

# 1 Analytical results for directional and quadratic selection 2 gradients for log-linear models of fitness functions

3 Michael B. Morrissey<sup>1</sup> and I. B. J. Goudie<sup>2</sup>

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5 <sup>1</sup>School of Biology, University of St Andrews  
6

## contact

email: michael.morrissey@st-andrews.ac.uk  
phone: +44 (0) 1334 463738  
fax: +44 (0) 1334 463366  
post: Dyers Brae House  
School of Biology, University of St Andrews  
St Andrews, Fife, UK, KY16 9TH

7 <sup>2</sup>School of Mathematics and Statistics, University of St Andrews  
8

## contact

email: ig@st-andrews.ac.uk  
phone: +44 (0) 1334 463705  
fax: +44 (0) 1334 463748  
post: School of Mathematics and Statistics, University of St Andrews  
St Andrews, Fife, UK, KY16 9SS

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# Abstract

1. Established methods for inference about selection gradients involve least-squares regression of fitness on phenotype. While these methods are simple and may generally be quite robust, they do not account well for distributions of fitness.
2. Some progress has previously been made in relating inferences about trait-fitness relationships from generalised linear models to selection gradients in the formal quantitative genetic sense. These approaches involve numerical calculation of average derivatives of relative fitness with respect to phenotype.
3. We present analytical results expressing selection gradients as functions of the coefficients of generalised linear models for fitness in terms of traits. The analytical results allow calculation of univariate and multivariate directional, quadratic, and correlational selection gradients from log-linear and log-quadratic models.
4. The results should be quite generally applicable in selection analysis. They apply to any generalised linear model with a log link function. Furthermore, we show how they apply to some situations including inference of selection from (molecular) paternity data, capture-mark-recapture analysis, and survival analysis. Finally, the results may bridge some gaps between typical approaches in empirical and theoretical studies of natural selection.

# 1 Introduction

The characterisation of natural selection, especially in the wild, has long been a major research theme in evolutionary ecology and evolutionary quantitative genetics (Endler, 1986; Kingsolver *et al.*, 2001; Lande & Arnold, 1983; Manly, 1985; Weldon, 1901). In recent decades, regression-based approaches have been used to obtain direct selection gradients (especially following Lande & Arnold 1983), which represent the direct effects of traits on fitness. These, and related, measures of selection have an explicit justification in quantitative genetic theory (Lande, 1979; Lande & Arnold, 1983), which provides the basis for comparison among traits, taxa, etc., and ultimately allows meta-analysis (e.g., Kingsolver *et al.* 2001). Selection gradients can characterise both directional selection and aspects of non-linear selection, and so are a very powerful concept in evolutionary quantitative genetics.

Formally, the selection gradient is the vector of partial derivatives of relative fitness with respect to phenotype, averaged over the distribution of phenotype observed in a population. Given an arbitrary function  $W(\mathbf{z})$  for expected fitness of a (multivariate) phenotype  $\mathbf{z}$ , a general expression for the directional selection gradient  $\boldsymbol{\beta}$  is

$$\boldsymbol{\beta} = \bar{W}^{-1} \int \frac{\partial W(\mathbf{z})}{\partial \mathbf{z}} p(\mathbf{z}) d\mathbf{z} \quad (1)$$

where  $p(\mathbf{z})$  is the probability density function of phenotype, and  $\bar{W}$  is mean fitness. Mean fitness can itself be obtained by  $\int W(\mathbf{z}) p(\mathbf{z}) d\mathbf{z}$ . A quadratic selection gradient can also be defined as the average curvature (similarly standardised), rather than the average slope, of the relative fitness function,

$$\boldsymbol{\gamma} = \bar{W}^{-1} \int \frac{\partial^2 W(\mathbf{z})}{\partial \mathbf{z}^2} p(\mathbf{z}) d\mathbf{z}. \quad (2)$$

The directional selection gradient has a direct relationship to evolutionary change, assuming that breeding values (the additive genetic component of individual phenotype, Falconer 1960) are multivariate normally-distributed, following the Lande (1979) equation

$$\Delta \bar{\mathbf{z}} = \mathbf{G} \boldsymbol{\beta} \quad (3)$$

50 where  $\Delta \bar{\mathbf{z}}$  is per-generation evolutionary change, and  $\mathbf{G}$  is the additive genetic covariance matrix,  
51 i.e., the (co)variances among individuals of breeding values. The quadratic selection gradient  
52 matrix has direct relationships to the change in the distribution of breeding values due to  
53 selection, but not with such simple relationships between generations as for the directional  
54 selection gradient and the change in the mean (Lande & Arnold, 1983).

55 The primary method for obtaining selection gradient estimates has been a simple and robust  
56 approach justified in Lande & Arnold (1983). The method involves least-squares multiple  
57 regression of relative fitness, i.e., absolute fitness divided by the mean observed in any comparable  
58 group of individuals over a specific period of the life cycle, potentially the entire life cycle, on  
59 measures of phenotype. Fitness, or any component of fitness, will typically have highly non-  
60 normal residuals in such a regression. Nonetheless, the simple least-squares methods are unbiased  
61 (see Geyer & Shaw 2010). However, methods that account for distributions of residuals that  
62 arise in regressions involving fitness as a response variable may provide better precision and  
63 more reliable statements about uncertainty (i.e., standard errors, p-values, etc.).

64 Some progress has been made at developing generalised regression model methods for  
65 inference of selection gradients. Janzen & Stern (1998) proposed a method for binomial responses  
66 (e.g., per-interval survival, mated vs. not mated). The Janzen & Stern (1998) method provides  
67 estimates of  $\beta$ , and requires fitting a logistic model with linear terms only, calculating the  
68 average derivatives at each phenotypic value observed in a sample, and then standardising  
69 to the relative fitness scale. Morrissey & Sakrejda (2013) expanded Janzen & Stern's (1998)  
70 basic approach to arbitrary fitness functions (i.e., not necessarily linear) and arbitrary response  
71 variable distributions, retaining the basic idea of numerically averaging the slope (and curvature)  
72 of the fitness function over the distribution of observed phenotype. Shaw & Geyer (2010)  
73 developed a framework for characterising the distributions of fitness (and fitness residuals) that  
74 arise in complex life cycles, and also showed how the method could be applied to estimate  
75 selection gradients by averaging the slope or curvature of the fitness function over the observed  
76 values of phenotype in a sample.

77 Of the many forms regression analyses of trait-fitness relationships might take, log-linear  
78 or log-quadratic models of the relationship between traits and expected absolute fitness may

79 be particularly useful. In generalised linear models, the log link function is often useful and  
 80 pragmatic. Fitness is a necessarily non-negative quantity, and expected fitness will typically best  
 81 be modelled as a strictly positive quantity. This will indeed be the case if expected fitness is an  
 82 exponential function of the sum of the predictors of the regression model, or, equivalently, a log  
 83 link is used. Also, a log link function is compatible with generalised linear models with various  
 84 distributions that could be useful for modelling fitness or fitness components. For example,  
 85 it can be used with the Poisson distribution (counts, e.g., number of mates or offspring),  
 86 the negative binomial distribution (for counts that are overdispersed relative to the Poisson  
 87 distribution, potentially including lifetime production of offspring), and the exponential and  
 88 geometric distributions (e.g., for continuous and discrete measures of longevity). The purpose  
 89 of this short paper is to investigate the relationships between log-linear and log-quadratic models  
 90 of fitness functions, and selection gradients.

## 91 **2 Log-linear and log-quadratic fitness functions, and se-** 92 **lection gradients**

93 Selection gradients turn out to have very simple relationships to the coefficients of log-  
 94 linear regression models predicting expected fitness from (potentially multivariate) phenotype.  
 95 Suppose that there are  $k$  traits in the analysis and that the absolute fitness function,  $W(\mathbf{z})$  takes  
 96 the form

$$W(\mathbf{z}) = e^{a+b_1z_1+b_2z_2+\dots+b_kz_k} \quad (4)$$

97 where  $a$  is a log-scale intercept, and the  $b_i$  are log-scale regression coefficients relating the traits  
 98 ( $z_i$ ) to expected fitness. The equation for the directional selection gradient (equation 1) can then  
 99 be simplified. Focusing on the selection gradient for a specific trait,  $i$ , in a log-linear model of  
 100  $W(\mathbf{z})$ ,

$$\frac{\partial W}{\partial z_i} = b_i W(\mathbf{z})$$

101 and hence

$$\begin{aligned}\beta_i &= \frac{\int b_i W(\mathbf{z}) p(\mathbf{z}) d\mathbf{z}}{\int W(\mathbf{z}) p(\mathbf{z}) d\mathbf{z}} \\ &= \frac{b_i \int W(\mathbf{z}) p(\mathbf{z}) d\mathbf{z}}{\int W(\mathbf{z}) p(\mathbf{z}) d\mathbf{z}} \\ &= b_i.\end{aligned}\tag{5}$$

102 This result could be quite useful. In any log-linear model regressing expected absolute fitness,  
103 or a component of fitness, on trait values, the linear predictor-scale regression coefficients are  
104 the directional selection gradients.

105 The situation is a little bit more complicated if a log-quadratic model is fitted. If  $W(\mathbf{z})$  takes  
106 the form

$$W(\mathbf{z}) = e^{a + \sum_i b_i z_i + \sum_i g_i (\frac{1}{2} z_i^2) + \sum_{i=1}^{k-1} \sum_{j=i+1}^k g_{ij} (z_i z_j)},\tag{6}$$

107 i.e., of a log-scale regression model with linear and quadratic terms, plus first-order interactions,  
108 then the  $b_i$  coefficients are not necessarily the directional selection gradients, nor are the  $g_i$  and  
109  $g_{ij}$  coefficients the quadratic and correlational selection gradients, as they would be in a least  
110 squares analysis following Lande & Arnold (1983). However, we can use the log-scale quadratic  
111 fitness function with the general definitions of selection gradients (equations 1 and 2) to obtain  
112 analytical solutions for  $\boldsymbol{\beta}$  and  $\boldsymbol{\gamma}$ .

113 The factor of  $\frac{1}{2}$  associated with the quadratic terms in equation 6 is a potential source of  
114 confusion, analogous to that surrounding a similar factor in Lande & Arnold's (1983) paper (see  
115 Stinchcombe *et al.* 2008). In order to obtain the correct values of the  $g_i$  coefficients, the covariate  
116 values for quadratic terms should be (1) mean-centred, then (2) squared, and then (3) halved.  
117 An alternative analysis is possible, where the squared covariate values are not halved, but the  
118 estimated coefficient estimates are doubled (analogous to procedures discussed by Stinchcombe  
119 *et al.* 2008). However, this alternative analysis leads to an additional, and potentially confusing,  
120 step in the calculation of standard errors (detailed in the appendix).

121 Define a vector  $\mathbf{b} = (b_1, \dots, b_k)'$  containing the coefficients of the linear terms in the exponent

of the model in equation 6, and a matrix  $\mathbf{g} = (g_{ij})$  containing the coefficients of the corresponding quadratic form. We can then write the fitness function more conveniently in matrix form

$$W(\mathbf{z}) = e^{f(\mathbf{z})} \quad (7a)$$

$$f(\mathbf{z}) = a + \mathbf{b}'\mathbf{z} + \frac{1}{2}\mathbf{z}'\mathbf{g}\mathbf{z}. \quad (7b)$$

Let  $\mathbf{d}$  be a vector of the expectations of the first order partial derivatives of  $W(\mathbf{z})$  and let  $\mathbf{H}$  be the matrix of expectations of the second order partial derivatives of  $W(\mathbf{z})$ . Thus the elements of  $\mathbf{d}$  are  $d_i = E\left[\frac{\partial W(\mathbf{z})}{\partial z_i}\right]$  and the elements of  $\mathbf{H}$  are  $H_{ij} = E\left[\frac{\partial^2 W(\mathbf{z})}{\partial z_i \partial z_j}\right]$ . We can now rewrite the expressions for directional and quadratic selection gradients as

$$\beta = \frac{\mathbf{d}}{E[W(\mathbf{z})]} \quad (8)$$

and

$$\gamma = \frac{\mathbf{H}}{E[W(\mathbf{z})]}. \quad (9)$$

Differentiating equation 7 gives

$$\frac{\partial W(\mathbf{z})}{\partial \mathbf{z}'} = (\mathbf{b} + \mathbf{g}\mathbf{z}) e^{f(\mathbf{z})}, \quad (10)$$

and

$$\frac{\partial^2 W(\mathbf{z})}{\partial \mathbf{z} \partial \mathbf{z}'} = (\mathbf{g} + (\mathbf{b} + \mathbf{g}\mathbf{z})(\mathbf{b} + \mathbf{g}\mathbf{z})') e^{f(\mathbf{z})}. \quad (11)$$

Assume that the phenotype  $\mathbf{z}$  is multivariate normal, with mean  $\boldsymbol{\mu}$  and covariance matrix  $\boldsymbol{\Sigma}$ , and denote its probability density by  $p_{\boldsymbol{\mu}, \boldsymbol{\Sigma}}(\mathbf{z})$ . Provided  $e^{f(\mathbf{z})}$  has a finite expectation, the function

$$K(\mathbf{z}) = \left(E\left[e^{f(\mathbf{z})}\right]\right)^{-1} e^{f(\mathbf{z})} p_{\boldsymbol{\mu}, \boldsymbol{\Sigma}}(\mathbf{z}) \quad (12)$$

is a probability density function. Define the matrix  $\boldsymbol{\Omega}^{-1} = \boldsymbol{\Sigma}^{-1} - \mathbf{g}$  and the vector  $\boldsymbol{\nu} = \boldsymbol{\mu} + \boldsymbol{\Omega}(\mathbf{b} + \mathbf{g}\boldsymbol{\mu})$ .

We show in the Appendix that  $\boldsymbol{\Omega}$  is symmetric. Provided it is also positive definite, it is a valid

136 covariance matrix, and, by equation A7,

$$K(\mathbf{z}) \propto p_{\nu, \Omega}(\mathbf{z}). \quad (13)$$

137 As  $K$  is a probability density function this implies,

$$K(\mathbf{z}) = p_{\nu, \Omega}(\mathbf{z}). \quad (14)$$

138 Define  $\mathbf{Q}^{-1} = \mathbf{\Omega}^{-1}\mathbf{\Sigma} = \mathbf{I}_k - \mathbf{g}\mathbf{\Sigma}$ . Combining equations 8, 10 and 14 yields  $\boldsymbol{\beta} = E[\mathbf{b} + \mathbf{g}\mathbf{z}]$ , where  
 139 the expectation is taken with respect to  $K$ . This is an expectation of a linear function of  $\mathbf{z}$ , and  
 140 so

$$\boldsymbol{\beta} = \mathbf{b} + \mathbf{g}\nu = (\mathbf{b} + \mathbf{g}\mu) + \mathbf{g}\mathbf{\Omega}(\mathbf{b} + \mathbf{g}\mu) = (\mathbf{I}_k + \mathbf{g}\mathbf{\Omega})(\mathbf{b} + \mathbf{g}\mu) = \mathbf{Q}(\mathbf{b} + \mathbf{g}\mu), \quad (15)$$

141 by use of equation A4.

142 Combining equations 9, 11 and 14 yields  $\boldsymbol{\gamma} = E[\mathbf{g} + (\mathbf{b} + \mathbf{g}\mathbf{z})(\mathbf{b} + \mathbf{g}\mathbf{z})']$ , where the expectation  
 143 is taken with respect to  $K$ . Hence

$$\begin{aligned} \boldsymbol{\gamma} &= \mathbf{g} + \text{Var}(\mathbf{b} + \mathbf{g}\mathbf{z}) + [E(\mathbf{b} + \mathbf{g}\mathbf{z})][E(\mathbf{b} + \mathbf{g}\mathbf{z})]' \\ &= \mathbf{g} + \mathbf{g}\mathbf{\Omega}\mathbf{g}' + \boldsymbol{\beta}\boldsymbol{\beta}' \\ &= \boldsymbol{\beta}\boldsymbol{\beta}' + (\mathbf{I}_k + \mathbf{g}\mathbf{\Omega})\mathbf{g} \\ &= \boldsymbol{\beta}\boldsymbol{\beta}' + \mathbf{Q}\mathbf{g}, \end{aligned} \quad (16)$$

144 where we have noted that  $\mathbf{g}$  is symmetric and used equation A4.

145 In univariate analyses, the matrix machinery necessary for implementing the general formulae  
 146 in equations 15 and 16 can be avoided. If the fitness function is  $W(z) = e^{a+bz+g\frac{1}{2}z^2}$  (note, again,  
 147 that the quadratic coefficient is that for centred, then squared, and then halved values of  $z^1$ ),  
 148 and  $z$  has a mean of  $\mu$  and a variance of  $\sigma^2$  and then  $\boldsymbol{\beta} = \frac{b+g\mu}{1-g\sigma^2}$  and  $\boldsymbol{\gamma} = \frac{(b+g\mu)^2+g(1-g\sigma^2)}{(1-g\sigma^2)^2}$ . These  
 149 expressions will hold for any univariate analysis, and can be applied to get mean-standardised,

<sup>1</sup>This can be accomplished easily in R. Assume that  $W$  and  $z$  are variables in memory representing absolute fitness and phenotypic data, and that residuals of  $W$  are assumed to follow a Poisson distribution. The regression could be implemented by `glm(W~z+I(0.5*(z-mean(z))^2),family=poisson(link="log"))`.



150 variance-standardised, and unstandardised selection gradients, when appropriate values of  $\mu$  and  
 151  $\sigma^2$  are used, and applied to log-quadratic models of  $W(z)$  where the phenotypic records have been  
 152 correspondingly standardised. For the common case where the trait is mean-centred and (unit)  
 153 variance standardised, the expressions simplify further to  $\beta = \frac{b}{1-g}$  and  $\gamma = \frac{b^2+g(1-g)}{(1-g)^2}$ .

154 The equivalence of the regression coefficients of a log-linear fitness model with directional  
 155 selection gradients (equation 5) of course requires that the regression model provides a reasonable  
 156 description of the relationship between a trait and expected fitness and makes reasonable  
 157 assumptions about fitness residuals. Otherwise, the relationship is relatively unburdened by  
 158 assumptions. For example, it does not require any specific distribution of phenotype. The use  
 159 of selection gradients obtained from log-linear regressions to predict evolution using the Lande  
 160 equation (equation 3) does assume that breeding values are multivariate normal (see Morrissey  
 161 2014 for a discussion of selection gradients and associated assumptions about multivariate  
 162 normality of phenotype and breeding values). The expressions for  $\beta$  and  $\gamma$  given a log-quadratic  
 163 fitness model (equations 15 and 16) do assume multivariate normality of phenotype. Equations  
 164 15 and 16 further require that  $\Omega$  is positive definite. In univariate analyses, this condition  
 165 reduces to  $g < \frac{1}{\sigma^2}$ , implying that the fitness function should not curve upwards too sharply  
 166 within the range of observed phenotype.

167 A very convenient feature of the expressions for  $\beta$  and  $\gamma$  in equations 5, 15 and 16 is that the  
 168 model (log) intercept does not influence the selection gradients. This means that the range of  
 169 modelling techniques that yield selection gradients can be even further expanded. For example,  
 170 adding fixed and random effects to Lande & Arnold's (1983) least squares analysis will generally  
 171 result in estimated regression coefficients that are not interpretable as selection gradients. For  
 172 example, it might be desirable to estimate a single selection gradient across two sexes, if data  
 173 are limited and sex-differences in selection are not anticipated. In such an analysis, it might  
 174 seem sensible to include an effect of sex, to account for differences in mean fitness between the  
 175 sexes. However, such an analysis would not yield correct selection gradients, because the theory  
 176 underlying the least squares-based regression analysis of selection requires that mean relative  
 177 fitness is one, and this would not be the case when different strata within an analysis have  
 178 different intercepts. On the other hand, adding such an effect to a log-scale model of absolute

179 fitness, and then deriving selection gradients using equations 5, 15 and 16 will yield correct  
180 selection gradients. Other effects, such as random effects to account for individual heterogeneity  
181 in expected fitness, beyond that explained by the traits (or correlated, unmeasured traits), will  
182 be usable as well, while still retaining the ability to obtain correct selection gradients.

### 183 3 Statistical uncertainty

184 The expressions for selection gradients, given the parameters of a log-quadratic fitness function  
185 (equations 15 and 16) give the selection gradients conditional on the estimated values of  $\mathbf{b}$  and  
186  $\mathbf{g}$ . However,  $\mathbf{b}$  and  $\mathbf{g}$  will not typically be known quantities in empirical studies of natural  
187 selection, but rather will be estimates with error. Because equations 15 and 16 are non-linear  
188 functions of one or more regression coefficients, unconditional estimators of  $\beta$  and  $\gamma$  would  
189 have to be obtained by integrating the expressions for  $\beta$  and  $\gamma$  over the sampling distributions  
190 of the estimated values of  $\mathbf{b}$  and  $\mathbf{g}$ . Such details are not normally considered in calculations  
191 of derived parameters (e.g., heritabilities) in evolutionary studies. Such integration could be  
192 achieved using approximations, bootstrapping, or MCMC methods. Alternatively, application  
193 of equations 15 and 16 directly to estimated values of  $\mathbf{b}$  and  $\mathbf{g}$  may be sufficient in practice.  
194 Similarly, while standard errors of the parameters  $\mathbf{b}$  and  $\mathbf{g}$  are not directly interpretable as  
195 standard errors of corresponding values of  $\beta$  and  $\gamma$ , approximations, bootstrapping, and MCMC  
196 methods may all potentially be useful in practice. In particular, approximation of standard  
197 errors by a first-order Taylor approximation (the “delta method”; Lynch & Walsh 1998) may  
198 generally be pragmatic. Formulae for approximate standard errors by this method are given in  
199 the appendix. For univariate analysis, with phenotype standardised to  $\mu = 0$  and  $\sigma^2 = 1$ , the  
200 approximate standard errors of  $\beta$  and  $\gamma$  are given by

$$SE[\beta] \approx \sqrt{\frac{\Sigma[b]}{(1-g)^2} + \frac{b^2 \Sigma[g]}{(1-g)^4} + \frac{2b \Sigma[b, g]}{(1-g)^3}}, \quad (17)$$

201 and

$$SE[\gamma] \approx \sqrt{\frac{4b^2 \Sigma[b]}{(1-g)^4} + \frac{(1+2b^2-g)^2 \Sigma[g]}{(1-g)^6} + \frac{4b(1+2b^2-g) \Sigma[b, g]}{(1-g)^5}}. \quad (18)$$

Where  $\Sigma[b]$  and  $\Sigma[g]$  represent the sampling variances of the estimated  $b$  and  $g$  terms. These are the squares of their standard errors.  $\Sigma[b, g]$  is the sampling covariance of the  $b$  and  $g$  terms. This is not always reported, but can usually be obtained. For example, in R, it can be extracted from a fitted glm object using the function `vcov()`.

We performed a small simulation study to assess the extent of any bias in the estimators  $\beta$  and  $\gamma$  and the adequacy of their standard errors. We simulated univariate directional selection, with values of  $b$  between -0.5 and 0.5, and with  $g = -0.5, 0$  and 0.2. Because  $\beta$  and  $\gamma$  are non-linear functions of  $g$ , it is not possible to simultaneously investigate ranges of parameter values with regular intervals of values of both  $g$  and selection gradients. These values of  $g$  represent a compromise between investigating a regular range of  $g$  and  $\gamma$ . We used a (log) intercept of the fitness function of  $a = 0$ . We simulated a sample size of 200 individuals. This sample size reflects a very modest-sized study with respect to precision in inference of non-linear selection, and is therefore a useful scenario in which to judge performance of different methods for calculating standard errors. Fitness was simulated as a Poisson variable with expectations defined by the ranges of values of  $b$  and  $g$ , and with phenotypes sampled from a standard normal distribution.

Firstly we analysed each simulated dataset using the OLS regression described by Lande & Arnold (1983), i.e.,  $w_i = \mu + \beta z_i + \gamma \left(\frac{1}{2} z_i^2\right) + e_i$ , using the R function `lm()`. For the OLS regressions, we calculated standard errors assuming normality using the standard method implemented in the R function `summary.lm()`, and by case-bootstrapping, by generating 1000 bootstrapped datasets by sampling with replacement, running the OLS regression analysis, and calculating the standard deviation of the bootstrapped selection gradient estimates. Secondly we fitted a Poisson glm with a linear and quadratic terms, using the R function `glm()`. We then calculated conditional selection gradient estimates using equations 15 and 16. We obtained standard errors by using a first-order Taylor series approximation (the “delta method”; Lynch & Walsh 1998, appendix A1). For each method of obtaining estimates and standard errors, we calculated the standard deviation of replicate simulated estimates. We could thus evaluate the performance of different methods of obtaining standard errors by their ability to reflect this sampling standard deviation. We also calculated mean absolute errors for both estimators of  $\beta$  and  $\gamma$  for all scenarios. Every simulation scenario and associated analysis of selection gradients was repeated 1000 times.

231 Selection gradient estimates obtained by all three methods were essentially unbiased (figure  
232 1a,d,g,j,m,p), except for small biases that occurred when the fitness function was very curved.  
233 Thus, glm-derived values of selection gradients, conditional on estimated values of  $b$  and  
234  $g$  performed very well as estimators of  $\beta$  and  $\gamma$  in our simulations. Similarly, first-order  
235 approximations of standard errors of the glm-derived estimates of  $\beta$  and  $\gamma$  closely reflected the  
236 simulated standard deviations of the estimators (figure 1). All methods for obtaining standard  
237 errors performed well for estimates of  $\beta$  in the pure log-linear selection simulations (figure 1h,k).  
238 OLS standard errors performed reasonably well under most simulation scenarios, except when  $g$   
239 was positive (figure 1n,q); across all scenarios bootstrap standard errors of the OLS estimators  
240 outperformed standard OLS standard errors. Mean absolute error of the glm estimators was  
241 always smaller than that of the OLS estimators of  $\beta$  and  $\gamma$ . This is unsurprising, as the simulation  
242 scheme corresponded closely to the glm model. These results demonstrate the usefulness of the  
243 conditional values of  $\beta$  and  $\gamma$  as estimators, and show that gains in precision and accuracy can  
244 be obtained when glm models of fitness functions fit the data well. It remains plausible that  
245 the OLS estimators motivated by Lande & Arnold's (1983) work could outperform glm-based  
246 analyses in some scenarios.

## 247 4 Other analyses that correspond to log-linear fitness 248 functions

249 In addition to generalised linear models with log link functions, there may be other cases  
250 where models of trait-fitness relationships may correspond to log-linear or log-quadratic fitness  
251 functions. In paternity inference, some methods have been proposed wherein the probability  
252 that candidate father  $i$  is the father of a given offspring is modelled according to

$$W(\mathbf{z}) \propto e^{f(\mathbf{z})},$$

253 and where realised paternities of a given offspring array are then modelled according to a  
254 multinomial distribution, potentially integrating over uncertainty in paternity assignments based

on molecular data (Hadfield *et al.*, 2006; Smouse *et al.*, 1999). When  $f(\mathbf{z})$  is a linear function, Smouse, Meagher & Korbak (1999; T. Meagher, personal communication) interpreted the analysis as analogous to Lande and Arnold's 1983, but not necessarily identical. For a linear  $f(\mathbf{z})$ , this analysis does in fact yield estimates of  $\beta$ , and for a quadratic function, directional and quadratic selection gradients can be obtained using equations 15 and 16. This can be seen by noting that expected fitness, given phenotype, of candidate fathers for any given offspring array will be, in the log-linear case,

$$W(\mathbf{z}) = ce^{a+b\mathbf{z}},$$

where  $c$  is a constant. In application of the expressions yielding equation 5,  $c$  appears in both the numerator and the denominator, yielding  $\beta = \mathbf{b}$ .

Another case where our formulae may be applicable pertains to inferences of survival rate. Often, data about trait-dependent survival rates may be assessed over discrete intervals. While the experimental unit of time may be an interval (e.g., a day or a year), the biologically-relevant aspect of variation in survival may be longevity, i.e., for how many intervals an individual survives. One such situation arises when per-interval survival rate is assessed via a logistic regression analysis, and trait-dependent survival rates are (or may be assumed to be) constant across intervals. A common case of logistic regression analysis that satisfies this first condition is often implemented in capture-mark-recapture procedures. Suppose that per-interval survival rate, given phenotype, may be assumed to be constant, and that fitness is defined to be the expected survival time. Then fitness will be given by the mean of a geometric distribution where death in a particular interval of an individual with phenotype  $\mathbf{z}$  occurs with probability  $\rho(\mathbf{z})$ ,

$$W(\mathbf{z}) = \frac{1 - \rho(\mathbf{z})}{\rho(\mathbf{z})}.$$

If trait-dependent per-interval survival probability is denoted  $\phi(\mathbf{z})$  ( $\phi$  being the standard symbol for survival rate in capture-mark-recapture analyses; Lebreton *et al.* 1992), then the fitness function in terms of expected number of intervals lived is  $W(\mathbf{z}) = \frac{1 - (1 - \phi(\mathbf{z}))}{1 - \phi(\mathbf{z})} = \frac{\phi(\mathbf{z})}{1 - \phi(\mathbf{z})}$ . If per-interval

279 survival rate has been modelled as a logistic regression, i.e.,

$$\phi(\mathbf{z}) = \frac{e^{f(\mathbf{z})}}{1 + e^{f(\mathbf{z})}}$$

280 where  $\phi(\mathbf{z})$  denotes the per-interval fitness function, and  $f(\mathbf{z})$  is the fitness function on the logistic  
281 scale, then the fitness function on the discrete longevity scale is

$$W(\mathbf{z}) = \frac{\frac{e^{f(\mathbf{z})}}{1+e^{f(\mathbf{z})}}}{1 - \frac{e^{f(\mathbf{z})}}{1+e^{f(\mathbf{z})}}} = e^{f(\mathbf{z})}.$$

282 Therefore, if  $f(\mathbf{z})$  is a linear function, then its terms are the directional selection gradients on  
283 the discrete-longevity scale. If  $f(\mathbf{z})$  is a quadratic function, then the corresponding directional  
284 and quadratic selection gradients, again if the relevant aspect of fitness is the number of  
285 intervals survived, can be obtained using equations 15 and 16. Waller and Svensson (2016; this  
286 issue) takes advantage of these relationships to compare inference of trait-dependent survival  
287 in capture-mark-recapture models to classical inference using Lande & Arnold's (1983) least-  
288 squares regression analysis where fitness is assessed as the number of intervals that individuals  
289 survive.

290 It must be stressed that these results do not justify interpretation of logistic regression  
291 coefficients of survival probability as selection gradients in a general way. Such coefficients  
292 differ from selection gradients for three reasons: (1) they pertain to a linear predictor scale, and  
293 natural selection plays out on the data scale, (2) they directly model absolute fitness, not relative  
294 fitness, and (3) they pertain to per-interval survival, which may not necessarily be the aspect  
295 of survival that best reflects fitness in any given study. It is only when the number of intervals  
296 survived is of interest (and mean survival can be assumed to be constant across intervals) that  
297 these three different aspects of scale cancel out such that the parameters of a logistic regression  
298 are selection gradients.

299 Finally, another situation where an important analysis for understanding trait-fitness  
300 relationships that has an immediate – but not necessarily immediately apparent – relationship  
301 to selection gradients, arises in survival analysis. In a proportional hazards model (Cox, 1972),  
302 the instantaneous probability of mortality experienced by live individuals, the hazard  $\lambda(t)$ , as a

303 function of their phenotype could be modelled as

$$\lambda(t) = \lambda_0 e^{f(z)}$$

304 where  $\lambda_0$  is the baseline hazard, and the  $e^{f(z)}$  part of the function describes individual deviations  
 305 from this baseline hazard. If the baseline hazard is constant in time, then survival distributions  
 306 conditional on phenotype are exponential, and have mean  $\lambda^{-1}$ . So, if fitness is taken to be  
 307 expected longevity (as a continuous variable now, not discrete number of intervals as in the  
 308 relations given above between logistic models of per-interval survival and selection gradients)  
 309 then

$$W(z) = \frac{1}{\lambda_0 e^{f(z)}} = \frac{1}{\lambda_0} e^{-f(z)}.$$

310 In expressions for selection gradients (equations 1 and 2),  $\frac{1}{\lambda_0}$  would be a constant in the integrals  
 311 in both the numerators and denominators, and therefore cancels in calculations of selection  
 312 gradients. Therefore, if proportional hazards are modelled with  $f(z)$  as a linear or quadratic  
 313 function, then the expressions for selection gradients (equations 5, 15 and 16) hold, but the  
 314 coefficients of the trait-dependent hazard function must be multiplied by -1.

## 315 5 Conclusion

316 We have provided analytical expressions for selection gradients, given the parameters of log-  
 317 linear and log-quadratic functions describing expected fitness. These functions can be applied  
 318 in conjunction with a range of generalised linear model approaches, specific situations in capture-  
 319 mark-recapture analysis, and relate to fitness functions used in theoretical studies. The general  
 320 relationship of selection gradients to the coefficients of log-linear and log-quadratic models, in  
 321 particular, various generalised linear models, are probably the most generally useful feature of  
 322 our results. In empirical applications, our preliminary simulation results indicate that, given  
 323 an appropriate model of a log-scale fitness function, inference using log-linear and log-quadratic  
 324 models may be very robust, and could provide more reliable statements about uncertainty (e.g.,  
 325 reasonable standard errors) than the main methods used to date. Furthermore, the relationships

given here between log-quadratic fitness functions and selection gradients could lead to better integration between empirical and theoretical strategies for modelling selection. In theoretical studies, Gaussian fitness functions are often used. These are simply log-quadratic functions that are parameterised in terms of a location parameter (phenotype of maximum fitness), and a width parameter. A relationship between the parameters of a Gaussian fitness function and directional selection gradients (Lande 1979; the expression we give for  $\beta$  is an alternative formulation) is already widely used in the theoretical literature. For any given distribution of phenotype, these parameters correspond directly to linear and quadratic (log-scale) regression parameters, and so can be directly related to selection gradients in empirical studies.

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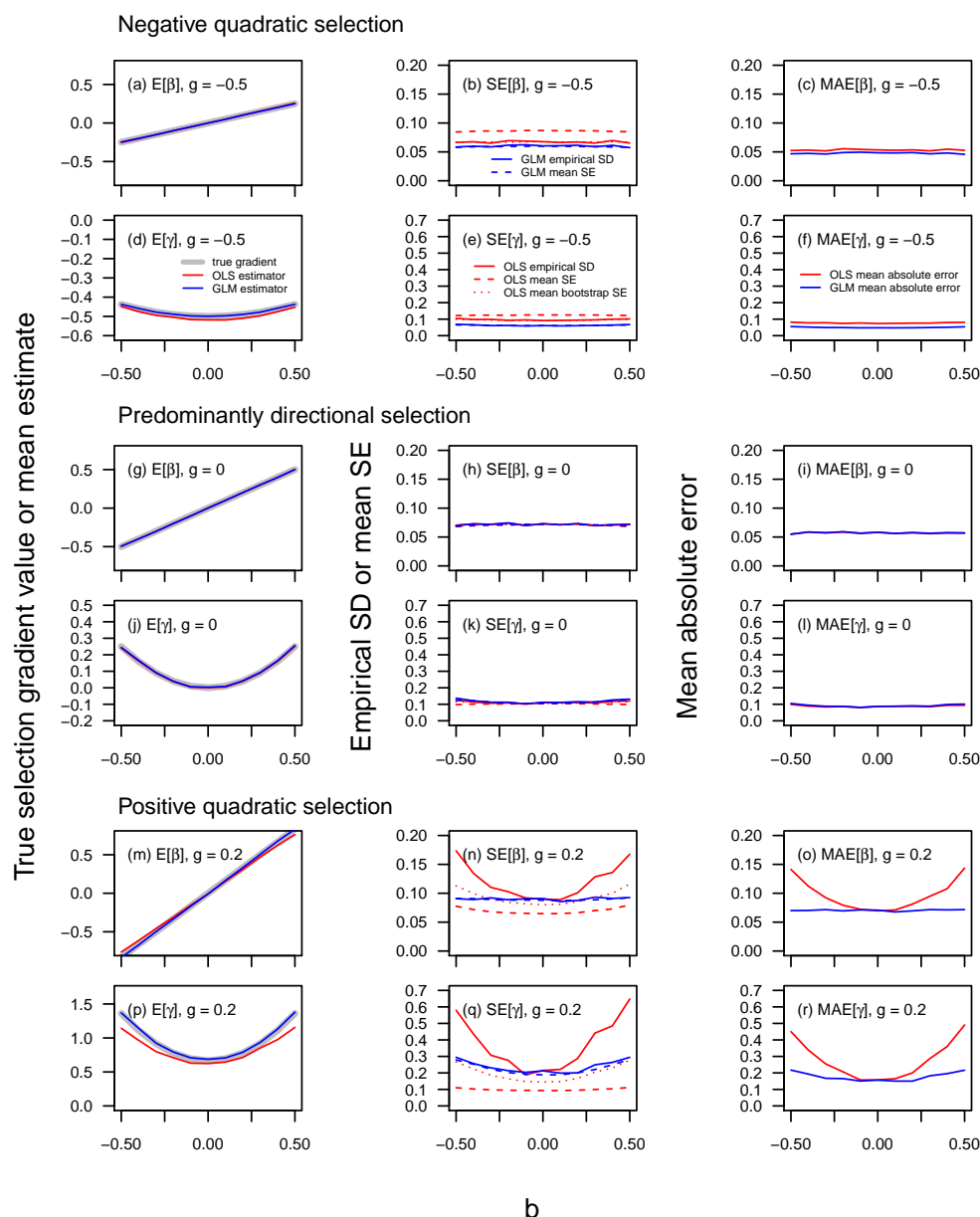


Figure 1: Simulation results for the performance of Lande & Arnold's (1983) least squares-based (OLS) estimators (red lines), and log-quadratic (GLM) estimators (blue lines), of directional and quadratic selection gradients. The first column shows bias in estimates of  $\beta$  and  $\gamma$ , where departure from the grey line (the simulated truth) indicates bias. The middle column shows the performance of OLS standard errors (red dashed lines), bootstrap standard errors (red dotted lines), and first-order approximations (blue dashed lines) of the standard errors of the GLM estimators. Ideally, all values of estimated mean standard errors would fall on the simulated standard deviation of their associated estimators, shown as solid lines. The right column shows the mean absolute errors of the OLS and GLM estimators.

## Appendix

Denote a vector containing all unique elements of  $\boldsymbol{\gamma}$  by  $\tilde{\boldsymbol{\gamma}}$ . The following assumes that  $\tilde{\boldsymbol{\gamma}}$  is composed by vertically stacking the columns of the diagonal and sub-diagonal elements of  $\boldsymbol{\gamma}$ . For example, in an analysis with three traits,  $\tilde{\boldsymbol{\gamma}} = [\gamma_{1,1}, \gamma_{2,1}, \gamma_{3,1}, \gamma_{2,2}, \gamma_{3,2}, \gamma_{3,3}]'$ . Let  $\mathbf{v}()$  denote the function mapping the distinct elements of a symmetric matrix  $\mathbf{r}$  onto the column vector  $\tilde{\mathbf{r}}$ .

The first-order approximation to the sampling covariance matrix of the elements of  $\boldsymbol{\beta}$  and  $\boldsymbol{\gamma}$  is then given by  $\mathbf{J}\tilde{\boldsymbol{\Sigma}}\mathbf{J}'$ , where  $\tilde{\boldsymbol{\Sigma}}$  is the sampling covariance matrix of a vector containing the elements of  $\mathbf{b}$  and  $\tilde{\mathbf{g}}$ , where the latter is a column vector containing the distinct elements of  $\mathbf{g}$  arranged according to the same scheme that defines  $\tilde{\boldsymbol{\gamma}}$ .  $\mathbf{J}$  is the Jacobian, or gradient matrix of first order partial derivatives, of  $\boldsymbol{\beta}$  and  $\tilde{\boldsymbol{\gamma}}$  with respect to  $\mathbf{b}$  and  $\tilde{\mathbf{g}}$ , i.e.,

$$\mathbf{J} = \begin{bmatrix} \frac{\partial \boldsymbol{\beta}}{\partial \mathbf{b}} & \frac{\partial \boldsymbol{\beta}}{\partial \tilde{\mathbf{g}}} \\ \frac{\partial \tilde{\boldsymbol{\gamma}}}{\partial \mathbf{b}} & \frac{\partial \tilde{\boldsymbol{\gamma}}}{\partial \tilde{\mathbf{g}}} \end{bmatrix},$$

evaluated at the estimated values of  $\mathbf{b}$  and  $\mathbf{g}$ .

Note that some users may prefer to fit the model 6 with  $g_{ii}$  replaced by  $2g_i$ , say. The formulae for  $\boldsymbol{\beta}$  and  $\boldsymbol{\gamma}$  are readily re-expressed in terms of these variables by making this substitution. If  $\boldsymbol{\Sigma}_1$  denotes the covariance matrix obtained when fitting this revised model, the required covariance matrix  $\tilde{\boldsymbol{\Sigma}}$  can be calculated using  $\tilde{\boldsymbol{\Sigma}} = \mathbf{D}\boldsymbol{\Sigma}_1\mathbf{D}'$ , where  $\mathbf{D}$  is a diagonal matrix with all the diagonal elements equal to one, apart from those corresponding to the variables  $g_{ii}$  which equal 2.

The four submatrices of  $\mathbf{J}$  can be treated separately. Noting that  $\boldsymbol{\beta} = \mathbf{Q}(\mathbf{b} + \mathbf{g}\boldsymbol{\mu})$  (equation 15),

$$\frac{\partial \boldsymbol{\beta}}{\partial \mathbf{b}} = \mathbf{Q}. \quad (\text{A1})$$

Let  $s = \frac{1}{2}k(k+1)$ , where  $k$  is the number of traits in the analysis, and let  $\mathbf{e}_1, \dots, \mathbf{e}_s$  be the standard basis for an  $s$  dimensional space (i.e.,  $\mathbf{e}_1 = [1, 0, \dots, 0]'$ , etc.). Define an indicator matrix  $\mathbf{C}_m = \mathbf{C}^{(i,j)}$  where  $\mathbf{C}^{(i,j)}$  is a  $k$  by  $k$  matrix in which

$$[\mathbf{C}^{(i,j)}]_{xy} = \begin{cases} 1, & (x,y) = (i,j) \text{ or } (j,i); \\ 0, & \text{otherwise.} \end{cases}$$

Using the standard expression for the derivative of the inverse of a matrix with respect to a

401 scalar, we can obtain  $\frac{\partial \beta}{\partial \tilde{\mathbf{g}}}$ , i.e., the upper-right sub-matrix of  $\mathbf{J}$ .

$$\begin{aligned}
 \beta = \Psi^{-1}(\mathbf{b} + \mathbf{g}\mu) &\Rightarrow \frac{\partial \beta}{\partial \tilde{\mathbf{g}}_m} = \frac{\partial \beta}{\partial g_{ij}} = -\Psi^{-1} \left[ \frac{\partial \Psi}{\partial g_{ij}} \right] \Psi^{-1}(\mathbf{b} + \mathbf{g}\mu) + \Psi^{-1} \left[ \frac{\partial (\mathbf{b} + \mathbf{g}\mu)}{\partial g_{ij}} \right] \\
 &= -\mathbf{Q} \left[ \frac{\partial \mathbf{I}_k - \mathbf{g}\Sigma}{\partial g_{ij}} \right] \mathbf{Q}(\mathbf{b} + \mathbf{g}\mu) + \mathbf{Q} \left[ \frac{\partial \mathbf{g}}{\partial g_{ij}} \right] \mu \\
 &= \mathbf{Q} \left[ \frac{\partial \mathbf{g}}{\partial g_{ij}} \right] [\Sigma \mathbf{Q}(\mathbf{b} + \mathbf{g}\mu)] + \mathbf{Q} \left[ \frac{\partial \mathbf{g}}{\partial g_{ij}} \right] \mu \\
 &= \mathbf{Q} \mathbf{C}^{(ij)} (\Sigma \beta + \mu) = \mathbf{Q} \mathbf{C}_m (\Sigma \beta + \mu) \\
 &\Rightarrow \frac{\partial \beta}{\partial \tilde{\mathbf{g}}} = \sum_{m=1}^s \frac{\partial \beta}{\partial \tilde{\mathbf{g}}_m} \mathbf{e}'_m = \mathbf{Q} \sum_{m=1}^s \mathbf{C}_m (\Sigma \beta + \mu) \mathbf{e}'_m
 \end{aligned} \tag{A2}$$

402 Let  $\mathbf{Q}_{[u]}$  denote the  $u^{\text{th}}$  column of  $\mathbf{Q}$ . Using the previous relation  $\frac{\partial \beta}{\partial \mathbf{b}} = \mathbf{Q}$ , we can obtain  $\frac{\partial \tilde{\gamma}}{\partial \mathbf{b}}$ ,  
 403 i.e., the lower-left sub-matrix of  $\mathbf{J}$ .

$$\begin{aligned}
 \gamma = \beta \beta' + \mathbf{Q} \mathbf{g} &\Rightarrow \frac{\partial \gamma}{\partial b_u} = \beta \left( \frac{\partial \beta}{\partial b_u} \right)' + \left( \frac{\partial \beta}{\partial b_u} \right) \beta' = \beta \mathbf{Q}'_{[u]} + \mathbf{Q}_{[u]} \beta' \\
 &\Rightarrow \frac{\partial \tilde{\gamma}}{\partial b_u} = \mathbf{v} (\beta \mathbf{Q}'_{[u]} + \mathbf{Q}_{[u]} \beta') \\
 &\Rightarrow \frac{\partial \tilde{\gamma}}{\partial \mathbf{b}} = \sum_{u=1}^k \mathbf{v} (\beta \mathbf{Q}'_{[u]} + \mathbf{Q}_{[u]} \beta') \mathbf{e}'_u
 \end{aligned} \tag{A3}$$

404 Let  $\mathbf{M}^{(m)} = \mathbf{Q} \mathbf{C}_m (\Sigma \beta + \mu) \beta'$ . Note that  $\mathbf{Q}^{-1} = \Omega^{-1} \Sigma$  implies  $\Omega = \Sigma \mathbf{Q}$ . Moreover  $\Omega^{-1} = \Sigma^{-1} - \mathbf{g}$   
 405 implies firstly that

$$\mathbf{I}_k + \mathbf{g}\Omega = \Sigma^{-1} \Omega = \mathbf{Q} \tag{A4}$$

406 and secondly that  $\Omega$  is symmetric, since  $\Sigma$  and  $\mathbf{g}$  are both symmetric. It follows that

$$\mathbf{Q}' = \mathbf{I}_k + (\mathbf{g}\Omega)' = \mathbf{I}_k + \Omega \mathbf{g}. \tag{A5}$$

407 The lower-right sub-matrix of  $\mathbf{J}$  can then be derived.

$$\begin{aligned}
 \frac{\partial \gamma}{\partial g_{ij}} &= \left[ \frac{\partial \beta}{\partial g_{ij}} \right] \beta' + \beta \left[ \frac{\partial \beta}{\partial g_{ij}} \right]' + \mathbf{Q} \mathbf{C}^{(ij)} + \mathbf{Q} \mathbf{C}^{(ij)} \Sigma \mathbf{Q} \mathbf{g} \\
 &= [\mathbf{Q} \mathbf{C}^{(ij)} (\Sigma \beta + \mu)] \beta' + \beta [\mathbf{Q} \mathbf{C}^{(ij)} (\Sigma \beta + \mu)]' + \mathbf{Q} \mathbf{C}^{(ij)} + \mathbf{Q} \mathbf{C}^{(ij)} \Omega \mathbf{g} \\
 &\Rightarrow \frac{\partial \tilde{\gamma}}{\partial g_{ij}} = \mathbf{v} [\mathbf{M}^{(m)} + (\mathbf{M}^{(m)})' + \mathbf{Q} \mathbf{C}_m (\mathbf{I}_k + \Omega \mathbf{g})] \\
 &\Rightarrow \frac{\partial \tilde{\gamma}}{\partial \tilde{\mathbf{g}}} = \sum_{m=1}^s \mathbf{v} [\mathbf{M}^{(m)} + (\mathbf{M}^{(m)})' + \mathbf{Q} \mathbf{C}_m \mathbf{Q}'] \mathbf{e}'_m,
 \end{aligned} \tag{A6}$$

408 by use of equation A5.

409 Finally note that equations A4 and A5 are also relevant to the derivation of formula 13. By  
 410 definition,  $f(\mathbf{z}) = a + \mathbf{z}'\mathbf{b} + \frac{1}{2}\mathbf{z}'\mathbf{g}\mathbf{z}$ , and we have  $\log[p_{\mu,\Sigma}(\mathbf{z})] = -\frac{1}{2}\mathbf{z}'\Sigma^{-1}\mathbf{z} + \mathbf{z}'\Sigma^{-1}\mu + \alpha$ , where  $\alpha$  does  
 411 not depend on  $\mathbf{z}$ . Thus, if  $\alpha' = \alpha + a$ , it follows that, as a function of  $\mathbf{z}$ ,

$$f(\mathbf{z}) + \log[p_{\mu,\Sigma}(\mathbf{z})] = -\frac{1}{2}\mathbf{z}'(\Sigma^{-1} - \mathbf{g})\mathbf{z} + \mathbf{z}'(\mathbf{b} + \Sigma^{-1}\mu) + \alpha' = -\frac{1}{2}\mathbf{z}'\Omega^{-1}\mathbf{z} + \mathbf{z}'\Omega^{-1}[\Omega(\mathbf{b} + \Sigma^{-1}\mu)] + \alpha',$$

412 Now, by A4 and A5, we have  $\Omega(\mathbf{b} + \Sigma^{-1}\mu) = \Omega\mathbf{b} + (\Sigma^{-1}\Omega)'\mu = \Omega\mathbf{b} + \mathbf{Q}'\mu = \Omega\mathbf{b} + (\mathbf{I}_k + \Omega\mathbf{g})\mu = \nu$ ,  
 413 implying that

$$f(\mathbf{z}) + \log[p_{\mu,\Sigma}(\mathbf{z})] = -\frac{1}{2}\mathbf{z}'\Omega^{-1}\mathbf{z} + \mathbf{z}'\Omega^{-1}\nu + \alpha' = -\frac{1}{2}(\mathbf{z} - \nu)'\Omega^{-1}(\mathbf{z} - \nu) + \alpha'', \quad (\text{A7})$$

414 where  $\alpha''$  is constant as a function of  $\mathbf{z}$ . The exponent of  $e^{f(\mathbf{z})}p_{\mu,\Sigma}(\mathbf{z})$  is thus identical, as a function  
 415 of  $\mathbf{z}$ , to that of  $p_{\nu,\Omega}(\mathbf{z})$ . Hence formula 13 holds.