion of convergence stability (Christiansen 1991), introduced by Eshel (1983) as the essential component of his CSS, and studied by Taylor (1989) under the name of  $m$ -stability. Under this definition, an equilibrium value  $\mu$  of the population mean is stable if for  $\bar{x}$  near  $\mu$ , the sign of  $S(\bar{x})$  is opposite to the sign of  $\bar{x} - \mu$ . This guarantees that the action of selection will move the population mean towards  $\mu$ . This will imply stability of  $\mu$  in a continuous-time model, but in a discrete time model, one must pay attention to the possibility of overshooting—if  $S$  is too large in magnitude, for example, if  $|S| > 2|\bar{x} - \mu|$ , departures from equilibrium might result in unbounded oscillations. In this case, comparisons between  $S$  and  $S\sim$  must take magnitude as well as sign into account, but this should not be a problem when selection is weak.

The above results show that  $S$  and  $S\sim$  are identical when fitness  $W$  is linear or exponential (eq. 18). When  $W$  is quadratic they have the same sign, and almost (assuming weak selection) the same magnitude. These results are true with or

without a group structure. In case  $W$  is gaussian, if there is no group structure, then  $S$  and  $S\sim$  have the same sign and almost (assuming weak selection) the same magnitude (eqs. 20–21); with a group structure,  $S$  and  $S\sim$  have almost (assuming weak selection) the same sign and the same magnitude (eqs. 24–25).

In the absence of group structure, there is a simple “geometric” argument which generalizes the above results for  $W$  quadratic or gaussian. If  $W$ , as a function of  $x$ , is symmetric about a mode  $\theta$ , and increasing for  $x < \theta$  and decreasing for  $x > \theta$ , then  $S$  and  $S\sim$  must have the same sign and indeed, both have the sign of  $\theta - \bar{x}$ . Indeed, with these assumptions,  $S\sim$  clearly has the sign of  $\theta - \bar{x}$  (eq. 7). To examine the sign of  $S$  it is mathematically simplest to rescale the  $x$ -axis so that  $\bar{x} = 0$ . Then:

$$\begin{aligned} \bar{W}S &= \int_{-\infty}^{\infty} (x - 0)W(x)p(x) dx \\ &= \int_0^{\infty} x[W(x) - W(-x)]p(x) dx. \end{aligned}$$

If we suppose  $\theta > 0$ , then the assumed form of  $W$  tells us that  $W(x) > W(-x)$  for all  $x > 0$ , and it follows that  $S > 0$ .

Finally, I mention that equation (11) provides the selection differential  $S$  for two quite different proposals for discrete dynamics. If we let  $p(x)$  be the trait density, then we can ask how  $p$  changes in one generation. The obvious proposal is to say that the new  $p$  will be the fitness-weighted average of the old:

$$p^*(x) = W(x)p(x)/\bar{W} \quad (31)$$

giving the “replicator” dynamic

$$\Delta p(x) = p^*(x) - p(x) = (W(x) - \bar{W})p(x)/\bar{W} \quad (32)$$

proposed by Maynard Smith (1982). The continuous-time version of this was introduced by Taylor and Jonker (1978) and studied by Hofbauer et. al. (1979) and Zeeman (1979). This is the dynamic behind equation (4); indeed, the change in the mean of  $x$  is

$$\Delta \bar{x} = \int x \Delta p(x) dx = S \quad (33)$$

as given by equation (4).

Another proposal for the change in  $p$  is related to a “learning” interpretation of fitness. Imagine that an  $x$ -individual looks to the right and to the left, (on the  $x$ -axis) and with some probability alters his  $x$ -value in the direction in which fitness is increasing, this probability proportional to the fitness gradient. Then the “mass flow” on the  $x$ -axis will, at each  $x$  be proportional to  $[dW/dx] p(x)$ , and the rate of accumulation of mass at  $x$  will be proportional to how fast this flow is changing with respect to  $x$  (the net inflow). This gives the “gradient” dynamics:

$$\Delta p(x) = - \frac{V}{\bar{W}} \frac{d}{dx} \left[ \frac{dW}{dx} p(x) \right] \quad (34)$$

where the constants  $V$  and  $\bar{W}$  are chosen to make the dynamics dimensionless, independent of a change of scale in either  $W$

or  $x$ . In the context of the application of evolutionary games to economic behaviour, this dynamic was proposed by Friedman and Yellin (pers. comm.); in another context, it is the Fokker-Planck equation for conservative fluid flow. Following equation (30) the change in the mean of  $x$  is

$$\Delta \bar{x} = \int x \Delta p(x) dx = \frac{V}{\bar{W}} E \left( \frac{\partial W}{\partial x} \right). \quad (35)$$

Equations (33) and (35) hold without any assumptions on the form of  $p$  or  $W$ . The nice observation is that equation (11) tells us that, for a normally distributed trait, the replicator dynamics (33) and the gradient dynamics (35) give the same change in the mean value of the trait.

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Corresponding Editor: J. B. Walsh

#### APPENDIX

Equations (14) and (15) can easily be obtained by a direct vector integration analogous to the derivation of equation (11) (Lande and Arnold 1983), but here I derive them in a statistically interesting manner. First of all, I show that if  $x$  and  $y$  are jointly normally distributed, then the partial regression coefficients can be expressed as

$$\beta_{Wx,y} = \frac{E(\text{cov}_y(W, x))}{E(\text{cov}_y(x, x))} \quad (A1)$$

and

$$\beta_{Wy,x} = \frac{E(\text{cov}_x(W, y))}{E(\text{cov}_x(y, y))} \quad (A2)$$

where the subscript signals that the covariance is to be calculated with the subscripted variable held fixed, and then the expectation  $E$  is taken over the subscripted variable.

To obtain (A1), take the covariance of  $W$  in equation (12) with  $x$ , holding  $y$  fixed, and then take the expectation over  $y$ :

$$E\text{cov}_y(W, x) = \beta_{Wx,y} E\text{cov}_y(x, x) + \beta_{Wy,x} E\text{cov}_y(y, x) + E\text{cov}_y(\delta, x) \quad (A3)$$

Since the middle term on the right is zero, (A1) will hold if  $E\text{cov}_y(\delta, x) = 0$ . What we know is that  $\text{cov}(\delta, x) = 0$ ; write this as a sum of within and between group components:

$$0 = \text{cov}(\delta, x) = E\text{cov}_y(\delta, x) + \text{cov}(E_y(\delta), E_y(x)) \quad (A4)$$

and we will be done if we show the last term is zero. This follows from the fact that  $E_y(x)$  is linear in  $y$ :

$$E_y(x) = ay + b \quad (A5)$$

which is a standard property of a bivariate normal distribution. Then

$$\text{cov}(E_y(\delta), E_y(x)) = a \text{cov}(E_y(\delta), y) = 0 \quad (A6)$$

since  $\delta$  is uncorrelated with  $y$ . The derivation of (A2) is similar.

Equations (A1) and (A2) are interesting because of their similarity to the standard single-variable regression coefficient, and they deserve to be better known. They are also valid when  $y$  and  $z$  are binary variables which take only the value 0 or 1 (as might occur, for example, in a model of altruism in which you are either an altruist ( $y = 1$ ) or not ( $y = 0$ )). Indeed, the crucial property for (A1) to hold is the linearity property (A5), and every function of a binary variable is trivially linear.

Now for the second step, we apply (11) to  $W(x, y)$ , with  $y$  held fixed:

$$E_y \left( \frac{\partial W}{\partial x} \right) = \frac{\text{cov}_y(W, x)}{\text{cov}_y(x, x)}. \quad (A7)$$

If we now take the expectation over all  $y$ , and note that the denominator of (A4) is in fact independent of  $y$ , then (A1) gives us equation (14); equation (15) is similarly derived.