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NONPARAMETRIC ESTIMATION OF NATURAL SELECTION ON A QUANTITATIVE TRAIT USING MARK-RECAPTURE DATA

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Abstract.—Assessing natural selection on a phenotypic trait in wild populations is of primary importance for evolutionary ecologists. To cope with the imperfect detection of individuals inherent to monitoring in the wild, we develop a nonparametric method for evaluating the form of natural selection on a quantitative trait using mark-recapture data. Our approach uses penalized splines to achieve flexibility in exploring the form of natural selection by avoiding the need to specify an a priori parametric function. If needed, it can help in suggesting a new parametric model. We employ Markov chain Monte Carlo sampling in a Bayesian framework to estimate model parameters. We illustrate our approach using data for a wild population of sociable weavers (*Philetairus socius*) to investigate survival in relation to body mass. In agreement with previous parametric analyses, we found that lighter individuals showed a reduction in survival. However, the survival function was not symmetric, indicating that body mass might not be under stabilizing selection as suggested previously.

Key words.—Bayesian inference, Cormack-Jolly-Seber model, fitness function, individual covariates, penalized splines, random effects, WinBUGS.

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Evolutionary ecologists are often interested in describing and quantifying the action of selection on phenotypic traits in a natural population (Endler 1986; Hoekstra et al. 2001; Kinksolver et al. 2001). For this purpose, the multiple regression method of Lande and Arnold (1983) is a popular and powerful method to measure coefficients of directional and quadratic selection intensity. There are several well-known difficulties with this method. Perhaps the most important one is the problem of environmental covariances (Mauricio and Mojonner 1997; Kruuk et al. 2003). However, there are other caveats when interpreting coefficients of directional and quadratic selection intensity. In particular, inferring the form of selection (directional, stabilizing, or disruptive) from these coefficients may be difficult if the shape of the underlying fitness surface is not quadratic. As a consequence, estimating the shape of the fitness surface is an important step in describing selection pressure on phenotypic traits (Schluter 1988; Schluter and Nychka 1994), and it is useful in understanding how selection acts on combinations of traits and how traits may be modified directly or indirectly through their correlations (Lande and Arnold 1983).

This surface, or fitness function, relates survival or reproductive success of individuals to a set of phenotypic traits

(Lande 1979; Lande and Arnold 1983). The main difficulty in estimating this surface is that it may have any shape, including several peaks, valleys, and ridges. To overcome this problem, it is desirable to use a statistical method with few a priori constraints on the possible shapes. For this purpose, Schluter (1988) and Schluter and Nychka (1994) introduced the use of cubic splines, a flexible and general nonparametric method. In addition, fitness traits such as survival are often difficult to measure directly in the field because unobserved individuals can be either dead or alive but undetected (Clobert 1995). Kingsolver and Smith (1995) proposed using mark-recapture (hereafter MR) statistical methods to estimate fitness functions that relate survival to quantitative traits. Note that, following Schluter and Nychka (1994), we consider survival a surrogate of fitness, despite it being only a component of true fitness, and thus we use the general term “fitness” throughout (see also Cooch et al. 2002).

There is an elaborate set of methods to describe detection and survival probabilities from MR data (Lebreton et al. 1992; Williams et al. 2002). However, these methods are generally restricted to linear or quadratic fitness functions, and they have the same potential limitations of the original

Lande and Arnold (1983) method. Although this approach has proved useful in several cases (Kingsolver 1995; Srygley and Kingsolver 2000; Lorenzon et al. 2001; Altwegg and Reyer 2002; Conroy et al. 2002; Covas et al. 2002; Grégoire et al. 2004; Blums et al. 2005), a more flexible approach combining cubic splines with the MR methods would be valuable in helping to better understand the form of selection in natural populations.

In this paper, we develop a nonparametric method for evaluating the form of natural selection on a quantitative trait using MR data. We first formulate survival as a nonparametric regression function of a trait. We use Markov chain Monte Carlo (MCMC) sampling in a Bayesian framework to estimate model parameters. We illustrate our approach using data for a wild population of sociable weavers (*Philetairus socius*) to investigate survival in relation to body mass. Finally, we briefly discuss how this method may be adapted to take into account breeding values instead of phenotypic values and other individual covariates (e.g., age, sex). This method may be useful in a variety of situations in extracting as much information as possible from MR data.

MODEL DEVELOPMENT

A MR protocol consists of J encounter occasions at which a total of I animals are recaptured. On each occasion, new unmarked animals are given unique marks and then released. Previously marked animals can also be encountered, and after their identity is recorded, they are also released back into the population. This experiment results in a set of animal encounter histories, made up of 1 and 0 values depending, respectively, on whether an animal is detected or not (for reviews, see Lebreton et al. 1992; Williams et al. 2002). The inclusion of explicative variables in MR models was reviewed by Pollock (2002), who noted that a particular treatment was needed for individual covariates (see Skalski et al. 1993; Hoffman and Skalski 1995). Clobert (1995) discussed the use and potential of MR methods for evolutionary ecology. Kingsolver and Smith (1995) applied MR methodology to show evidence of natural selection on quantitative traits. We first specify the survival function under a nonparametric form and then form the likelihood for MR data. Because the combination of these two steps results in a complex multidimensional integral, an explicit formula would be intractable. However, with the improving capacities of recent computers, the use of computational intensive algorithms now offers a solution for tackling such complex problems, especially in the analysis of data arising from marked animals (for a review see Brooks et al. 2000). We thus opt for MCMC methods (e.g., Gilks et al. 1996) for estimating model parameters, and we conduct the analysis in a Bayesian framework using noninformative priors.

Nonparametric Regression of Survival Probabilities

We denote ϕ_{ij} as the probability that an animal i survives to time t_{j+1} given that it is alive at time t_j . We consider a nonparametric regression model for this survival probability of the form

$$\text{logit}(\phi_{ij}) = f(x_{ij}) + \varepsilon_{ij}, \quad i = 1, \dots, I \quad \text{and} \\ j = 1, \dots, J, \quad (1)$$

where x_{ij} is the value of the covariate for the i th individual at the j th sampling occasion, ε_{ij} are i.i.d $N(0, \sigma_\varepsilon^2)$, ε_{ij} is independent of x_{ij} , f is a smooth function, and $\text{logit}(x) = \log[x/(1-x)]$. Because the survival must lie between zero and one, the logit link is often preferred in equation (1) (but for a discussion see Kingsolver and Smith 1995). We used random effects ε_{ij} to cope with the residual variation in survival not handled by the covariate alone. Several alternatives are available to model the nonparametric relationship between the survival probability and the individual covariate specified by the function f , for example, loess smoothing (Cleveland and Devlin 1988), kernel smoothing (Silverman 1986), natural cubic splines (Schluter 1988), and multivariate adaptive regression splines (Friedman 1991; for reviews, see Hastie and Tibshirani 1990; Ruppert et al. 2003). In this paper, we opted for penalized splines (P-splines) introduced by Ruppert et al. (2003), because they can be easily implemented (Crainiceanu et al. 2005), allow straightforward extensions to several covariates that may enter the model linearly or nonlinearly (Gimenez et al. 2006), and automatically cope with several issues associated with the use of splines (see below). We used the truncated polynomial basis to model the smooth function

$$f(x|\eta) = \beta_0 + \beta_1 x + \dots + \beta_P x^P + \sum_{k=1}^K (b_k - \kappa_k)_+^P, \quad (2)$$

where $P \geq 1$ is the degree of the P-spline, $\eta = (\beta_1, \dots, \beta_P, b_1, \dots, b_K)^T$ is a vector of regression coefficients to be estimated, $(u)_+^p = u^p I(u \geq 0)$, and $\kappa_1 < \kappa_2 < \dots < \kappa_K$ are fixed knots. The problem in using equation (2) is the choice of the number and the position of the knots. A small number of knots may result in a smoothing function that is not flexible enough to capture variability in the data, whereas a large number of knots may lead to overfitting. A trade-off can be achieved by imposing a penalty, which attenuates the influence of the regression coefficients, and thus yields a smoother curve.

Technically, we first chose a fixed number of knots $K = (J/4, 35)$ that was large enough to ensure the desired flexibility (Ruppert 2002; Ruppert et al. 2003). We let κ_k be equally spaced sample quantiles, that is, the sample quantile of the x_{ij} values corresponding to probabilities $k/(K+1)$ (Ruppert 2002). Because the b_k values are the jumps in the second derivatives of the smooth function at the knots, a quadratic penalty is placed on b so that with equation (2) we associate the constraint $b^T b \leq \lambda$, where λ is the smoothing parameter (Ruppert et al. 2003). We note that equation (2) can be easily implemented in a mixed model framework (Ruppert et al. 2003), and in this context, imposing a roughness penalty is equivalent to considering the penalized regression parameters (the b_k values) as random, whereas the unpenalized coefficients (the β_p values) are treated as fixed. Considering this structure, the degree of smoothness is data driven and controlled by the smoothing parameter estimated as a by-product as $\lambda = \sigma_b^2/\sigma_\varepsilon^2$ (Ruppert et al. 2003). Once a minimum number of knots is reached, the fit given by a P-spline is nearly independent of the knot number and location (Ruppert 2002).

Mark-Recapture Data Likelihood

We consider the encounter history for individual i

$$h_i = (\delta_{i1}, \dots, \delta_{ij+1}), \tag{3}$$

where δ_{ij} denotes whether individual i is observed ($\delta_{ij} = 1$) or not ($\delta_{ij} = 0$) at time t_j . Then the likelihood component corresponding to individual i is given by

$$[h_i | \phi, p] \propto \left\{ \prod_{j=e_i}^{l_i-1} \phi_{ij} \right\} \left\{ \prod_{j=l_i+1}^{l_i} p_j^{\delta_{ij}} (1 - p_j)^{1-\delta_{ij}} \right\} \chi_{il_i} \tag{4}$$

(Skalski et al. 1993; Hoffman and Skalski 1995), where $[X]$ denotes the distribution of X , p_j , $j = 2, \dots, J + 1$, denotes the encounter probability of being detected at time t_j . We note e_i the occasion where individual i is captured for the first time; similarly l_i is an index for the last occasion where individual i is recaptured. We denote χ_{ij} the probability that animal i , alive at time t_i , is not subsequently encountered. This is calculated recursively as $\chi_{ij} = 1 - \phi_{ij}[1 - (1 - p_{j+1})\chi_{ij+1}]$, with $\chi_{ij+1} = 1$. Note that we adopt the convention that a null sequence has a product of one.

Assuming independence among individuals, the likelihood is the product of the probabilities of all individual encounter histories (Skalski et al. 1993; Hoffman and Skalski 1995) given by equation (4):

$$[h | \phi, p] \propto \prod_{i=1}^I h_i. \tag{5}$$

Implementation via Markov Chain Monte Carlo Methods

To estimate the model parameters, a frequentist approach would require maximizing the likelihood, which is obtained by integrating the distribution $[h|\phi, p]$ over the random effects ϵ_{ij} and b_k , involving a high dimensional integral. To overcome this difficulty, we make use of MCMC sampling (e.g., Gilks et al. 1996) in a Bayesian framework. The Bayesian analysis combines the likelihood (eq. 5) and prior probability distributions for the parameters and uses Bayes' theorem (Gilks et al. 1996) to obtain the posterior distribution as the basis for inference. The MCMC methods simulate values for the unknown quantities of interest following a Markov chain whose stationary distribution is the required posterior distribution. A burn-in period ensures that the Markov chain has reached its stationary distribution. Inference is then based on the remaining simulated values, by computing numerical summaries such as empirical medians and confidence intervals for quantities of interest.

To specify the Bayesian nonparametric model, we provide noninformative prior distributions for all parameters. Specifically, we chose uniform distributions on $[0,1]$ for the detection probabilities, and normal distributions with mean zero and variances 1,000,000, σ_b^2 , and σ_ϵ^2 for the β , the b , and the ϵ_{ij} values, respectively. The priors for the hyperparameters σ_b^2 and σ_ϵ^2 were chosen as inverse-gamma with both parameters equal to 0.001. All priors were selected as sufficiently vague to induce little prior knowledge. Generally, if the data are informative enough, the likelihood dominates the non-informative priors and the posterior summaries using MCMC samples are close to the results of a frequentist analysis.

We used software WinBUGS (Spiegelhalter et al. 2003) to implement our approach. The codes used for fitting the model are available from the first author on request.

APPLICATION

To illustrate our approach, we used a long-term dataset on the relationship between body mass and survival of adult sociable weavers (*P. socius*) at Benfontein Game Farm, in the Northern Cape Province, South Africa (Covas et al. 2002). From 1993 to 2000, the birds were captured with mist nets and individually banded with a numbered metal band. Age of birds was determined based on developmental indices. A total of 977 birds weighted as adults were banded and released. Covas et al. (2002) provide further details on the MR protocol. The theoretical prediction is that body mass represents a trade-off between the risks of starvation at low mass and predation at high mass. A previous analysis of the data (Covas et al. 2002) suggested that a nonlinear relationship held across years (i.e., $\epsilon_{ij} = \epsilon_i$).

Body mass was measured to the nearest 0.5 g each time a bird was captured (so that some individuals were weighed several times). In general, individual body mass may not remain constant over time. For instance, it may vary with individual age or with more or less favorable environmental conditions (seasons or years). As a consequence, incorporating time-dependent individual covariates in MR models is not straightforward (Pollock 2002). For instance, Covas et al. (2002) averaged body mass over all captures for each individual (hereafter, standardization 1). However, we subsequently discovered that there is substantial interannual variability in measurements of body mass in this dataset. In particular, body mass was lower and less variable in the more recent years, perhaps due to a change in capture protocols, and this introduces a potential bias in estimating survival. To eliminate these temporal effects, we standardized body mass so that its mean and variance were equal among years (see Conroy et al. 2002). We then averaged these standardized values over all captures for each individual (hereafter, standardization 2).

We generated two chains of length 200,000, discarding the first 100,000 as burn-in. These simulations took approximately 40 h on a PC (512 Mo RAM, 2.6 GHz CPU). Convergence was assessed using the Gelman and Rubin statistic, also called the potential scale reduction, which compares the within to the between variability of chains started at different and dispersed initial values (Gelman 1996).

We applied our model to the sociable weaver dataset using quadratic P-splines (i.e., $P = 2$). Unfortunately, clear guidelines do not exist for choosing the degree of a P-spline. However, as a rule of thumb, the higher the P-spline order, the smoother the fitted curve. For our example, we checked visually that cubic P-splines (i.e., $P = 3$) did not significantly improve the fit.

With standardization 1, we found a lower survival for adult birds that were lighter or heavier than the mean (the survival being maximal around the mean phenotype over the whole sample). This analysis would support the idea that body mass is under stabilizing selection (Fig. 1A, dashed line), in agreement with the earlier analysis of Covas et al. (2002). The

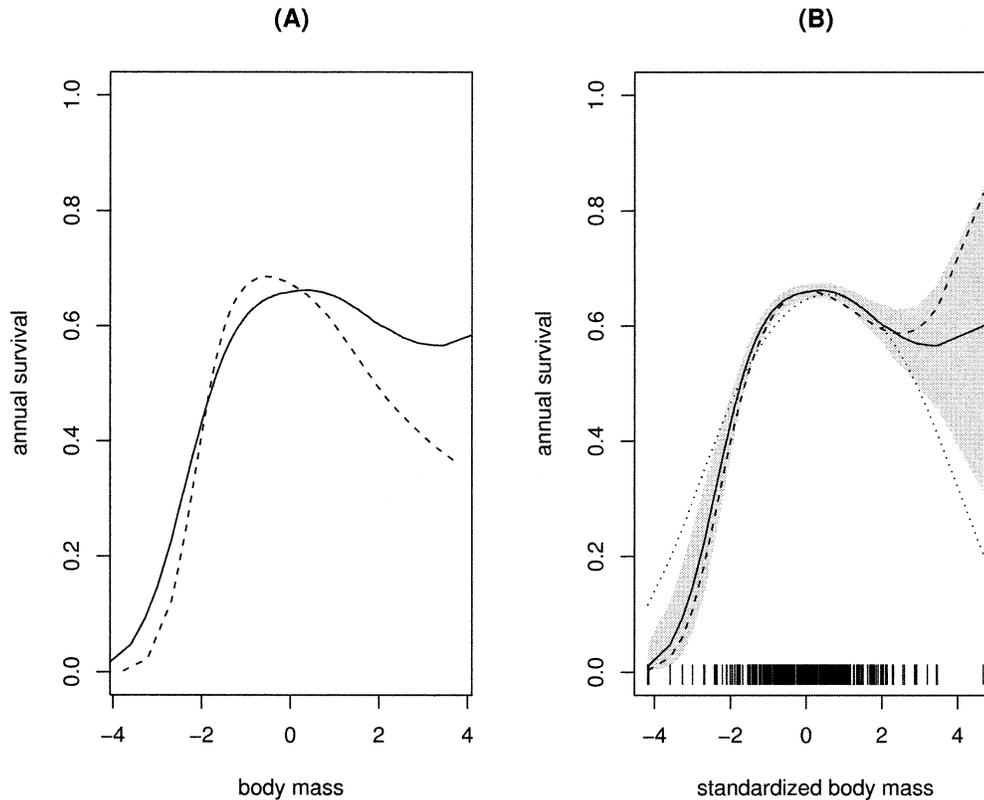


FIG. 1. Relationship between survival and body mass in sociable weavers. (A) P-splines medians are displayed using standardization 1 (dashed line) and standardization 2 (solid line). (B) Medians (solid line) with 95% pointwise credible intervals (shaded area) for the P-splines approach, along with medians for the quadratic (dotted line) and cubic (dashed line) models are displayed. In (B), the covariate values are also shown on the x-axis using standardization 2.

adjusted P-spline also shows that heavier individuals survive better than the lighter ones. With standardization 2, we also found a lower survival for adult birds that were lighter than the mean. However, we also found that heavier individuals survived much better (Fig. 1A, solid line). The two analyses clearly indicate that the effect of body mass on survival depends on the standardization. Because standardization 2 takes into account annual variability in measures of variance, it should yield the more robust approach. As a consequence, this reanalysis gives less support for stabilizing selection on body mass in this species.

We can compare this P-spline approach to the parametric alternatives used in Covas et al. (2002). Conveniently, a polynomial adjustment can be obtained as a particular case of the penalized splines approach with $b_k = 0$ for all k in equation (2). We can therefore adjust the quadratic relationship between body mass and survival (using $P = 2$), the best model in Covas et al. (2002), to more directly compare the P-spline and parametric approach. For this, we used standardization 2. The quadratic model differs markedly from the P-spline: with the quadratic model (Fig. 1B, dotted line), lighter individuals have a higher survival while the heavier ones have a lower one, compared to the P-spline (Fig. 1B, solid line). The quadratic model is nearly symmetrical: individual with body mass at either extreme of the distribution have similarly low survival. In contrast the P-spline is very asymmetrical, with heavier individuals surviving better than the lighter

ones. However, we emphasize that these conclusions are based in each case on a small number of observations at each end of the phenotype distribution, especially for the very heavy individuals. Nevertheless, this comparison shows that the precise shape of the body mass–survival relationship is overconstrained when fitted with the quadratic model. Our reanalysis challenges the stabilizing selection hypothesis and shows that this dataset does not unambiguously disentangle directional and stabilizing selection on body mass.

The P-spline may help in suggesting alternative and more appropriate parametric models if desired. In our case, the shape of the adjusted P-spline suggests that a cubic relationship between survival and body mass would be more appropriate. This adjusted cubic relationship (Fig. 1B, dashed line) is, overall, a better match to the P-spline, although it predicts even higher survival for the heavier individuals.

To compare more formally these different models (quadratic, cubic, and P-spline), we used the mean square predictive error (MSPE; Gelfand and Ghosh 1998). In our case, the MSPE compares the observed frequencies with the predicted frequencies of the individual capture histories. The posterior mean of the MSPE can be computed when estimating parameters of a given model and measures its adequacy (the most adequate model corresponding to the lowest MSPE). Based on this criterion, the cubic model is more adequate than the quadratic one (0.340 vs. 0.347), whereas the P-spline is similar to the latter (0.347). Using a frequentist

analysis and program MARK (White and Burnham 1999), model selection based on the standard AIC (e.g., Burnham and Anderson 2002) gives the same outcome, the cubic being a better model than the quadratic (AIC scores 1946 and 1941, respectively).

DISCUSSION

We developed a nonparametric model for assessing the form of natural selection on a quantitative trait using longitudinal studies based on MR data. Our approach may be viewed as a combination of that by Kingsolver and Smith (1995) of using MR models to cope with imperfect detection of individuals and the method proposed by Schluter (1988) of using cubic splines to model nonparametrically the fitness function.

Survival and Body Mass in Sociable Weavers

Our reanalysis of the variation in survival with body mass in *P. socius* illustrates the kind of information that can be obtained with our method. First, and in agreement with previous parametric analyses (Covas et al. 2002), we found that lighter individuals suffer a drastic reduction in survival. Second, we found that the survival function is not symmetric: individuals that are average or heavier than average have broadly similar survival, in both the P-spline or the cubic model approach. This result indicates that body mass may not be under stabilizing selection as suggested previously, although any conclusion contains considerable uncertainty because of the few very heavy birds sampled (see Fig. 1B). A more intensive sampling effort of heavy individuals would probably be necessary to establish more firmly whether stabilizing or directional selection is operating on body mass. More technically, the asymmetry in the fitness surface was not captured by a simple quadratic regression of survival on body mass. However, a cubic regression would have detected this caveat. This situation illustrates how the spline-fitting method can suggest the appropriate parametric model, increasing the chances that no essential feature of the fitness surface is overlooked. Finally, this case study shows that uncontrolled time variation in the individual covariates (standardization 1 vs. 2) may significantly affect model adjustment and the resulting conclusions. A more explicit modeling of the time dependence in the individual covariates would be a significant expansion of the methods described here.

Method's Limitations and Prospects

Natural selection may act on combinations of traits. As a consequence, detecting apparent stabilizing selection on a focal trait may be due to phenotypic correlation of the focal traits with traits under direct stabilizing selection. To disentangle direct and correlated stabilizing selection requires incorporating as many traits as possible in a multivariate analysis, even if it seems impossible to include them all (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Brodie et al. 1995). Our method is incomplete in this respect, and further developments are needed to extend it to the multivariate case. More generally and like with the Lande and Arnold method, the inclusion of several possible covariates

(e.g., age, sex), if available, is important in making robust inferences on the form of selection on a particular trait or set of traits. For instance, if young birds are lighter and old individuals are heavier and both have low survival for a reason unrelated to their body mass, the analysis of a dataset containing individuals of different ages may indicate (spuriously) that body mass is under stabilizing selection (when this effect is not controlled for by an age covariate). Our approach can be generalized by considering a semiparametric alternative in simple cases (Ruppert et al. 2003; Gimenez et al. 2006), where fitness is defined as an additive function of several traits that are entered either nonlinearly or linearly into a model. For instance, in our case, if the sex of individuals was available, the same spline could be adjusted for male and female mean body size, along with a binary indicator variable to allow for a potential difference between them.

As with many multivariate analyses, the measurement of correlated traits can lead to numerical instabilities. To cope with this multicollinearity issue, one solution would be to reduce the set of traits under study (Lande and Arnold 1983; Phillips and Arnold 1989) and then plot selection as a function of one or two principal components. Although the proportion of explained variance can be high in phenotype datasets, the main drawback of this method is that the major axes are determined for phenotypic variation alone, regardless of the fitness surface. A more satisfying method has been proposed by Schluter and Nychka (1994), who estimated and visualized fitness surfaces using projection pursuit regression. This method reduces the number of dimensions by finding new linear combinations of the original predictors that explain most of the variation in fitness. These new synthetic summaries are then related to fitness using univariate cubic splines. The extension of the Schluter and Nychka (1994) approach to MR data is the object of ongoing work.

Environmentally induced covariances between fitness and traits or inbreeding may lead to bias in estimating the effect of selection (Willis 1996; Kruuk et al. 2003). To disentangle confounding effects, a path analysis (Shipley 2000) appears to be an efficient method (Kingsolver and Schemske 1991; Scheiner et al. 2000), because it allows for partitioning the correlations among variables by identifying a priori causal relationships between traits. Because we permit the survival to vary as a function of several traits with additional random effects ε_{ij} , an a priori model may be specified under the form of a structured covariance matrix for the ε_{ij} values, and therefore provide a structural equation modeling MR data. Alternatively, breeding values may be used if available in lieu of phenotypic values in a way analogous to Rausher's (1992) method, to correct the bias resulting from environmental covariances.

Our approach requires the efficient comparison of models. A model selection procedure may allow for distinguishing between competing link functions (Kingsolver and Smith 1995) or for proposing alternative parametric forms to the nonparametric model if desired (as we did here). Model selection in a Bayesian framework is still under debate and the subject of ongoing research (e.g., Johnson and Omland 2004). We opted for computing the MSPE criterion proposed by Gelfand and Ghosh (1998), given its straightforward com-

putation from the MCMC samples. We could have used other alternatives, such as the AIC (Burnham and Anderson 2002) or the deviance information criterion (DIC) introduced by Spiegelhalter et al. (2002). The MSPE, AIC, and DIC each seek a compromise between the goodness-of-fit of a model and its complexity. Nevertheless, for the AIC, it is not clear how to compute the number of parameters in the presence of random effects, and thus the AIC is not well suited for our purposes here. Also, it has been shown that the DIC may be misleading in the context of hierarchical models such as ours (Spiegelhalter et al. 2002), and thus we do not recommend its use. We did not explicitly investigate goodness-of-fit in this study, as Covas et al. (2002) earlier showed that fit of models was not problematic for these data. However, if needed, Bayesian p -values may be obtained, as explained in Brooks et al. (2000).

When using MR data to estimate natural selection on a quantitative trait, it is important to distinguish between individual covariates that are fixed (typically some attribute of the individual measured at the time of marking such as sex), or time varying (a characteristic measured at each encounter occasion that may vary over time such as body condition). The implementation of the former is straightforward (Hoffman and Skalski 1995; Kingsolver and Smith 1995), and in our example we considered body mass to be a fixed variable by averaging its values over all captures for each individual. We realize that body mass is likely to show significant temporal variation over the life span of the individual and therefore could be considered a time-varying individual covariate. However, because the covariate values can only be known upon capture, the individual histories inevitably exhibit missing values when individuals are not encountered.

The issue of handling missing data in MR analyses is difficult to address, and there is not a definitive way to do it at the moment. In our example, year variation was accounted for prior to computing mean individual body mass. This method implicitly copes with the problem of missing values of the covariate. A more refined correction could be performed by correcting in the same way for individual age variation if age is available (Conroy et al. 2002). Other approaches are possible to handle time-varying covariates. One possibility requires quantitative traits to be classified into discrete categories and data analyzed using multistate MR models (Arnason 1973; Schwarz et al. 1993) that allow transitions between the covariate states and account for missing covariate values (Nichols et al. 1992). However, besides the loss of information, the number of parameters grows exponentially with the number of states, therefore causing numerical problems that have to be dealt with (Gimenez et al. 2003, 2005). Alternatively, as a Bayesian analysis treats missing data as parameters to be estimated, our method could be extended to cope with this issue (e.g., Bonner and Schwarz 2005). However, this would require strong assumptions regarding the distribution generating the missing covariate values, which might obscure the true relationship between survival probability and the covariate. Consequently, although methods for handling missing data are still the object of active research, we suggest that a useful step would consist of comparing the three approaches described above, based on sim-

ulations contrasting hypotheses on the amount of missing data and the process generating the missing data.

Overall, this new method may be applied in a variety of contexts where the dependency of a covariate to a fitness trait is under study. In particular, it may be helpful to better understand how survival changes with age in a natural population, which so far has only been attempted using a cumbersome piecewise regression approach (Loison et al. 1999; Bryant and Reznick 2004).

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