Appendix: Proof that regressing individuals' reproductive values on vital rates yields Hamilton's sensitivities.

Directional selection is the change in the mean of a trait under selection (but before transmission to the next generation); this is given by the trait's covariance with relative fitness (Robertson 1966, Price 1970, 1972) taken over all individuals in the population. When selection acts on a trait indirectly through correlated traits that are also under investigation, then the partial covariance is used instead to identify the direct contribution. To apply this concept to specific vital rates in a manner consistent with conventional life history theory, then we must define the partial covariance between relative fitness and one specific vital rate that holds all other vital rates constant. Given this definition of a covariance taken over all individuals i in the population, direct selection for p_x, or survival from some age x to age $x + 1$, is

$$\mathrm{cov}_i(v_0, p_x) = \sum_{y=x+1}^{\infty} \lambda^{-y}\, \mathrm{cov}\left(l_{yi} m_y, p_{xi}\right). \qquad \text{[A.1]}$$

This is the sum of partial covariances between later age reproduction $l_{yi}m_y$ and age-specific survival, discounted by future population growth. Note that an individual's cumulative survival is necessarily binary, but the population mean is not. Also, note that population means are used for age-specific reproduction because the partial covariance holds those values constant.

Phenotypic selection is often expressed in terms of products of trait variances and selection gradients, or slopes. To express [A.1] in this way, the individual's cumulative survival at age y can be rewritten as a product series that includes the individual's cumulative survival to age x, its survival rate at x, and age-specific survival rates at all future ages,

$$l_{yi} = p_{xi} l_{xi} \prod_{z=x+1}^{y-1} p_{zi}\ . \qquad \text{[A.2]}$$

Substituting [A.2] in to [A.1] and holding future survival constant (because this is a partial covariance) yields

$$\mathrm{cov}_i(v_0, p_x) = \sum_{y=x+1}^{\infty} \lambda^{-y} m_y \, \mathrm{cov}(p_{xi} l_{xi}, p_{xi}) \prod_{z=x+1}^{y-1} p_z \ . \qquad \text{[A.3]}$$

The covariance term on the right-hand side of [A.3] can be partitioned into among- and within-group components of covariance, where there are groups of individuals that either do or do not survive to age *x*. As the survival probability p_x is conditioned upon survival to age *x*, there is no among-group covariance, and the group of non-survivors contributes no within-group covariance to the total. Thus,

$$\mathrm{cov}(p_{xi} l_{xi}, p_{xi}) = l_x \, \mathrm{var}_i(p_x), \qquad \text{[A.4]}$$

where the variance in [A.4] quantifies dispersal from the mean among only those individuals that survive to age *x*. Substituting [A.4] into the series in [A.3] and simplifying yields the partial covariance between relative fitness and survival at some age *x*,

$$\mathrm{cov}_i(v_0, p_x) = \mathrm{var}_i(p_x) \sum_{y=x+1}^{\infty} \lambda^{-y} m_y l_x \prod_{z=x+1}^{y-1} p_z \ . \qquad \text{[A.5]}$$

This can be re-arranged into a product of a selection gradient and a variance by noting that the cumulative survival equation [A.2] applies to both individual and population-mean values of cumulative and age-specific survival. Re-arranging the relationship using the population means gives $l_x \prod_{z=x+1}^{y-1} p_z = \frac{l_y}{p_x}$. Substituting the right-hand term of this equality into [A.5] yields

$\mathrm{cov}_i(v_0, p_x) = \beta_{v(0),p(x)} \, \mathrm{var}_i(p_x)$, where

$$\beta_{v(0),p(x)} = \frac{\sum_{y=x+1}^{\infty} \lambda^{-y} l_y m_y}{p_x}. \qquad \text{[A.6]}$$

This is the selection gradient that describes the strength of selection acting to increase survival at age *x*. From Hamilton's implicit differentiation method (1966), the sensitivity of the Malthusian parameter *r* to changes in age-specific survival over one time interval is

$$\frac{\partial r}{\partial p_x} = \frac{\partial \lambda}{p_x \lambda \partial} = \frac{\sum_{y=x+1}^{\infty} \lambda^{-y} l_y m_y}{p_x T}, \qquad \text{[A.7]}$$

where $T = \sum_{y=0}^{\infty} y \lambda^{-y} l_y m_y$ is generation time (Hamilton 1966, Charlesworth 1994). Comparing [A.6] and [A.7] reveals that sensitivities from implicit differentiation and selection gradients from multiple regressions express the same measure; the sole difference is that sensitivities quantify selection on the unit-time scale and selection gradients quantify selection on the scale of the generation.

The same property of equivalence can be shown to apply to age-specific reproduction m_x. From [1], it can be seen that this value has a direct effect on the relative fitness only at age *x*. Thus, the partial covariance between relative fitness and age-specific reproduction is simply

$$\operatorname{cov}_i(v_0, m_x) = \lambda^{-x} \operatorname{cov}_i(l_{xi} m_{xi}, m_{xi}) = \beta_{v(0),m(x)} \operatorname{var}_i(m_x), \qquad \text{[A.8]}$$

where

$$\beta_{v(0),m(x)} = l_x \lambda^{-x}. \qquad \text{[A.9]}$$

From Hamilton (1966), the sensitivity of the Malthusian parameter to changes in age-specific reproduction is

$$\frac{\partial r}{\partial m_x} = \frac{l_x \lambda^{-x}}{T} \; ; \qquad \text{[A.10]}$$

this is the same as the generation-scaled selection gradient for age-specific reproduction derived in [A.9].

LITERATURE CITED

Charlesworth, B. 1994. Evolution in Age-structured Populations. Cambridge University Press, Cambridge, UK.

Hamilton, W. D. 1966. Moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Price, G. R. 1970. Selection and covariance. Nature 227:520–521.

Price, G. R. 1972. Extension of covariance selection mathematics. Annals of Human Genetics 35:485–490.

Robertson, A. 1966. A mathematical model of culling process in dairy cattle. Animal Production 8:95–108.