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ESTIMATING AND VISUALIZING FITNESS SURFACES USING MARK–RECAPTURE DATA

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Understanding how selection operates on a set of phenotypic traits is central to evolutionary biology. Often, it requires estimating survival (or other fitness-related life-history traits) which can be difficult to obtain for natural populations because individuals cannot be exhaustively followed. To cope with this issue of imperfect detection, we advocate the use of mark-recapture data and we provide a general framework for both the estimation of linear and nonlinear selection gradients and the visualization of fitness surfaces. To quantify the strength of selection, the standard second-order polynomial regression method is integrated in mark-recapture models. To visualize the form of selection, we use splines to display selection acting on multivariate phenotypes in the most flexible way. We employ Markov chain Monte Carlo sampling in a Bayesian framework to estimate model parameters, assessing traits relevance and calculating the optimal amount of smoothing. We illustrate our approach using data from a wild population of Common blackbirds (*Turdus merula*) to investigate survival in relation to morphological traits, and provide evidence for correlational selection using the new methodology. Overall, the framework we propose will help in exploring the full potential of mark-recapture data to study natural selection.

KEY WORDS: **Bayesian inference, correlational selection, individual covariates, natural selection, nonlinear selection, reversible Jump MCMC.**

Understanding how selection operates on a set of phenotypic traits is central to evolutionary biology. Although confirmation of selection relies on the experimental manipulation of traits, modern regression methods provide correlational evidence for selection by describing its shape and quantifying its magnitude.

There are currently two powerful and complementary approaches that are routinely used to estimate and visualize the relationship between "fitness" (e.g., survival, reproductive success of individuals or other combinations of other fitness-related traits) and a suite of phenotypic traits (e.g., various morphological traits), referred to as fitness surface (e.g., Schluter and Nychka 1994). First, the second-order polynomial regression proposed by Lande and Arnold (1983) allows the estimation of any selection gradients (directional, stabilizing/disruptive and correlational) that can be described as linear, quadratic, or cross-product terms. Second, although fitness surfaces can be represented by the best quadratic approximation of the surface, nonparametric methods have also been advocated as they allow more flexibility in visualizing fitness as they require no prior model (e.g., linear or quadratic) for the relationships between fitness and traits. Schluter (1998) and Schluter and Nychka (1994) introduced the use of cubic splines, a nonparametric method, that can be used to visualize in two and three dimensions the action of selection on phenotypic traits.

Obviously, both approaches require that fitness can be estimated. For this purpose, longitudinal studies that monitor cohorts of individuals over time are often used, but they have several difficulties. The most important is that individuals in natural populations cannot be followed exhaustively, so detectability should be incorporated in models for estimating fitness (Clobert 1995), otherwise any inference may be flawed (Gimenez et al. 2008). Because they incorporate detectability and uncertainty associated with the death of individuals (Lebreton et al. 1992), the use of mark-recapture (MR) methods allowing the estimation of important fitness components such as survival has been recommended to address questions in evolutionary biology (Gimenez et al. 2008). To date, however, the full potential of MR methods has been little explored in the study of natural selection (Clobert 1995; Kingsolver and Smith 1995; Cam 2009). First, only a part of the information contained in MR data is usually used with the standard approaches described above. For example, several authors have only considered the subset of individuals that are alive at the end of the study (Barbraud 2000; Bjorklund and Senar 2001). Others have used more correct survival estimates, but did not take uncertainties associated with the model fitting process into account (Altwegg and Reyer 2003). Second, when MR models are used to study selection, the focus is either on linear gradients (Kingsolver and Smith 1995; Clobert et al. 2000; Møller and Szép 2002) or quadratic gradients (Conroy et al. 2002; Covas et al. 2002; Schulte-Hostedde et al. 2002; Grégoire et al. 2004; Benkman et al. 2005; Blums et al. 2005). Rarely have several traits been considered, and never to our knowledge has the analysis of cross-product terms been properly conducted, which might add to the difficulty of detecting nonlinear selection in the wild. Finally, tools to visualize selection acting on several traits are not yet fully developed for MR models. Although it is straightforward to represent the best quadratic approximation, little has been done to allow surfaces to be explored in a more flexible way. Recently, Gimenez et al. (2006a) have developed a flexible nonparametric method to study the form of selection, but the approach is limited to a single phenotypic trait.

In this article, we develop general and flexible tools to provide a unifying framework to assess selection acting on a suite of phenotypic traits making optimal use of MR data. More specifically, our contribution is twofold. First, to quantify the strength of selection on combinations of traits, the second-order polynomial regression method is integrated in MR models. Procedures are provided to test selection gradients. Second, to visualize the form of selection, we employ bivariate smoothing to generalize the approach developed by Gimenez et al. (2006a) to the case of two-dimensional phenotypes. We use Markov chain Monte Carlo (MCMC) sampling in a Bayesian framework to estimate and test selection, as well as to control the amount of smoothing to visualize fitness surfaces. We illustrate our approach using data for a wild population of Common blackbirds (*Turdus merula*) to investigate survival in relation to morphological traits. Using the framework we propose, we provide evidence for correlational selection gradients, which emphasizes the great potential of MR data to investigate nonlinear selection.

Methods

We consider standard MR protocols involving I individuals that are captured and marked, then recaptured or resighted over J encounter occasions (for reviews, see Lebreton et al. 1992; Williams et al. 2002). We focus on survival and model ϕ_{ij} the probability that an animal i survives to time t_{j+1} given that it is alive at time t_j. We estimate and visualize survival as a function of P phenotypic traits measured in I individuals. We consider fixed individual covariates (i.e., measured at the time of marking), but our approach can also be applied to time-varying individual covariates (i.e., measured at each encounter occasion that may vary over time).

ESTIMATING FITNESS SURFACES

We model the survival probability using second-order polynomial regression to assess nonlinear selection (Lande and Arnold 1983; Brodie et al. 1995; Blows and Brooks 2003)

$$\operatorname{logit}(\phi_{ij}) = \beta_0 + \sum_{p=1}^{P} \beta_p x_i^p + 1/2 \sum_{p=1}^{P} \sum_{q=1}^{P} \gamma_{pq} x_i^p x_i^q + \varepsilon_i + b_j, \quad i = 1, \ldots, I \quad \text{and} \quad j = 1, \ldots, J \tag{1}$$

where x_i^p is the value of the pth covariate for the ith individual, b_j are fixed yearly effects, ε_i are i.i.d $N(0, \sigma_\varepsilon^2)$ and $\operatorname{logit}(x) = \log[x/(1-x)]$. We use the fixed effects b_j to account for time variation in survival, whereas the random effect ε_i is incorporated to cope with the individual residual variation in survival (Gimenez et al. 2006a; Royle 2008). In particular, this term usually referred to as a frailty (e.g., Cam et al. 2002) allows us to deal with individual heterogeneity which may cause bias in estimation and inference if it is not accounted for (Cam et al. 2002). Linear selection gradients (β) are calculated using the model described in equation (1), but where quadratic and cross-product coefficients are dropped, then a distinct regression is carried out using all terms in equation (1) to calculate the nonlinear selection gradients (γ) (Phillips and Arnold 1989; Brodie et al. 1995). Key model parameters are summarized with their posterior median and standard deviation. To determine relevant combinations of selection gradients, we view the problem as a variable selection exercise. We use an extension of the MCMC algorithm—Reversible Jump MCMC (RJMCMC; Green 1995)—to search among the large number of combinations of selection gradients and thereby exhibit the best-fitting model. We discriminate between different models by calculating the posterior model probability of each model. Technical details are given below.

VISUALIZING FITNESS SURFACES

To visualize the fitness function in two dimensions, we opt for thin-plate splines that are usually used in geostatistical applications to incorporate spatial coordinates in multiple regressions

(Green and Silverman 1994; Nychka 2000). Our objective in exploring fitness surfaces is to detect interesting and actual patterns that are not just due to sampling variation; in other words, the challenge is to find the compromise between too much roughness and too much smoothness. We consider a semiparametric model for the survival where two continuous phenotype traits *s* and *t* enter the model under the form of a nonparametric interaction, whereas the remaining covariates enter linearly the model in a parametric component (Ruppert et al. 2003):

$$\text{logit}(\phi_{ij}) = f\left(x_i^s, x_i^t\right) + \sum_{p=1,\, p\neq s,t}^{P} \beta_p x_i^p + \varepsilon_i + b_j, \qquad i = 1, \ldots, I \quad \text{and} \quad j = 1, \ldots, J \qquad (2)$$

where x_i^s and x_i^t are the values of two focal traits for individual i, f is a smooth function and the other quantities are defined in equation (1). To estimate the function f, Gimenez et al. (2006a,b) opted for penalized splines. This technique uses a set of piecewise polynomials (splines) and imposes a penalty on the associated splines coefficients to achieve a smooth fit. Note that penalized splines can be fruitfully expressed as generalized linear mixed models, which have various advantages (Ruppert et al. 2003). Among others, the amount of smoothing or the penalty parameter is obtained as a by-product of this formulation as a ratio of variances (see Gimenez et al. 2006b for a demonstration in the MR context). Because they show good numerical stability and are moderately computer intensive, we use radial basis functions (French et al. 2001; Ruppert et al. 2003; Crainiceanu et al. 2008) to extend the approach proposed by Gimenez et al. (2006a) to the bivariate setting (Gimenez and Barbraud 2009). The problem is then to choose the number and the location of the points, or knots, at which the splines are fitted. Considering as many knots as there are individuals might cause overfitting, whereas using too few knots might cause them to be placed in regions with little data. We consider a number of knots that is large enough to ensure the desired flexibility, specifically $K = \max\{20, \min(I/4, 150)\}$ knots as suggested by Ruppert et al. (2003). We use the space-filling algorithm of Nychka and Saltzman (1998) to select the location of these knots. This algorithm automatically places knots in regions with a high density of observed values while maximizing the average spacing between knots of those regions. Ruppert et al. (2003) demonstrated that, once a minimum number of knots is achieved, the fit given by the penalized splines approach was independent of the location and the number of knots.

Finally, to plot the fitness surface, we obtain contours of the posterior median survival by generating a 30 × 30 grid of values for the two focal traits in equation (2), calculating the corresponding survival probability for each point of the grid and for each MCMC iteration, and taking the median over the MCMC draws. Note that we consider other things being equal by setting the remaining covariates to their means in equation (2). Predicted values for all individuals were also added on the contour plot to see the number of individual that supported each local pattern of the surface.

MR MODEL FITTING USING MCMC METHODS

To estimate the model parameters and perform inference, we adopted a Bayesian approach in conjunction with MCMC methods, a flexible and powerful framework for building and fitting complex models. In a Bayesian analysis, the likelihood and the prior probability distributions are combined using the Bayes' theorem to obtain the posterior distribution of the unknown parameters of interest (see McCarthy 2007 for an introduction). The MCMC algorithms then generate values from a Markov chain whose stationary distribution is the required posterior distribution (e.g., Gilks et al. 1996). 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 credible intervals for parameters of interest.

Here, standard MCMC algorithms are used to visualize fitness surfaces, whereas we use RJMCMC (Green 1995) to fit the second-order polynomial curves. RJMCMC extends MCMC by allowing transitions between models, or "jumps," to assess the presence or absence of a covariate. In our case, this algorithm searches over the different models to determine the best combination of selection gradients. It requires an extension of the standard Bayes Theorem, where the posterior distribution of all parameters is now defined over both the parameter and model space. In addition to posterior summaries for parameters, we also obtain the posterior probability for each model obtained as the proportion of the time the RJMCMC simulation spends in each model. This is achieved by exploring simultaneously the parameter and model space within a single Markov chain. See King et al. (2006) for a recent application of the RJMCMC algorithm in a MR context and Gimenez et al. (2009) for more details. Note that in the fit of the second-order polynomial curves, we allowed the RJMCMC to act only on second order terms to avoid fitting models with interactions without main effects.

In both analyses, we need to write down the likelihood and select priors for the parameters. Assuming independence among individuals, the likelihood is the product of the probabilities of all individual encounter histories, each of those probabilities involving complex nonlinear functions of the survival and detection probabilities (Skalski et al. 1993; Hoffman and Skalski 1995; Gimenez et al. 2007). Based on previous analyses of the data (Grégoire et al. 2004), we assume that the detection probability varies over time.

Regarding the a priori distributions for all parameters, we select vague priors to induce little prior knowledge because, if the data are informative enough, the likelihood dominates those priors and the posterior summaries are close to the results of a maximum likelihood analysis. Specifically, we choose uniform distributions on [0,1] for the detection probabilities, a uniform distribution on [0,10] for σ_ε as advocated by Gelman (2006; see also Royle 2008), and normal distributions with mean 0 and variances 1000 for the βs. In addition to those priors, we specify an equal prior probability on all possible models in the RJMCMC analysis, which corresponds to an independent prior probability of 0.5 for each covariate. We conducted a prior sensitivity analysis to assess the influence of prior specifications on posterior distributions. In particular, the posterior model probabilities may be more sensitive to the prior specification than the posterior distribution of the parameters themselves. In addition to the priors used above, we considered inverse-gamma distributions for σ_ε^2 with parameters (0.001, 0.001) or (3, 2), and normal distributions with mean 0 and variances 1 or 10 for the βs. The posterior inference was unchanged, although increasing the variance in the prior for the regression parameters decreased the posterior probability that covariates influences the survival probability.

We generate two chains of length 1,000,000, discarding the first 500,000 as burn-in. The large number of iterations was needed because good mixing (the movement of the MCMC chain around the parameter space) was difficult to achieve in the bivariate smoothing model. When applied to the example, these simulations took between 7 and 10 h on a PC (512Mo RAM, 2.6GHz CPU). Convergence was assessed using the Gelman and Rubin statistic which compares the within to the between variability of chains started at different and dispersed initial values (Gelman 1996). Note that there is no formal convergence diagnostic for the RJMCMC algorithm, so we run two chains starting either with all or without any covariates in the model and checked that estimation and inference results were similar. The mixing of the RJMCMC algorithm (how often the MCMC chain switches between including a selection gradient vs. excluding it) was satisfying, exploring most of the model space. All covariates were standardized to improve convergence.

The simulations were performed using WinBUGS v1.4 (Spiegelhalter et al. 2003) and its Jump extension (Lunn et al. 2006) to implement RJMCMC. To plot the fitness surfaces, the R (Ihaka and Gentleman 1996) package R2WinBUGS (Sturtz et al. 2005) was used to call WinBUGS and export results in R. We also used the R package FIELDS (Nychka 2004) to implement the space-filling algorithm. The WinBUGS code is available on request from the first author.

DATA

To illustrate our approach, we use a long-term dataset on the relationship between morphological traits and survival of adult Common blackbirds (*T. merula*) in an urban park in Dijon, France (47°19′N 5°02′E). From 1998 to 2002, birds were captured with mist-nets, and each individual was fitted with a numbered metal ring and a unique combination of plastic color rings. Grégoire et al. (2004) provide further details about the MR protocol. A total of 199 birds were banded, measured for morphological traits, and released. The tarsus length, phalanx length, and beak height were measured with a calliper to the nearest 0.02 mm, and wing length and rectrice length using a ruler to the nearest 0.5 mm. These morphological traits have been demonstrated to have a significant heritable component in birds (Boag and van Noordwijk 1987; Merilä and Gustafsson 1993; Charmantier and Garant 2005) and are closely related to flight and feeding efficiency (Grant 1986; Norberg 1990). They are therefore potentially subject to natural selection.

Using correlated explanatory variables in a multiple regression can cause problems in estimation and inference (Graham 2003), the analysis of MR data making no exception. Because we detected multicollinearity in the original suite of traits of our dataset, we performed a principal component analysis (PCA) to produce a new set of standardized uncorrelated synthetic traits variables (Joliffe 2002). Usually, only those principal components (PCs) explaining most of the phenotypic variations are retained (Lande and Arnold 1983; Phillips and Arnold 1989), although there is no guarantee that these PCs are the most related to fitness. We thus included all PCs in our analyses. Note that the correlation matrix was used in the PCA.

Results

The trait loadings obtained from the PCA are given in Table 1 and show how the original traits contribute to the new PCs. PC1 was considered an index of overall size because of consistent direction and relatively high loadings of each original traits (except beak height). PC2 contrasts the wing length and beak height with the tarsus length and phalanx length. PC3 consists of high positive loading from beak height only and was therefore considered a measure of beak height. PC4 contrasts the wing length with the rectrice length, two traits closely related to flight performances, and was therefore referred to as agility (the longer is the rectrice and the shorter are the wings, the higher is agility; Norberg 1990). Finally, PC5 contrasts the phalanx length and tarsus length and was considered an index of leg shape.

Posterior model probabilities of linear and nonlinear selection gradients (see eq. 1) obtained from the RJMCMC model selection are presented in Table 2.

Regarding linear effects, the model that includes an intercept only had the highest posterior probability, which means that no directional selection was detected on either PCs. Regarding nonlinear effects, the model with highest posterior probability was that including no quadratic selection on either PCs, but an interaction

Table 1. **Principal components analysis of the five original Common blackbird phenotypic traits (the matrix correlation was used).**

Principal component	PC1	PC2	PC3	PC4	PC5
Beak	0.37	0.50	0.78	0.04	0.08
Tarsus	0.75	−0.55	0.06	−0.15	0.34
Phalanx	0.77	−0.47	0.17	0.27	−0.30
Wing	0.66	0.48	−0.45	0.34	0.15
Rectrice	0.80	0.34	−0.20	−0.41	−0.19
Percentage of overall variance	47.26	22.23	17.49	7.52	5.51
Eigenvalue	2.36	1.11	0.87	0.38	0.28
Interpretation	Overall size	Wing length and beak height vs. the tarsus length and phalanx length	Beak height	Agility	Leg shape

between PC3 and PC4. In other words, we detected a correlational gradient between PC3 and PC4, with a high marginal posterior probability for this coefficient of being included in the model (Table 3). This correlational gradient between beak height and agility was negative (Table 3), which means that Common blackbirds share a particular combination of these two components, such that an increase in agility (corresponding to an increase in the rectrice length and a decrease in the wing length, i.e., a decrease in PC4 values) is always associated with an increase in beak height (i.e., increase in PC3 values).

Table 2. **Top 10 models incorporating linear and nonlinear effects for the Common blackbird mark-recapture data. Two distinct analyses were carried out, one with linear effects only (left column), and the other with second order terms with linear effects always included (right column). In the model structure, a 1/0 indicates the presence/absence of the corresponding covariate (note that the intercept is always included in the model and therefore not represented in this notation). Regarding the linear effects, the 5 numbers stand for PC1, PC2, PC3, PC4, and PC5. For example, 00000 denotes a model with the intercept only, whereas 00101 is a model with a linear effect of both PC3 and PC5. Regarding the nonlinear effects, the 5 first numbers stand for quadratic effects (PC1^2, PC2^2, PC3^2, PC4^2, PC5^2) and the 10 remaining numbers stand for cross-product effects, PC1∗PC2, PC1∗PC3, PC1∗PC4, PC1∗PC5, PC2∗PC3, PC2∗PC4, PC2∗PC5, PC3∗PC4, PC3∗PC5, and PC4∗PC5. For example, 001000000000100 denotes a model with a quadratic effect of PC3 and a cross-product effect of PC3 and PC4.**

Linear effects		Nonlinear effects	
Model structure	Posterior model probability	Model structure	Posterior model Probability
00000	0.738	00000 0000000100	0.206
00001	0.108	00000 0000000001	0.045
00100	0.045	00000 0000000101	0.035
01000	0.034	00000 0000000000	0.030
00010	0.033	00000 0000000110	0.029
10000	0.015	00001 0000000100	0.022
00101	0.006	00000 0000010000	0.021
01001	0.005	00000 0000010100	0.018
00011	0.004	00000 0000010001	0.018
00110	0.002	00000 0000000011	0.014

Correlational selection on the morphological traits was confirmed by plotting the fitness surface (eq. 2) generated by the two components PC3 and PC4; it is displayed in Figure 1 using a contour plot. Overall, this surface reveals a ridge of high survival (from the top left to the bottom right of the figure). This is consistent with the negative correlational selection between PC3 and PC4 detected when fitting the parametric model in equation (1) (see the red contour on the figure illustrating the direction and strength of correlational selection fitted by the parametric model). However, the fitness surface also displays more subtle features. For instance, it indicates a small "valley" (centered on $\mathrm{PC4} \approx 0.5$, $\mathrm{PC3} \approx -0.5$). Whether this is due to insufficient smoothing or to a bimodal fitness function is difficult to evaluate. In our example, it does not matter much because this detail corresponds to small survival differences. However, this example points out that the method may be very useful to reveal complex fitness functions.

Discussion

SURVIVAL IN COMMON BLACKBIRDS

If a traditional approach had been adopted, we would not have detected nonlinear selection acting on morphological traits of the Common blackbird using MR data. In particular, the evidence for a correlational selection is important because little is known about it in the wild (Kingsolver et al. 2001). In addition, the tools we have developed to visualize fitness surfaces as estimated by MR models revealed important details of the phenotype under selection. This additional step may prove important to avoid overlooking complex features in the fitness surface or inferring erroneous conclusions from the sole examination of selection gradient (e.g., Brodie et al.

Table 3. Vector of directional selection gradients (β), and the matrix of quadratic and correlational selection gradients (γ)—on the logit scale (cf. eq. 1). Posterior medians are provided as well as standard deviations between parentheses. Below these two values, the marginal posterior probability of each coefficient being included in the model is also given.

		γ				
	β	PC1	PC2	PC3	PC4	PC5
PC1	−0.004 (0.070)	0.051 (0.157)				
	0.028	0.156				
PC2	0.002 (0.105)	−0.003 (0.054)	0.117 (0.391)			
	0.041	0.021	0.139			
PC3	0.017 (0.153)	0.005 (0.073)	0.040 (0.219)	0.004 (0.084)		
	0.056	0.029	0.068	0.030		
PC4	−0.188 (0.649)	−0.014 (0.156)	0.068 (0.462)	−1.673[1] (0.481)	−0.220 (0.652)	
	0.148	0.048	0.083	0.813	0.174	
PC5	0.005 (0.292)	−0.008 (0.177)	0.014 (0.229)	0.123 (0.577)	0.193 (0.900)	−0.008 (0.416)
	0.071	0.046	0.062	0.115	0.156	0.082

[1] A covariate selected by the RJMCMC simulation (cf. Table 2).

1995). Overall, the integration of two well-established methods in selection analyses—second-order polynomial regression and bivariate smoothing—within MR models provides a powerful approach to make an optimal use of MR data to explore fitness surfaces.

The fact that an increased agility (i.e., long tail relatively to short wing; Norberg 1990) was associated with a better survival is not surprising in the studied urban area. It has recently been argued that in Western Europe the Common blackbird is the second species that suffers the most from collisions with moving vehicles (Erritzoe et al. 2003). Thus, it seems reasonable to consider that less agile birds are at least more prone to this risk of death, especially in town. On the other hand, beak shape has been demonstrated to be linked with the diet of a bird, selection favoring longer beaks when diet hardness increases (e.g., Grant 1986). In the present case, we observed that birds with medium beaks survived better. It is not surprising because colonization of urban areas has been associated with a higher proportion of dry seeds in the diet of the Common blackbird (Luniak and Muslow 1988).

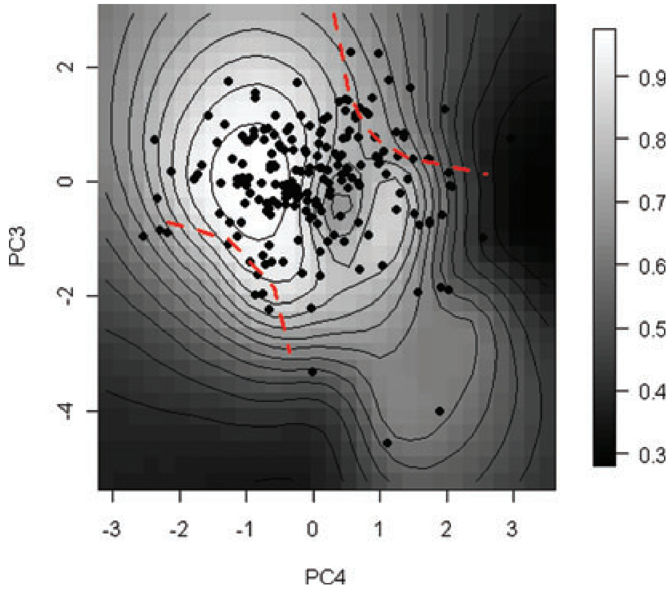

Figure 1. Bayesian thin-plate spline visualization of the fitness (survival probability) surface PC4 (*x*-axis) vs. PC3 (*y*-axis) for the Common blackbird mark-recapture data. A two-dimensional contour plot of posterior medians is provided (gray levels). For a comparison, the parametric model fitted (eq. 1) is illustrated by the contour corresponding to a survival equal to 0.8 (dashed lines).

It should be noted that MR models estimate survival conditional upon presence, so that dispersal from the local study area and mortality cannot be dissociated. In the present study, this means that we could not exclude the possibility that birds with specific morphological features dispersed more than others. If this was the case, the observed variation in survival between individuals might actually correspond to some form of habitat selection where birds that have nonoptimal traits with respect to local selective pressures (e.g., food) leave the area for places where the traits better fit the local pressures. Whenever habitat selection is expected to induce costs (e.g., Lin and Batzli 2002), one way to access actual survival is to combine MR data with information on mortality obtained from ring-recovery or radio-tracking data in which the date of death is known (Williams et al. 2002).

METHOD'S LIMITATIONS AND PROSPECTS

Although we adopted a Bayesian framework to estimate survival, a classical frequentist analysis using maximum likelihood theory could have been conducted using the free programs MARK (White and Burnham 1999) or E-SURGE (Choquet et al. 2009).

However, because individual random effects have only been made available within the Bayesian framework so far, one would have to ignore potential unexplained variance while testing significance, which might lead to biased estimates and flawed inference (Cam et al. 2002). Besides, regarding the visualization of fitness surfaces, a frequentist implementation of the penalized splines has not yet been proposed in the context of MR models. The main difficulty lies in calculating the amount of smoothing because it requires the use of multiple random effects which involves coping with high dimensional integrals in the maximization of the likelihood (Gimenez et al. 2006b). The Bayesian framework associated with the MCMC machinery offers a straightforward solution to cope with this issue.

One may be interested in stratifying the data to cope with known sources of heterogeneity or to assess differences in selection according to some qualitative variables (e.g., sex or presence/absence of a predator). To this aim, Chenoweth and Blows (2005) introduced a sequential model building approach using *F*-tests to assess whether the fitness surfaces differ in linear, quadratic, and/or correlational selection. This approach can be easily translated in the framework we proposed using a variable selection approach through the RJMCMC methodology by adding extra relevant covariates to the model.

We used thin-plate splines to visualize the action of selection. This approach can be generalized to incorporate additional variables entering linearly in the model for fitness (cf. eq. 2) as well as categorical variables (Gimenez et al. 2006b). The latter might reveal itself to be particularly useful to compare fitness surfaces according to a binary indicator (e.g., sex or presence/absence of a predator) without making prior assumption on the different ways in which the traits affect fitness.

We emphasize that, similarly to Lande and Arnold (1983) method, the main assumption of our approach is that the shape of the underlying fitness surface is indeed quadratic, while it may actually have any shape, including one or more peaks, valleys or ridges. To relax this assumption, Schluter and Nychka (1994) proposed to estimate fitness surfaces using projection pursuit regression. This method not only reduces the number of dimensions in a way similar to what PCA does, but also relates the new synthetic variables to fitness using flexible splines. The extension of the Schluter and Nychka (1994) approach to MR data is the object of ongoing work, and we feel confident in that the introduction of spline smoothing in MR data modeling is an important step toward this extension.

Finally, we note that a complete selection analysis should include a canonical analysis (Box and Wilson 1951; Box and Draper 1987) of the matrix of quadratic and cross-product parameters to find the major axes of nonlinear selection that indicate important directions of the surface fitness, for example, multivariate stabilizing/disruptive selection (Phillips and Arnold 1989; Blows and Brooks 2003; Blows 2007). Of particular importance, Blows and Brooks (2003) showed that nonlinear selection can be overlooked if a canonical analysis is not performed after a second-order polynomial regression. The extension of our approach to combine the second-order polynomial regression with the canonical rotation in a MR model is straightforward. For each of the samples obtained from the MCMC algorithm, one just needs to perform a canonical analysis of the γ matrix to obtain the posterior distributions of the eigenvectors that indicates how the traits contribute to the major axes of the response surface, together with associated eigenvalues that give the strength of nonlinear selection along each eigenvector. Although in our case the canonical rotation did not detect patterns not shown by the second-order polynomial regression (unpublished results), it may not be always the case (Blows and Brooks 2003; Blows et al. 2003).

To conclude, as suggested by Blows and Brooks (2003), the response surface methodology should be incorporated in the evolutionary biologist's toolbox to properly assess nonlinear selection without neglecting correlational selection. In this context, MR recapture models implementing second-order polynomial regressions as well as flexible methods for fitness visualization constitute a powerful framework to address evolutionary questions using longitudinal data collected in the wild.

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