

ESTIMATING SELECTION ON NEONATAL TRAITS IN RED DEER USING ELASTICITY PATH ANALYSIS

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Abstract.—Van Tienderen recently published a method that links selection gradients between a phenotypic trait and multiple fitness components with the effects of these fitness components on the population growth rate (mean absolute fitness). The method allows selection to be simultaneously estimated across multiple fitness components in a population dynamic framework. In this paper we apply the method to a population of red deer living in the North Block of the Isle of Rum, Scotland. We show that (1) selection on birth date and birth weight can operate through multiple fitness components simultaneously; (2) our estimates of the response to selection are consistent with the observed change in trait values that we cannot explain with environmental and phenotypic covariates; (3) selection on both traits has fluctuated over the course of the study; (4) selection operates through different fitness components in different years; and (5) no environmental covariates correlate with selection because different fitness components respond to density and climatic variation in contrasting ways.

Key words.—Birth date, birth weight, *Cervus elaphus*, elasticity, elastogram, selection gradient.

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Although ecology defines the arena within which natural selection operates, there is perhaps a tendency for some evolutionary biologists to ignore ecological processes and for some ecologists to overlook dynamic changes that are a result of responses to selection. However, recent research that explores selection in an ecological framework has proved illuminating (Merilä et al. 2001; Kruuk et al. 2002) and has demonstrated that ecological variation can generate a response to selection (Réale et al. 2003). Recently published methods now allow ecological and evolutionary dynamics to be linked using detailed long-term individual-based data (e.g., Van Tienderen 2000) but have not been widely applied. We use detailed long-term individual-based data from a study of red deer (*Cervus elaphus*; Clutton-Brock et al. 1982) to explore selection and the response to selection on birth date and birth weight in a population dynamic framework. We focus on these two traits because birth weight is considered a key trait associated with individual fitness in this population (Clutton-Brock et al. 1982; Kruuk et al. 1999a,b) and more generally (Metcalf and Monaghan 2001; Lindstrom and Kokko 2002) and red deer on Rum give birth comparatively late in the year for large northern ungulates and later than spring grass flush (Clutton-Brock and Coulson 2002). The timing of breeding (birth date) is considered a classic example of a heritable trait under directional selection (Price et al. 1988) and influences first-year survival within our study population (Clutton-Brock et al. 1982).

Lande (1982) demonstrated how selection and population dynamic analyses could be linked in a matrix-modeling framework. Van Tienderen (2000) extended Lande's work by developing a hierarchical modeling framework of λ , the population growth rate (mean absolute fitness) based on elasticities of λ . Under the hierarchical framework of the Lande model, λ depends on elements in a matrix model, which themselves depend on state-dependent fitness components, which in turn can depend on phenotypic traits. The trick to

linking phenotype, fitness components, and population growth is to estimate each association on the same scale. Van Tienderen (2000) primarily concentrated on the proportional scale, which relies on elasticities, defined as the proportional change in a response variable resulting from a proportional change in a model parameter. Van Tienderen's method, along with research by Benton and Grant (2000) and Rose et al. (2002), demonstrated that elasticities can be used to estimate selection, which is in contrast to Caswell's (2001, p. 295) view that selection should be estimated with sensitivities. Lande (1982) originally proposed the use of sensitivities.

In the hierarchical framework we apply, we estimate the proportional change in λ resulting from a hypothetical proportional change in birth weight and birth date. The method involves the estimation of the elasticity of a trait of λ via all fitness components used to construct the matrix elements in the model of λ . These multiple elasticities can be summed to estimate selection on a trait acting via multiple fitness components. Furthermore, the method allows phenotypic trait correlations to be incorporated if the proportional response of one trait to a proportional change in the value of the correlated trait can be estimated and the expected response to selection to be estimated if the additive genetic variation of the trait(s) is known. To our knowledge this is the first application of the hierarchical modeling framework to field data. But given the obvious complexity to the approach, why would anyone want to apply this method?

Primarily the greatest advantage is to allow population dynamics to be linked to evolutionary dynamics. As long as the relationships between traits, fitness components, matrix elements, and λ can be elucidated, it is feasible to explore the consequences of environmental variation on selection and the expected response to selection. Although it is beyond the scope of this paper, these relationships could be functions of density and environmental stochasticity, allowing the effects of environmental change on trait evolution to be explored.

A second related advantage, which we consider in detail in this paper, is that the method allows selection on a trait to be decomposed into relative contributions from multiple fitness components and for temporal variation in these contributions to be explored. For example, estimates of natural selection from field data are often made using selection gradients, which describe the association between a phenotypic trait and survival, fecundity, or dispersal (Kingsolver et al. 2001). One potential limitation of this approach is that selection on the phenotypic trait may be operating simultaneously through other fitness components. For example, a selection gradient may be estimated between a measure of juvenile condition and juvenile survival but this estimate of selection would overlook any survival cost to a parent of producing an offspring in good condition. Although parent-offspring trade-offs between offspring birth size and timing have been the focus of much research, studies of selection on such traits rarely consider gradients across offspring and parental generations. If there are trade-offs between fitness components resulting from conflicts between offspring and parents, then estimating selection between a trait and one fitness component could generate a biased estimate of selection. The hierarchical decomposition of selection (HDS) approach allows selection to be estimated across multiple fitness components and for the relative importance of each path via which selection can operate to be assessed.

In this paper we use the HDS approach to estimate selection on two key traits in a wild mammal, birth weight and birth date, within a population of red deer living within the North Block on the Isle of Rum, Scotland (Clutton-Brock et al. 1982). Our objectives are to estimate selection on birth weight and birth date, to decompose selection on these traits into contributions from selection gradients across multiple fitness components, and to explore whether these associations vary over time and whether this variation is associated with environmental covariates.

MATERIALS AND METHODS

The methods we use are designed to elucidate how a change in the population mean value of a trait alters λ (population growth rate, and under some circumstances mean fitness; Lande et al. 2002). The methods we use fall into two categories: (1) simple algebra of deterministic Leslie matrices; and (2) general and generalized linear and linear mixed-effects models. The matrix algebra links mean values of fitness components to λ , and the statistical modeling uses individual data to estimate the association between a trait and each fitness component. Our choice of matrix model, fitness components, and the associations between traits and fitness components incorporated into analyses are all guided by our biological understanding of the study system (see Discussion).

Definitions

λ is the proportional change in population size between $t(1)$ and $t(2)$ and is calculated as $N_{t(2)}/N_{t(1)}$ where N refers to the population size at times $t(1)$ and $t(2)$. We describe λ with a Leslie matrix model consisting of multiple matrix elements. Each matrix element is a function of underlying fitness components. These fitness components consist of state-dependent

(age and sex in our analyses) mean values for survival, emigration, and reproduction for individuals in the state that the matrix element represents. For example, if λ is defined as N_{2000}/N_{1974} as in the analyses for the whole dataset (see below), then the fitness components are the mean values of age- and sex-specific survival, fecundity, and dispersal between 1974 and 2000. The proportional effect on λ of a proportional change in one fitness element is the elasticity of the fitness component of λ and can be calculated either analytically or by simulation. The proportional change in a fitness component resulting from a proportional change in a trait value is the selection gradient. It should be noted that these selection gradients are the slope of a linear regression of the mean standardized trait on the mean standardized fitness component. The data used to calculate these selection gradients are at the individual level but are the same data used to estimate mean values for the matrix elements. The elasticity of a trait of λ is the product of a selection gradient between a trait and a fitness component and the elasticity of that fitness component of λ . It measures the proportional change in λ resulting from a proportional change in the trait value via that fitness component. Each elasticity of a trait of λ is a unique path between the trait and λ in Figure 1. Selection on a trait is the sum of all elasticities of the trait of λ (paths). The expected response to selection is the product of selection on a trait scaled to generation length and the additive genetic variance of the mean standardized trait. The observed phenotypic response to selection is a change in mean value of a trait over the course of the study that cannot be explained with environmental and individual-based covariates.

Study Population

We used data from a population of red deer (*C. elaphus*) living in the North Block of Rum, Scotland. Within this population females can be sexually mature at 2.5 years of age and can give birth to their first offspring aged 3 years, although at high density many females delay their first breeding attempt until aged 3.5 years (Albon et al. 1989). Many females breed every other year. Births occur in late May to June and calves are weaned by October. The mating season takes place in late September to October. The population is food limited during winter, and most mortality occurs between January and April.

Life-history data have been collected on marked individuals living in the study area since 1971. Life-history data consist of sex, date of birth (transformed into days since January 1), weight at birth (kg), date of death or emigration, and the outcome of all breeding attempts. Calves are caught and marked with unique ear tags within hours of birth. Just over 3000 individuals have been marked throughout the course of the study. Further details of the study area and data collection procedures have been published elsewhere (Clutton-Brock et al. 1982).

Standardized census data have been collected since January 1974. A set route is walked each census, and the identity and position of animals seen is recorded. Census routes differ slightly between summer and winter. Censuses of the study area are conducted up to five times per month in all months except June, August, and November (Coulson et al. 1997).

For this analysis animals that are seen in 10% or more of winter censuses (January–May) and known to be alive on May 15 (a date prior to calving yet after all winter mortality) are considered as being resident in the population.

Temporal Trends in Trait Values

The observed phenotypic response to selection was estimated as the change in the value of a mean standardized trait over time, having corrected for other environmental covariates associated with variation in the trait. Temporal trends in birth weight and birth date were estimated using linear mixed effect models with mother's identity fitted as a random effect to remove potential nonindependence within the data resulting from multiple measures on the same mother (Verbeke and Molenberghs 1998; Milner et al. 1999; Pinheiro and Bates 2000). The significance of mother's age (linear and quadratic), calf sex, mother's reproductive status, population size (linear and quadratic, detrended and not; measured as the number of animals > 12 months old, the number of females > 12 months old, and number of males > 12 months old), weather covariates, and year (linear and quadratic) were examined. If year was significant following correction for all other significant terms, a trend in trait value is suggested. Mother's reproductive status is a categorical variable with five levels: (1) first time breeders, animals that had not previously bred; (2) true yields, females that had previously bred, but did not breed in the previous year; (3) summer yields, females whose calf died before October 1 of the previous year; (4) winter yields, females whose calf died between October 1 of the previous year and the beginning (May 15) of the current year; and (5) milk hinds, females that raised a calf to one year of age.

The following climatic variables were considered: the winter North Atlantic Oscillation measured between Iceland and Lisbon (Hurrell 1995), the monthly mean of the mean daily temperature range and total monthly precipitation. Each weather variable was fitted into models independently. Composite weather variables were defined by grouping monthly variables based on the similarity of their regression estimates. The four most significant of these composite weather variables were then fitted into the linear mixed effects models, and the most parsimonious model was selected using standard model selection methods. Birth weight and birth date were mean standardized prior to analyses to allow comparison with estimates of selection from mean standardized data. To explore the correlation between focal traits, birth weight was fitted into the birth date model and birth date was fitted into the birth weight model.

Population Model

We initially constructed a population model that distinguished survival between yearling females, yearling males, prime adult females (aged 2 to 10 years), prime adult males (aged 2 to 8 years), older adult females (aged 11 or more years), and older adult males (aged 9 or more years). This classification was identified as the most parsimonious age structure from a mark-recapture-recovery analysis (Fan et al. 2003; for methods, see Catchpole et al. 1998). Recruitment

rates per female (the number of offspring produced and surviving to 1 year of age) were zero for hinds aged less than 3 years and were considered identical across all other ages. Three-year-old females do have lower recruitment rates than older individuals (Albon et al. 1989), but there were insufficient numbers of 3 year olds breeding to allow this difference to be incorporated into the population model.

The model was a prebreeding partitioned Leslie matrix model (Caswell 2001) of the following form:

$$\mathbf{T} = \begin{pmatrix} \mathbf{T}_1 & \mathbf{0} \\ \mathbf{T}_2 & \mathbf{T}_3 \end{pmatrix} \quad (1)$$

with components

$$\mathbf{T}_1 = \begin{pmatrix} 0 & 0 & RF & \cdots & RF \\ SF_Y & 0 & 0 & \cdots & 0 \\ & SF_A & 0 & \cdots & 0 \\ & & SF_A & \cdots & 0 \\ & & & \ddots & SF_O \end{pmatrix}, \quad (2a)$$

$$\mathbf{T}_2 = \begin{pmatrix} 0 & 0 & RM & RM & \cdots & RM \\ & & 0 & 0 & \cdots & 0 \end{pmatrix}, \quad \text{and} \quad (2b)$$

$$\mathbf{T}_3 = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 \\ SM_Y & 0 & 0 & \cdots & 0 \\ & SM_A & 0 & \cdots & 0 \\ & & SM_A & \cdots & 0 \\ & & & \ddots & SM_O \end{pmatrix}, \quad (2c)$$

where RF is the recruitment rate of female calves to the population per adult female (birth rate to female calves \times neonatal survival rate of female calves [from birth to October 1]) \times winter survival rate of female calves [from October 1 to May 14]) and RM is the recruitment rate of male calves to the population per adult female. SF_Y , SM_Y , SM_A , and SM_O are, respectively, the probabilities of female yearlings, male yearlings, prime-aged male adults and older male adults, of remaining in the population and are calculated as the product of the age- and sex-specific survival rates and one minus the age- and sex-specific emigration rates. SF_A and SF_O are, respectively, the probabilities of prime-aged and older adult females of remaining in the population. They are calculated as:

$$SF_A = [NF_{A(f)} + NF_{A(m)} + NF_{A(\cdot)}NF_{A(e)}]/NF_{A(t)} \quad \text{and} \quad (3a)$$

$$SF_O = [NF_{O(f)} + NF_{O(m)} + NF_{O(\cdot)}NF_{O(e)}]/NF_{O(t)}, \quad (3b)$$

where NF is the number of females in each subscripted category and $A(t)$ represents all prime-aged adult females, $O(t)$ represents all old adult females, $A(f)$ represents prime-aged adult females that produced a female calf, $A(m)$ represents prime-aged adult females that produced a male calf, $A(\cdot)$ represents prime-aged adult females that did not breed, and $A(e)$ represents adult females that emigrated. Note that no females who produced a calf emigrated in that year, and immigration into the population is negligible (Clutton-Brock et al. 2002). Our motivation in defining SF_A and SF_O as we did was to allow the possibility that selection operates through a survival cost of reproduction.

A

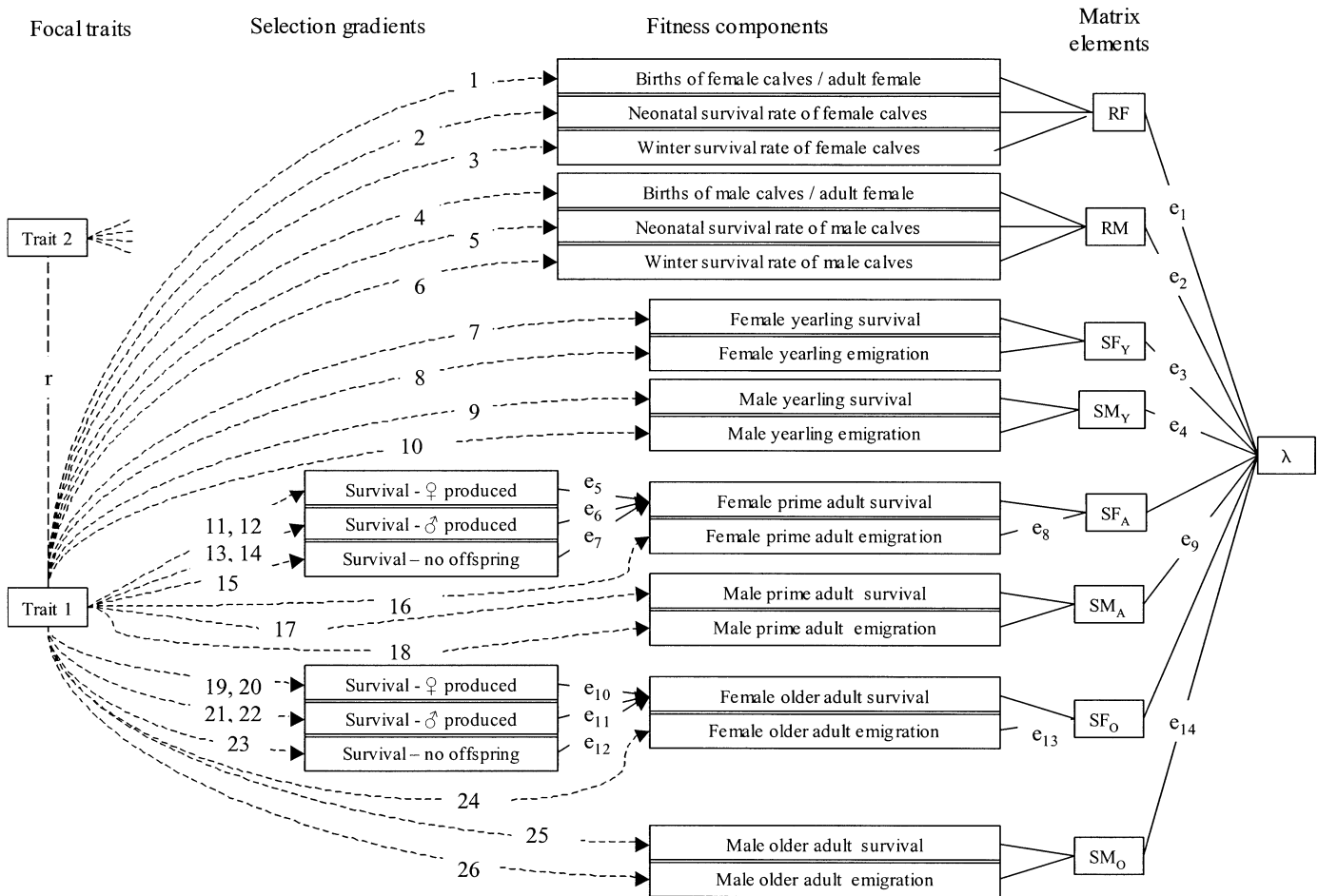


FIG. 1. Elasticity path diagram or elastogram demonstrating the association between traits, fitness components, matrix elements, and λ . Solid lines without arrows represent elasticities of matrix elements and fitness components of λ , which are labeled with an e and a subscripted number. Dashed lines with arrows represent selection gradients between focal traits and fitness components and are labeled with a number. Each number also represents a unique path, and each unique path represents an elasticity of the focal trait of λ via a fitness component. All paths between focal trait 1 and λ are represented; identical paths exist for focal trait 2 but for clarity are not displayed. The vertical dashed line labeled r, represents the correlation between focal traits 1 and 2. (A) The elastogram used for estimates of selection using data for the whole study and for the three periods 1974–1980, 1981–1990, and 1991–2000. Setting trait 1 to birth weight, selection gradients are: (1) female’s (> 2 years old) birth weight against probability of producing a female calf (Clutton-Brock et al. 1987); (2) female calf birth weight against neonatal survival; (3) female calf birth weight against survival from October 1 to May 15 $t + 1$ (Coulson et al. 1997); (4–6) as (1–3) but for male offspring; (7) birth weight against female yearling survival (Clutton-Brock and Coulson 2002); (8) birth weight against female yearling emigration; (9–10) as (7–8) but for males (Clutton-Brock et al. 2002); (11) mother’s birth weight on survival of prime-aged mother’s that produced a female calf; (12) calf’s birth weight on survival of prime-aged mother’s that produced a female calf; (13–14) as (11–12) but for prime-aged mother’s who produced male calves (Clutton-Brock et al. 1982); (15) birth weight on prime-aged survival of females who did not breed; (16) birth weight on emigration of prime-aged females; (17) birth weight on prime-aged male survival; (18) birth weight on prime-aged male emigration (Clutton-Brock et al. 2002); (19–26) as (11–18) but for older adults. References represent previous work on red deer suggesting these associations are significant and therefore should be considered in the HDS framework. (B) The simplified elastogram used to estimate selection in each year (see text for description of simplification from the elastogram in Fig. 1A).

We were able to use this framework to construct one matrix model for the whole study period (1974–2000) and one for each decade of the study (1974–1980, 1981–1990, 1991–2000) to explore whether the strength of selection differed between periods when the population was increasing (1974–1980), had recently reached ecological carrying capacity (1981–1990), or had been at carrying capacity for at least a generation (1991–2000). Sample sizes of older males and older females were insufficient in many years to use this framework to estimate selection for annual time steps to ex-

plore interannual variation in selection pressures. Consequently, we simplified the population model by merging the prime and older adult age classes.

Calculation of Elasticities

Elasticities of a matrix element of λ (de Kroon et al. 2000; Caswell 2001) are defined as $\delta \log \lambda / \delta \log a_{rc}$, where a_{rc} is the value of the matrix element in row r and column c and were calculated for each matrix element (e.g., RF, RM, \dots ,

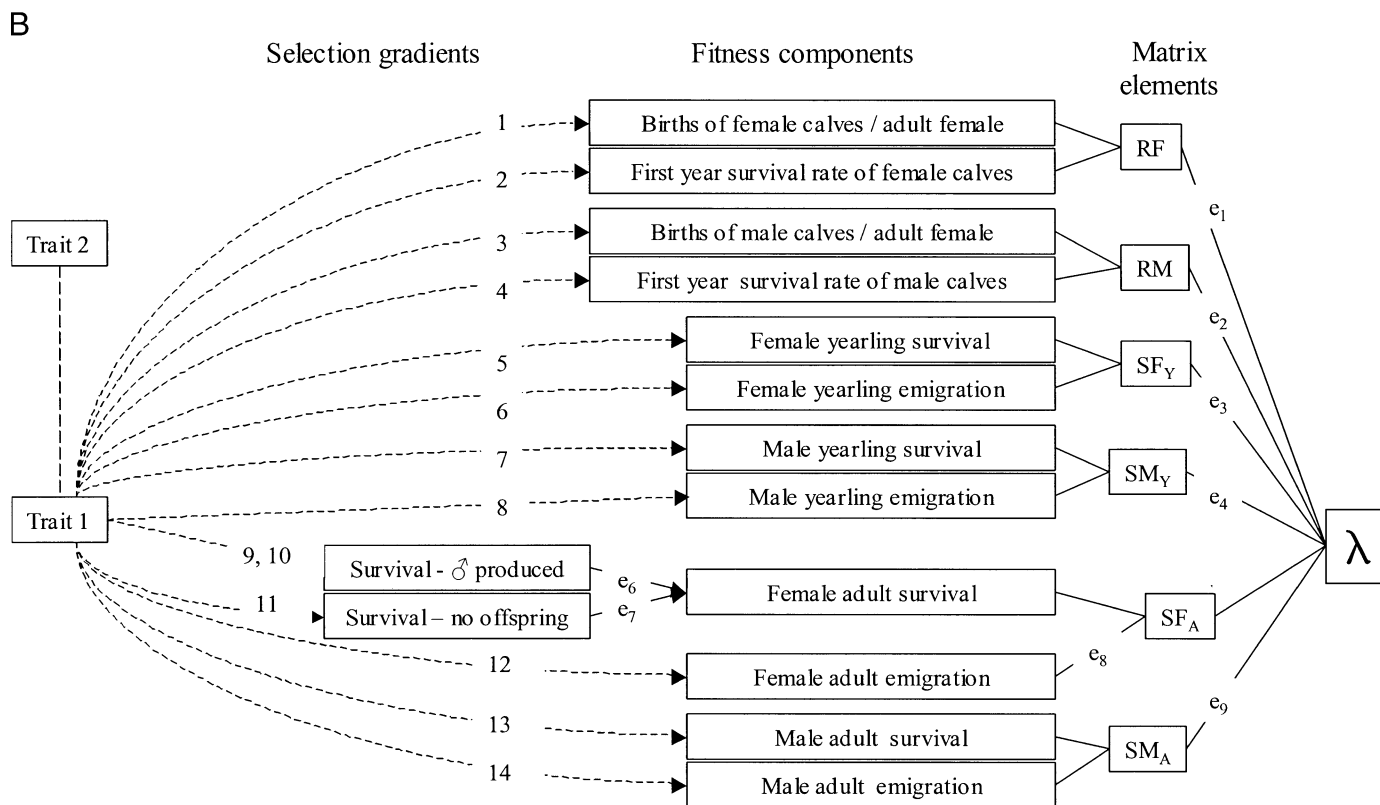


FIG. 1. Continued.

SM_O). The elasticities of matrix elements were used to estimate elasticities of fitness components. For transition matrices for the whole time series (1974–2000) and for each decade (1974–1980, 1981–1990, and 1991–2000) elasticities were calculated analytically assuming the stable age- and sex-structure (de Kroon et al. 2000; Caswell 2001). For transition matrices calculated for each year, the assumption of the stable age- and sex-structure was relaxed, with elasticities estimated using the observed age- and sex-structure by perturbing each matrix element independently (Caswell 2001).

When a matrix element is simply the product of two or more fitness components (e.g., RF , RM , SM_A , and SM_O), the elasticities of these fitness components of λ are the same as the elasticity of the matrix element of λ . When matrix elements involve the addition of different fitness components (e.g., SF_A , SF_O), we decomposed the elasticity of the matrix element into the contribution of each fitness component to the matrix element using the chain rule (Caswell 2001, p. 232).

Estimation of Selection Gradients

Selection gradients on a mean standardized scale were calculated between each fitness component and each focal trait using multiple linear regression analysis. Prior to each analysis, fitness components and traits were standardized by dividing through by their respective means. Because data representing fitness components in these analyses were binary, linear model regression fits did not fit the data well, making estimates of significance problematic. Estimates of signifi-

cance were calculated from logistic regressions of the non-standardized fitness components (Mitchell-Olds and Shaw 1987; McCullagh and Nelder 1989; Crawley 2002). In the few cases (in analyses for each year) where the logistic regression analyses failed to converge, selection gradients were set to zero and P -values to unity.

Selection gradients for birth weight and birth date were estimated by including both traits in the multiple linear regression analyses. Independent variables other than the focal traits fitted in the multiple linear regressions were year as a factor (when more than one year was included in estimates of selection), age (for adult survival and emigration within each age class of the population model) and mother's reproductive status (for birth rate, neonatal survival, and winter survival).

Linking Elasticities of Fitness Components of λ with Selection Gradients

Selection gradients and elasticities of fitness components of λ can be linked in a path diagram known as an elastogram or elasticity path diagram (Van Tienderen 2000), which incorporates all paths between the focal trait and λ (Fig. 1). Elasticities of a trait of λ via a specific fitness component (i.e., via each path) are calculated by multiplying the selection gradient for the trait on a fitness component by the elasticity of the fitness component of λ . Selection on a trait is found by summing the product of all paths between the focal trait and λ .

After simplifying the population model (see Population Model section), we also reduced the number of selection gradients estimated by combining some fitness components. Specifically, we combined neonatal survival and winter survival for each sex to generate first year survival for males and females and we pooled female adult survival into those that produced a calf (regardless of the calf sex) and those that did not. By doing this we generated two elastograms, the full elastogram with 26 selection gradients that was used to estimate selection on birth weight and birth date for the whole study period (1974–2000) and for each of the three periods 1974–1980, 1981–1990, and 1991–2000 (Fig. 1a) and the simplified elastogram with 14 selection gradients to estimate selection for each year (Fig. 1b).

Phenotypic correlation between focal traits can be incorporated into estimates of selection using elastograms (van Tienderen 2000), by estimating the proportional change in a trait resulting from a proportional change in another trait with which it is correlated. These values are linear regression estimates from mean standardized data. If the estimate of selection on traits *A* and *B* is *x* and *y*, respectively, then selection on *A*, including its correlation with trait *B* is $x + cor(x,y) \times y$ where $cor(x,y)$ is the slope between mean standardized values of *x* and *y* from a linear regression.

Analyses of Factors Affecting Selection

Once selection on birth weight and birth date was estimated for each year of the time series using the elastogram in Figure 1b, temporal variation in selection was analyzed using general linear models to explore how population density (linear and quadratic, detrended and not) and climatic variables influenced selection (McCullagh and Nelder 1989).

Estimates of the Expected Response to Selection

The expected response to selection per generation on a mean standardized scale is the product of selection per generation multiplied by the additive genetic variance of the mean standardized trait (the trait's evolvability; Houle 1992; Van Tienderen 2000). We estimate generation length as the average age of breeding females over the full course of the study. The additive genetic variance of the mean standardized trait values were estimated from pedigree data using the animal model in the program VCE (Groeneveld 1995). We do not give further details of these methods as their application to our data has been published elsewhere (Kruuk et al. 2000, 2002).

RESULTS

Temporal Trends in Trait Values

Birth date has gotten significantly earlier over the course of the study, even following correction for environmental and phenotypic covariates. In contrast, there is little evidence that birth weights have significantly changed. These results provide correlational evidence suggesting birth date may have responded to selection.

The most parsimonious linear mixed effects model of birth date with mother's identity fitted as a random factor contained mother's reproductive status, mother's age (quadratic), total September–December precipitation during gestation, popu-

lation size of adult females, and year as fixed effects (Table 1a). Birth date has on average decreased by 0.37 days/year, corresponding to a change in mean birth date by approximately 10 days over the course of the study. This model (AIC = -3108.22) outperformed a model with year fitted as a categorical fixed effect instead of total September–December rain (AIC = -3115.64), demonstrating that the weather covariate we identified captures much interannual environmental variation associated with birth date.

In a linear mixed effects model of birth weight with mother's identity fitted as the random factor and mother's age (quadratic), mother's reproductive status, calf sex, year of birth (continuous variable), and average temperature between February and March, there was no evidence of a significant temporal trend in birth weights (Table 1b).

Estimates of Selection: All Years Combined

Each elasticity of a trait of λ is labeled with a unique integer (1 to 26 in Fig. 1a). Different elasticities of a trait can operate through the same matrix element. For example, the elasticity of trait 1 of λ via the path labeled 4 refers to: (1) the selection gradient estimated from the regression of whether adult females gave birth to a male calf or not against the values of trait 1 for the adult females; (2) the elasticity of the birth rate of adult females to male calves of matrix element *RM*; and (3) the elasticity of matrix element *RM* of λ (elasticity e_2). Similarly, the elasticity of trait 1 of λ via the path labeled 5 refers to: (1) the selection gradient between neonatal survival of male calves and their values of trait 1; (2) the elasticity of male neonatal survival of matrix element *RM*; and (3) the elasticity of matrix element *RM* of λ (again, elasticity e_2). The different selection gradients are described in the legend to Figure 1a. Those solid lines that are not labeled all have an elasticity of one because the matrix elements are simply products of the constituent fitness components (see above; Van Tienderen 2000; Caswell 2001).

We demonstrate how to interpret our results and link Figure 1a to Figure 2a–c using another elasticity of trait 1 of λ as an example. The path we chose is path 6 in Figure 1a, which represents: (1) the selection gradient between trait 1 and winter survival of male calves; (2) the elasticity of winter survival of male calves on matrix element *RM*; and (3) the elasticity of *RM* of λ (elasticity e_2). The value of elasticity e_2 is 0.086 (see arrow in Fig. 2a), the value of the selection gradient when trait 1 is birth weight is 0.657 and when trait 1 is birth date is -1.568 (Fig. 2b also highlighted by arrows). Finally, the elasticity of trait 1 of λ when trait 1 is birth weight is $0.657 \times 0.086 = 0.0565$ (Fig. 2c highlighted by an arrow) and when trait 1 is birth date is $-1.568 \times 0.086 = -0.135$ (Fig. 2d highlighted by an arrow).

Elasticities of matrix elements of λ and elasticities of fitness components of λ are displayed in Figure 2a. SF_A and SF_O are the sum of multiple elasticities of fitness components of λ because we incorporate reproductive costs of survival. Matrix elements SF_A (e_5 to e_8) and SF_O (e_{10} to e_{13}) have the largest elasticities. Fitness components associated with adult female and adult male survival and emigration had the highest elasticities.

Selection gradients (represented by the dotted lines in Fig.

TABLE 1. Results from a linear mixed effects model of (a) birth date and (b) birth weight.

(a) Birth date				
Random effects				
Mother's identity	Intercept	Residual		
SD	0.03653	0.071945		
Fixed effects				
	Value	SE	<i>t</i>	<i>P</i>
Intercept	5.5669	0.9969	5.5844	<0.0001
Mother's reproductive status				
First time breeder	0.0000			
Milk hind	0.0072	0.0043	1.6600	0.0970
Summer yield	-0.0187	0.0022	-8.4687	<0.0001
True yield	-0.0051	0.0013	-3.7650	<0.0001
Winter yield	0.0091	0.0014	6.6632	<0.0001
Mother's age	-0.0119	0.0042	-2.7975	0.0050
(Mother's age) ²	0.0008	0.0002	3.6177	<0.0001
No. females > 12 months	0.0004	0.0001	3.2383	<0.0001
Precipitation (Sep-Dec)	0.0001	0.0000	5.4743	<0.0001
Year	-0.0024	0.0005	-4.6935	<0.0001
Birth weight	0.0522	0.0114	4.5956	<0.0001
No. observations	1486			
No. groups	399			
(b) Birth weight				
Random effects				
Mother's identity	Intercept	Residual		
SD	0.125964	0.144854		
Fixed effects				
	Value	SE	<i>t</i>	<i>P</i>
Intercept	2.1690	1.9145	1.1329	0.2575
Mother's reproductive status				
First time breeder	0.0000			
Milk hind	0.0113	0.0093	1.2127	0.2255
Summer yield	0.0270	0.0048	5.5662	<0.0001
True yield	0.0135	0.0029	4.7323	<0.0001
Winter yield	-0.0141	0.0030	-4.6302	<0.0001
Mother's age	0.0556	0.0091	6.1192	<0.0001
(Mother's age) ²	-0.0033	0.0005	-6.9930	<0.0001
Mean temp (Feb-Apr)	0.0393	0.0062	6.3906	<0.0001
Sex				
Female	0.0000			
Male	0.0254	0.0042	5.9737	<0.0001
Birth date	0.2813	0.0549	5.1224	<0.0001
No. observations	1486			
No. groups	399			

1a) were steepest for fitness components associated with the recruitment of calves into the population (*RM* and *RF*) and flattest for fitness components associated with adults remaining within the population, and this pattern held for both birth weight and birth date (Fig. 2b,c). Either one or both of the focal traits (birth weight or birth date) was significantly associated with neonatal survival, calf winter survival, and yearling survival of males and females. Selection gradients between the focal traits and fitness components comprising the probability of prime-aged and older adult females and males remaining in the population tended to be nonsignificant.

Those paths with large elasticities consequently tended to have small selection gradients. When only the significant selection gradients were considered, the negative correlation between elasticities and selection gradients were significant for birth date ($F_{1,8} = 5.372$, $r^2 = 0.41$, $P = 0.046$) and for birth weight ($F_{1,8} = 6.898$, $r^2 = 0.46$, $P = 0.034$).

The elasticities of focal traits of λ (the product of the selection gradient and elasticity encountered on each path from the focal trait to λ) varied between paths (Fig. 2c,d). The majority of the paths describing the elasticities of birth date of λ were negative (Fig. 2c), suggesting an advantage to being born earlier in the year. Paths associated with *RM* and *RF* had the most negative elasticities (Fig. 2c) and tended to have significant selection gradients. There was only one significant positive path, and that was for adult males not emigrating: those animals born relatively late in the calving season were less likely to emigrate as adults. The elasticities of birth weight of λ tended to be positive (Fig. 2d), meaning being born heavy was a good thing. The only significant negative path was path 14, the influence of the birth weight of male calves on the survival of prime-aged adult females; those animals that produced a heavy male calf were more likely to die.

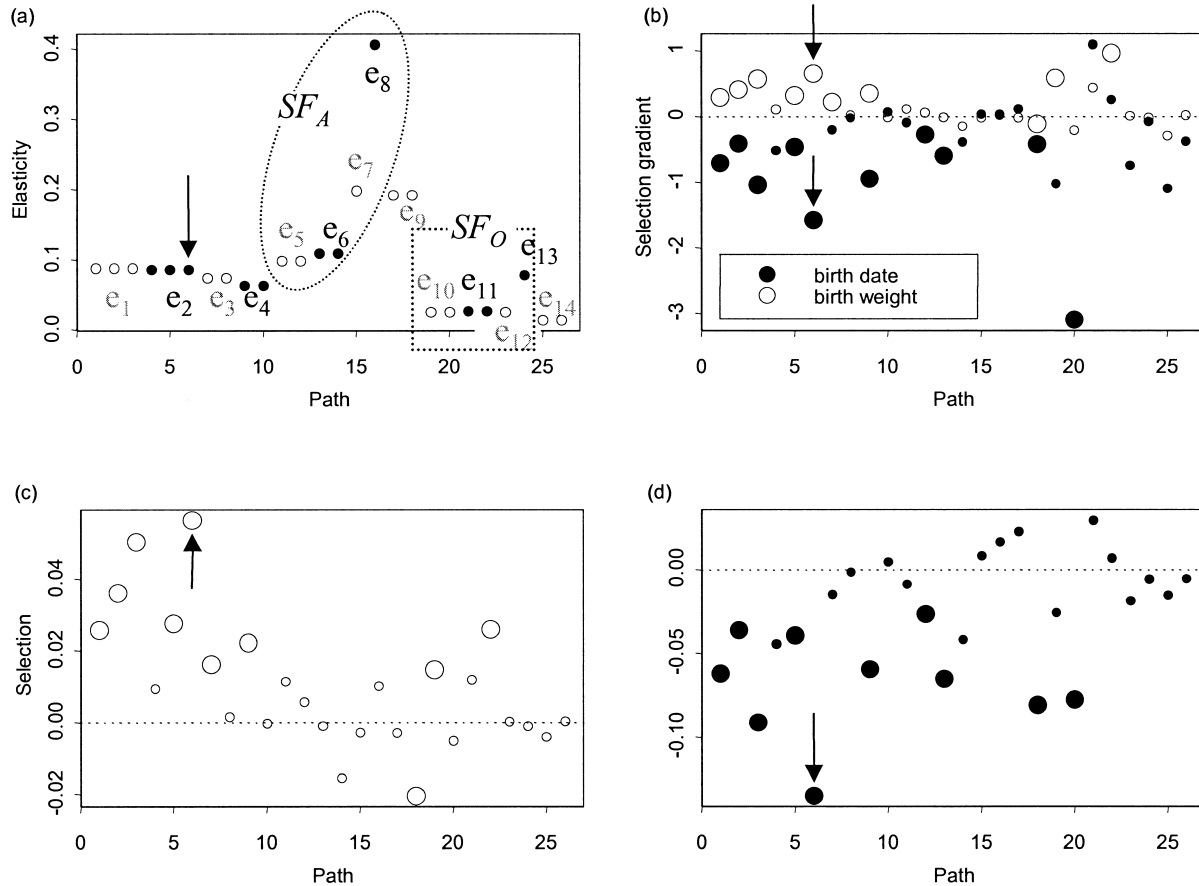


FIG. 2. Results from the analysis of selection using the entire dataset (1974–2000). (a) Plots of the values of elasticities against the path number for the elastogram for the full dataset (Fig. 1a). The x-axis represents each of the unique paths highlighted in Figure 1a. The elasticities of the matrix elements are marked in alternating open and filled circles. For example, the first three paths all have the same elasticities for the fitness component of λ (e_2), which corresponds to matrix element *RF* (see Fig. 1). Dotted lines group together the elasticities of fitness components of λ for those matrix elements in which the elasticities of fitness components are not simple products. (b) The values of the selection gradient for each path for birth weight and birth date. Larger symbols represent significance at $P < 0.05$, small symbols nonsignificance. The contribution of each path to overall selection for (c) birth weight and (d) birth date. As in (b) symbol size represents significance or not at $P < 0.05$. The arrows highlight the values of elasticities (in a), selection gradients (in b) and the strength of selection on birth weight (in c) and birth date (in d) via path 6 in Figure 1A (see text).

Selection on birth weight estimated from the elastogram (i.e., the sum of the elasticities of birth weight of λ) was 0.242 when we considered only selection gradients that were significant at $\alpha = 0.05$. This means that an increase in mean birth weight of 1% would increase λ by 0.242%. Selection on birth date was -0.647 , meaning a 1% increase in mean birth date would result in a 0.647% decrease in λ . Including the significant correlations between birth weight and birth date (see Table 1) reduced selection on birth weight to $0.242 - (0.647 \times 0.2813) = 0.060$ and reduced selection on birth date to $-0.647 + (0.242 \times 0.0522) = -0.634$.

Estimates of Selection by Decade

Having estimated selection for the entire study period (1974–2000), we next examined whether selection had varied over the course of the study. Estimates of selection for 1974–1980, 1981–1990, and 1991–2000 were broadly consistent in that selection on birth date was always negative and on birth weight was always positive (Table 2). Selection was always greater for birth date than birth weight. Although the

values of elasticities of matrix elements of λ were remarkably similar among periods (Fig. 3), the dominant elasticities of our focal traits of λ varied between periods (Table 2). Although selection typically operated strongest through first winter survival, both yearling and prime adult survival also influenced selection in some decades.

Estimates of Selection by Year

Next we generated a time series of selection on birth weight and birth date by estimating selection for each year of the study. Due to sample size restrictions we were unable to use the full model, so we simplified the elastogram from Figure 1a to Figure 1b. The full and simplified elastograms gave similar estimates of selection using the whole dataset and the datasets for each period. For example, the value for selection on birth weight was estimated at 0.242 from the full model and 0.229 from the simplified model, and selection for birth date was estimated at -0.647 from the full model and -0.750 from the simplified model.

The time series of selection on birth date is shown in Figure

TABLE 2. Summary of results for analyses of the three separate periods 1974–1980, 1981–1990, 1991–2000. Estimates of selection for birth weight and birth date are given, excluding the correlation between the traits. The correlation between the traits in each period are shown; bold values represent significance. Estimates of selection include the correlation between traits. Finally, the two most dominant paths through which selection operated are listed.

	1974–1980	1981–1990	1991–2000	All years
Selection				
birth weight	0.075	0.139	0.430	0.242
birth date	-0.356	-0.334	-0.465	-0.647
Correlation	0.095	0.205	0.247	0.207
date-wt	0.022	0.037	0.037	0.0347
birth weight	0.041	0.070	0.315	0.108
birth date	-0.349	-0.306	-0.449	-0.639
Selection including trait correlations	birth rate male calves, winter survival male calves	winter survival male calves, winter survival female calves	neonatal survival female calves, winter survival female calves	winter survival male calves, winter survival female calves
Dominant paths	birth rate male calves, winter survival male calves	winter survival male calves, winter survival female calves	winter survival male calves, winter survival female calves	winter survival male calves, winter survival female calves
	birth date	winter survival male calves, winter survival female calves	winter survival male calves, prime female survival—calf birth weight	winter survival male calves, winter survival female calves

4a. The temporal variation is due to variation in both the size of the elasticities of each fitness component of λ and the selection gradients. Selection fluctuates considerably between years: in six of the 26 years there was no significant selection on birth date, in 17 of the remaining 20 years it was negative, and in 1994, 1997, and 2000 it was significantly positive. Mean birth date was significantly earlier during the later part of the study than in earlier years (see above), hinting that the strength of selection may be declining, although a linear trend through these data was not quite significant ($F_{1,24} = 4.225$, $P = 0.051$). Selection on birth date was strongly positive in 2000 because of a strong significant selection through birth rate—those females born later were significantly more likely to reproduce in 2000 than those born earlier. This result remained significant following bootstrapping, although it is unclear how to interpret this result. Incorporating the weak but significant correlation between birth date and birth weight (see above) had virtually no impact on selection on birth date (the two lines in Fig. 4 are indistinguishable). Mean selection on birth date over this period (averaging the time series) was -0.229 (SD = 0.524).

Selection on birth weight also fluctuated considerably between years. Birth weight was selectively neutral in six of 26 years, significantly positive in 17 years, and significantly negative in 1977, 1981, and 1998. When the positive covariation with birth date was included in estimates of selection, the time series of selection on birth weight changed (Fig. 4b). Positive selection on birth weight was observed in 12 years, negative values in 10 years, and zero values in the remaining four years. Mean selection on birth weight over the period (averaging the time series) was 0.042 (SD = 0.244).

In all years, with the exception of 1975 when SM_A had the highest elasticity, SF_A had the largest elasticities. However, the path that contributed the most to the estimates of selection varied greatly between years (Table 3).

Environmental Covariates Affecting Selection

There was no significant effect of population density (linear or quadratic, detrended or not) or any weather covariates in either the current year or in the previous year on the time series of selection of either birth date or birth weight. For brevity we do not report these nonsignificant results, but all P -values were greater than 0.2.

Expected Response to Selection

We estimated additive genetic variation for mean standardized (evolvability; Houle 1992) birth weight as 0.005, for mean standardized birth date as 0.050, and their covariation as 0.002. Generation length was estimated as 7.98 years (the average age of breeding females between 1974 and 2000). Because our study was 26 years in length, we estimate the response to selection of birth date over the study as the product of the evolvability ($26/[7.93 \times 0.05]$) and selection (-0.229 averaged over the time series) plus the product of the evolvability of birth weight over the study ($26/[7.96 \times 0.005]$) and selection on birth weight (0.042 averaged across the time series) and the genetic covariance between birth weight and birth date (0.002). This gives us an estimate of

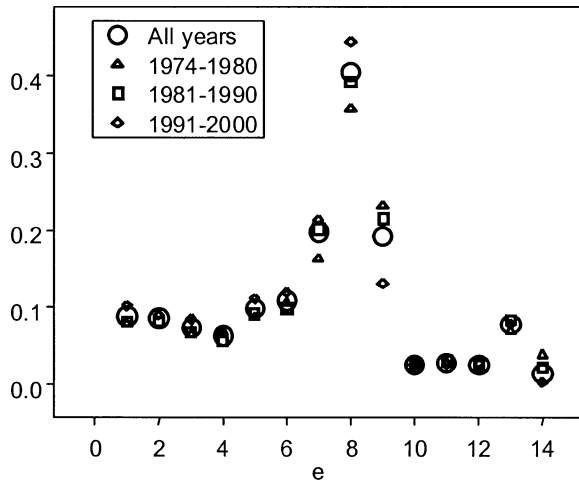


FIG. 3. The value of elasticities e_1 to e_{14} in Figure 1a for the whole study period and for the three periods 1974–1980, 1981–1990, and 1991–2000.

the expected response to selection of birth date as -0.0371 averaged across the time series. The observed response to selection is -0.0024 per year (the slope of year in the birth date model in Table 1a), giving an observed response to selection over the study period of $-0.0024 \times 26 = -0.0624$ (95% CI = -0.0369 to -0.08788); which just encompass our estimate of the response to selection from averaging across the time series. A preliminary analysis of breeding values for both traits supports the rather crude estimates of the responses to selection reported above (L. E. B. Kruuk, unpubl. data).

DISCUSSION

In this paper we apply a method recently described by Van Tienderen (2000) to parameterize the Lande (1982) model of selection, which estimates selection gradients between a focal trait and multiple fitness components; estimates the impact of each fitness component on the population growth rate, λ , using elasticities; and combines these estimates to measure selection across the life cycle. We show that our estimates of the observed changes in trait values that we cannot explain with phenotypic or environmental covariates and the expected response to selection are remarkably similar. Selection fluctuates over time and can operate through multiple fitness components in any one year. The fitness component most strongly correlated with selection varies between years, and no environmental covariates correlate with selection, presumably because different fitness components respond to density and climatic variation in contrasting ways.

Many studies using selection gradients only consider a gradient between a trait and one fitness component (e.g., Kingsolver et al. 2001). The HDS approach is appealing as it allows multiple selection gradients between a trait and multiple fitness components to be combined (Lande 1982; Van Tienderen 2000). One drawback of considering only one fitness component is that selection may act simultaneously through more than one fitness component, possibly across generations. For example, there may be advantages to both an offspring and a parent of the offspring being born heavy,

but there may also be a survival cost to a mother of raising a heavy offspring if it reduces her probability of reproducing in the future. We incorporate the possibility for selection to operate simultaneously through multiple fitness components across generations by considering age-specific survival probabilities as a function of whether a female bred or not and by estimating selection gradients between a breeding female's survival probability and both her and her offspring's birth weight and date. Our results (Fig. 2c,d) demonstrate that indeed selection can operate simultaneously via multiple paths and that the direction of selection (the elasticity of a trait of λ) can vary across fitness components. So, although selection is generally expected to act to increase birth weight if any individual path is considered, the strength of selection does vary across paths and in one case acts significantly in an opposing direction (Fig. 2). Only considering selection between a trait and one fitness component runs the risk of generating a biased estimate of selection. Given Lande's (1982) framework and Van Tienderen's (2000) demonstration of how to apply the framework, it is now feasible and comparatively easy to estimate selection across multiple fitness components assuming sufficient data exist.

A second appealing feature of the HDS approach is that it allows temporal variation in selection to be explored across multiple fitness components. Selection can be decomposed into the contribution from all elasticities of a trait of λ via each fitness component incorporated into the analysis both within and between years. One advantage of this approach is it allows exploration of the possibility that selection on a trait may vary over an individual's life span both within and between fitness components—possibly as a function of environmental conditions—and enables selection to be decomposed into contributions from different age groups. For example, in some years there may be positive selection for producing an offspring born early in the year acting through survival of the offspring, whereas in other years there may be no advantage of producing an offspring that is born early in the year. Although estimates of selection between a trait and surrogates of individual fitness such as individual λ -values and lifetime reproductive success (Brommer et al. 1998; Korpelainen 2000; Kruuk et al. 2000; Kirk et al. 2001) do estimate selection across all fitness components, they do not allow a simple decomposition into contributions from different fitness components, nor do they allow an exploration of temporal variation in selection pressures during an individual life span. Furthermore, the ability of these surrogate measures to really capture individual fitness is questionable (Grafen 1988; Benton and Grant 2000). The ability to explore temporal variation in fitness and whether the relative importance of different elasticities of a trait of λ fluctuated with time proved illuminating in our analyses. In some years the largest elasticity of birth date of λ operated through calf winter survival, in other years through yearling survival, and in yet other years through the survival of females that produced a calf (Table 3). The result that selection operates via different paths in different years is not surprising. Different fitness components, which are associated with birth weight or birth date, are associated with density and weather in contrasting ways. For example, the birth rate is associated with density in the year of conception (Albon et al. 1983), whereas first winter survival is associated with density in the year of birth (Coulson

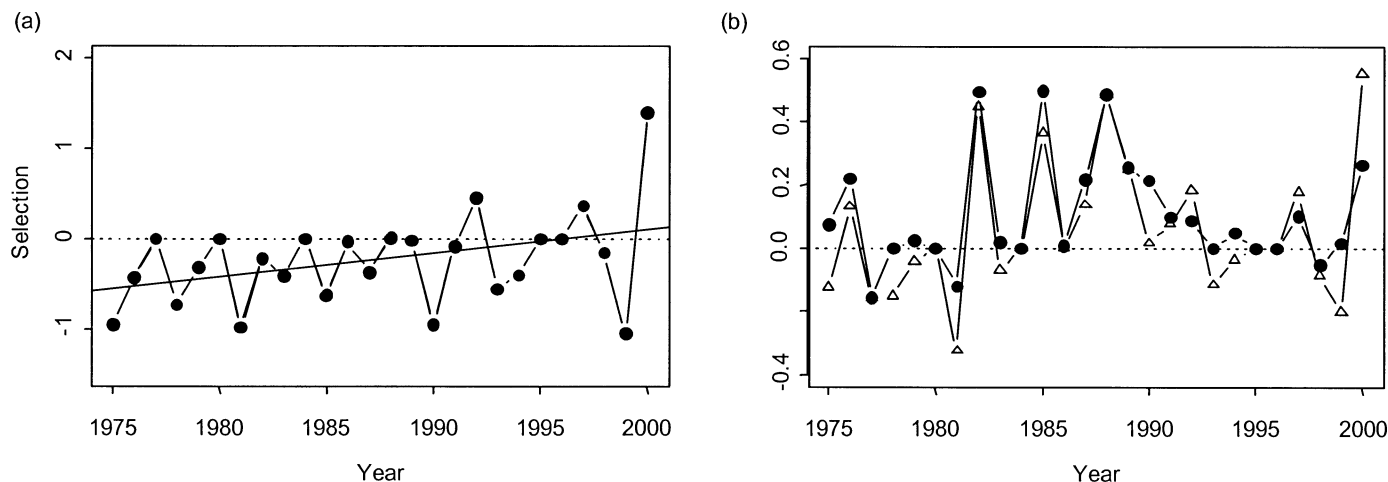


FIG. 4. Time series of selection estimated for each year from the elastogram in Figure 1B for (a) birth date and (b) birth weight. Solid lines and filled circles represent selection ignoring the correlation between traits; solid lines and open triangles represent selection incorporating the correlation between traits.

et al. 1997). Similarly, the birth rate is associated with January-to-March temperature in the winter prior to birth (Coulson et al. 2000), calf winter survival with total precipitation between October and January (Coulson et al. 1998), and adult survival with the North Atlantic Oscillation (Fan et al. 2003). The influence of population density and climatic variables on selection will vary from year to year as a function of climate variability within a year and this will influence which paths most strongly influence selection.

The absolute strength and direction of selection fluctuated greatly from year to year for both of our traits (Fig. 4). This was a function of which fitness components were most strongly associated with selection, which in turn are likely to be a result of within-year environmental conditions. For example, if January-to-March temperatures are low, selection may act on the birth rate as many females give birth. However, if rainfall between October and January is high, selection may be expected to act through calf survival, as calf survival is low in years of high rainfall. The variation in the fitness components that contributed most to selection over time, and the observation that different fitness components are affected to different extents and in different ways by environmental conditions, makes it unsurprising that we were unable to find a single environmental covariate that was associated with variation in selection. In our study, selection is a complex phenomenon operating via multiple fitness components in different ways in different years. We have no reason to believe that this complexity is unique to our study system.

Despite the complexity underlying selection and temporal fluctuations in the strength and direction of selection on each trait, we still observed significant directional selection over the study period for earlier birth date. We also observed a significant decrease in birth date over the course of the study that we could not explain with environmental or ecological variables. Our estimate of the response to selection was similar to the observed change in birth date, suggesting an evolutionary response. Although further research is required to examine trends in breeding values (Falconer and Mackay

1996; Merilä et al. 2001; Kruuk et al. 2002), this is correlational evidence that selection has been realized. In contrast, we did not see any persistent significant directional selection on birth weight over the course of the study. However, there was also no significant change in birth weight over the course of the study, again suggesting that our estimate of the strength and expected response to selection (i.e., none) has been realized. We believe this lends support for the utility of the HDS method, although it is possible that the addition of more phenotypic traits into the analyses could alter results.

The HDS approach does require the identification of a model of λ and the fitness components that should be included (Lande 1982; Van Tienderen 2000). This was relatively straightforward for the red deer study, as there has been considerable research identifying age and sex variation in fitness components (Clutton-Brock et al. 1982, 1987, 1997; Albon et al. 1986; Coulson et al. 1997, 2000; Kruuk et al. 1999a) and demonstrations that birth weight and date can affect a range of fitness components and lifetime reproductive success (Clutton-Brock et al. 1982, 1987; Coulson et al. 1999; Kruuk et al. 1999b). We used this biological understanding to guide our choice of fitness components and selection gradients. The elastograms are complex, but we ensured we had sufficient data to permit sensible linear regression fits (i.e., > 10 points in all cases and often > 50 points). We believe that the good correspondence between observed changes in trait values and the predicted response to selection support our choice of model. In other studies the choice of model of λ may be more difficult, although matrix models have proved useful in describing the dynamics of many vertebrate populations. However, several other ungulate studies have sufficient data to use these methods (Festa-Bianchet et al. 1995; Gaillard et al. 1998, 2000). In cases where data exist on individual sizes, and where size may be a better predictor of survival, dispersal, and reproduction, then integral projection models may provide a better modeling framework (Easterling et al. 2000).

There are assumptions behind the HDS approach that Van Tienderen (2000) discusses. Probably the most important as-

TABLE 3. The dominant path and fitness component via which selection operated in each year. The path number represents the selection gradients in Figure 1b, the sign of selection gradient represents a positive or negative slope between birth date or birth weight, and the fitness component and N (sig selection gradients) represents the number of significant selection gradients in each year. There were insufficient data in 1974 to estimate selection.

Year	Birth date				Birth weight			
	Vital rate	Path number	Sign	N (sig selection gradients)	Vital rate	Path number	Sign	N (sig selection gradients)
1975	prime survival of females who bore a calf	10	+	3	prime survival of females who bore a calf	10	-	3
1976	first year female survival	2	-	3	first year female survival	2	+	2
1977					adult male survival	13	-	1
1978	first year male survival	4	-	2				
1979	prime survival of females who bore a calf	10	-	2	survival of females who bore a calf	10	-	3
1980								
1981	yearling female survival	5	-	3	yearling female survival	3	+	1
1982	first year male survival	4	-	1	adult male emigration	14	-	4
1983	first year female survival	2	-	2	survival of females who did not breed	11	+	2
1984								
1985	first year male survival	4	-	1	first year male survival	4	+	2
1986	first year female survival	2	-	2	survival of females who did not breed	11	+	1
1987	first year male survival	4	-	2	first year male survival	4	+	1
1988					survival of females who bore a calf	10	-	3
1989	yearling male emigration	8	-	1	survival of females who bore a calf	9	+	1
1990	first year male survival	4	-	3	first year female survival	2	+	4
1991	yearling male emigration	8	-	1	first year female survival	2	+	3
1992	prime male survival	13	+	2	first year male survival	4	+	1
1993	first year male survival	4	-	2				
1994	prime survival of females who bore a calf	9	-	1	first year male survival	4	+	2
1995								
1996								
1997	first year male survival	4	+	2	first year male survival	4	+	1
1998	first year female survival	2	-	4	survival of females who bore a calf	10	-	4
1999	prime survival of females who bore a calf	9	-	3	survival of females who did not breed	11	+	1
2000	birth rate of male calves	3	+	3	first year male survival	4	+	1

sumption we make is of linearity (Lande and Arnold 1983; Caswell 2001). We are assuming that the association between a fitness component and λ is linear, and we do not report quadratic terms in our selection gradients. These assumptions could theoretically be relaxed, but previous work on the Rum red deer (Kruuk et al. 2002) has failed to find quadratic selection gradients between traits and fitness components. Another important assumption is reliance on the stable age- and sex-structure. Although we do assume this for analyses considering the whole time series and for analyses of each decade, we relax this assumption for analyses of each individual year.

The HDS approach has advantages over estimates of selection based on the association between one trait and one fitness component or a surrogate measure of individual fitness (Kingsolver et al. 2001). Our analyses suggest that the change in trait values that we have observed over the course of the study are similar to the expected response to selection calculated as the product of our estimates of selection and additive genetic variation for birth date. The results also suggest that selection on a trait can operate via multiple paths si-

multaneously in one year and that the dominant path can vary between years. We believe that further application of the HDS method to analyses of selection will prove illuminating.

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