SHORT COMMUNICATION

Stabilizing natural selection on the early expression of a secondary sexual trait in a passerine bird

A. GREGOIRE,*,† M. PREAULT,* F. CEZILLY,* M. J. WOOD,* R. PRADEL‡ & B. FAIVRE*

*Equipe Ecologie Evolutive, UMR CNRS 5561 Biogéosciences, Université de Bourgogne, Dijon, France
†Department of Zoology, Stellenbosch University, Stellenbosch, South Africa
‡CEFE-CNRS, Montpellier, France

Keywords:

capture-mark-recapture;
European blackbird;
natural selection;
sexual selection;
Turdus merula.

Abstract

Natural selection is a central tenet of evolutionary theory, yet the estimation of the direction and intensity of selection remains problematic. Here, we assess the strength of selection on the early expression of a secondary sexual ornament, bill colour, in male European blackbirds (*Turdus merula*) using 5 years of capture-mark-recapture (CMR) data. The best-fitting model consisted of a quadratic relationship between survival rate and bill colour, indicating stabilizing natural selection on the early expression of a secondary sexual trait. There was no evidence for sexual selection acting on bill colour in the first year. We suggest that the consideration of early selection and the adoption of refined statistical methods may reveal patterns of selection in the wild that have, as yet, remained undetected.

Introduction

It is widely accepted that the advantages obtained by males displaying exaggerated sexual characters, in terms of enhanced reproductive success (Andersson, 1994), can be countered by the effects of natural selection on the same traits. The costs of such traits could be explained in terms of direct visibility to predators or energetic investments to elaborate these ornaments (Harvey & Bradbury, 1991). However, the survival consequences of investment in secondary sexual traits have been difficult to detect. Owens & Bennett (1994) suggested that the costs of sexual traits may arise mainly during early stages of development, but studies probing the survival consequences of investment in secondary sexual traits have been carried out almost exclusively in the mature adult stage (reviewed in Jennions *et al.*, 2001), too late to detect early selection. Rohwer *et al.* (1980) suggested that the early costs of secondary sexual traits may explain the evolution of delayed plumage maturation. Thus, species where young individuals can express the same secondary

Correspondence: Arnaud Grégoire, Department of Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa.
Tel.: +27 21 808 2596; fax: +27 21 808 2405;
 e-mail: agregoire@sun.ac.za

sexual traits as matures ones offer relevant contexts to study the cost of early expression of these characters.

Quantitative methods have been developed to measure both natural and sexual selection patterns in the wild (Brodie *et al.*, 1995; Van Tienderen, 2000). In the last three decades, studies using these methods have broadened considerably our knowledge of natural selection on free ranging populations. However, recent studies (e.g. Kingsolver *et al.*, 2001) have demonstrated that the strength of selection in the wild is weak. The difficulty of obtaining measurements of survival in wild populations (Lebreton *et al.*, 1992) has also hindered the study of natural selection. In open populations, the return rate that corresponds to the fraction of individuals recaptured in the next year does not distinguish survival and recapture probabilities. Capture-mark-recapture (CMR) analysis is a sophisticated statistical tool that accounts for this difficulty, and may also consider the expression of a trait as a covariate of survival (Lebreton *et al.*, 1992), thus allowing the examination of selection coefficients on quantitative traits (Kingsolver & Smith, 1995).

In this study, we analyse patterns of survival and reproduction in male European blackbirds *Turdus merula* in relation to a secondary sexual trait: bill colour. Previous studies on this species suggest that bill colour

might indicate male quality (Faivre *et al.*, 2001, 2003; Hatchwell *et al.*, 2001). In addition, yearling male blackbirds can exhibit the same bill colour as adult males, or express a less intense signal (Préault, 2003). Thus, following the delayed maturation hypothesis (e.g. Rohwer *et al.*, 1980), the development of a showy bill colour may be costly in yearlings. We examined patterns of natural selection on bill colour using capture-mark-recapture methods on longitudinal survival data. In addition, we evaluated the selection coefficients on bill colour in relation to components of reproductive success.

Methods

Measuring bill colour, survival and reproductive success

Data were collected from 1997 to 2001 in a 5.5 ha urban park (Jardin de l'Arquebuse) in Dijon, France (47°19′N 5°02′E). Yearling males (i.e. birds in their second year of life, when they first reproduced) were captured during each breeding season using mist-nets, and their bill colour was assessed by comparison with a colour fan (Roche, Neuilly-sur-Seine, France) ranging from index 1 (pale yellow) to 15 (orange, Faivre *et al.*, 2001, 2003). Bill colour of blackbirds did not vary significantly within each breeding season (Préault, 2003). Recapture data corresponded to birds resighted during weekly standardized censuses. We evaluated the pairing status (paired or unpaired) and the number of offspring produced during a male's first breeding season from a close monitoring of reproductive attempts (Faivre *et al.*, 2001).

Evaluation of survival selection on bill colour

The time scale at which survival was estimated corresponded to the delay between two successive capture (resighting) sessions, from one year to the other. Survival and recapture probabilities were estimated for each yearling male sampled, using a maximum likelihood procedure from the capture-recapture history of each bird (MARK: White & Burnham, 1999). The validity of the estimates obtained from the models requires that several assumptions are met (Lebreton *et al.*, 1992). The absence of structural problems in the data set and the assumption that animals behave independently (e.g. capture does not affect recapture probability) must be verified. The test of these assumptions is usually made on the CJS, Cormack-Jolly-Seber, model (Φ_t; p_t) that assumes both survival (Φ) and recapture (p) probabilities to be dependent on time (t). The test of goodness of fit on CJS model (U-CARE: Choquet *et al.*, 2000) indicated that this model offered a satisfactory fit to the data set (Goodness of fit test, global test, quadratic $\chi^2_6 = 0.372$, n.s.). Thus, there were no significant departures from assumptions, allowing the use of CMR statistics. Only models with an *a priori* biological interpretation were considered (Burnham & Anderson, 1998), generating three classes of model. First, we generated models of time-dependent survival (without considering the covariate of bill colour or age-dependent effects) from the general Cormack-Jolly-Seber model (Φ_t; p_t), where survival and recapture probabilities were either dependent or independent of time (Table 1a). Secondly, we gener-

Table 1 Models of selection of yearling male blackbird bill colouration.

Model	AICc	delta AICc	Parameters	Deviance	AICc weight (%)	Model explanation
(a)						
Φ_t;p_t	116.9	6.1	7	101.1	2.61	Survival and recapture time-dependent
Φ_t;$p_.$	116.2	5.4	5	105.3	3.62	Survival time-dependent, recapture constant
$\Phi_.$;p_t	117.7	6.9	5	106.7	1.77	Survival constant, recapture time-dependent
$\Phi_.$;$p_.$	119.0	8.2	2	114.9	0.88	Survival and recapture constant
(b)						
$\Phi_{Bill colour}$	115.0	4.2	3	108.6	6.79	Directional selection on bill colour at yearling
$\Phi_{Bill colour, bill colour^2}$	110.8*	0.0	4	102.3	53.79	Stabilizing or disruptive selection on bill colour at yearling
(c)						
$\Phi_{1st(.); subs(.)}$	121.2	10.4	3	114.8	0.30	First year survival different from subsequent
$\Phi_{1st(Bill colour, bill colour^2);subs(.)}$	113.5	2.7	5	102.6	14.04	Selection on bill colour at yearling restricted to the interval between the first and second capture sessions
$\Phi_{1st(Bill colour, bill colour^2); subs (Bill colour, bill colour^2)}$	113.2	2.4	7	97.4	16.21	Selection on bill colour different between the interval from the first to the second capture sessions and subsequent intervals between capture sessions

(a) Cormack-Jolly-Seber model of survival estimates (Φ) and resighting probability (p), nested for time-dependence and tested for goodness of fit. (b) Models incorporating bill colour as a covariate. (c) Models incorporating age-dependent effects.
The lowest value of AICc indicates the best-fitting model (*). Delta AICc corresponds to the difference in AICc between the best fitting model and the model in consideration. AICc weight gives the relative likelihood of each model.
1st′ = effect present during first year of survival following release; 'subs' = effect present in subsequent years. For model classes (b) and (c), p was omitted as it was considered to be constant.

ated models of bill-colour-dependent survival. We examined the slope of the best linear approximation (β) to indicate directional selection and the best quadratic approximation (γ) for stabilizing or disruptive selection (Lande & Arnold, 1983; Kingsolver & Smith, 1995; Table 1b). Finally, we incorporated age-dependent effects. Considering two age groups, the year after first release and subsequent survival, we considered models of selection acting in one or both age groups (Table 1c). To select the most parsimonious model, each model was assessed using the Akaike Information Criterion (Akaike, 1973; Burnham & Anderson, 1998). Means and model parameters are shown as mean ± SE.

Evaluation of sexual selection on bill colour

We estimated sexual selection coefficients on bill colour according to two components of reproductive success: (i) the paring status and (ii) the number of offspring produced. We examined coefficients of regression terms from the best linear relationship (β) for directional selection and the second order term (γ) in the best quadratic relationship for stabilizing or disruptive selection (Lande & Arnold, 1983). We considered a binomial error for pairing status and a poisson error for the number of offspring produced.

Results

Evaluation of survival selection on bill colour

Over the 5 years of the study we captured 55 blackbirds as yearlings, and recorded their bill colour. The best model included a function consistent with stabilizing selection on bill colour (Table 1b: $\Phi_{\text{billcolour,billcolour}^2}$; *p.*). The presence of stabilizing selection was indicated by the negative and significant quadratic function in the retained model ($\gamma = -0.704 \pm 0.282$, $P < 0.01$, Fig. 1).

Evaluation of sexual selection on bill colour

There was no significant influence of bill colour on pairing status (maximum model, $\chi_2^2 = 2.071$, n.s., 7.42% of deviance explained). There was no evidence for directional selection ($\beta = -0.085 \pm 0.288$, $t_{53} = -0.294$, n.s.), nor for stabilizing or disruptive selection ($\gamma = -0.359 \pm 0.270$, $t_{53} = -1.332$, n.s.) on bill colour when considering pairing status. In addition, the number of offspring produced was not significantly associated with bill colour (Fig. 2, maximum model, $\chi_2^2 = 2.642$, n.s., 3.80% of deviance explained). There was no evidence for directional selection ($\beta = 0.144 \pm 0.327$, $t_{13} = 0.439$, n.s.), nor for stabilizing or disruptive selection ($\gamma = -0.564 \pm 0.532$, $t_{13} = 1.062$, n.s.) on bill colour when considering the number of offspring produced.
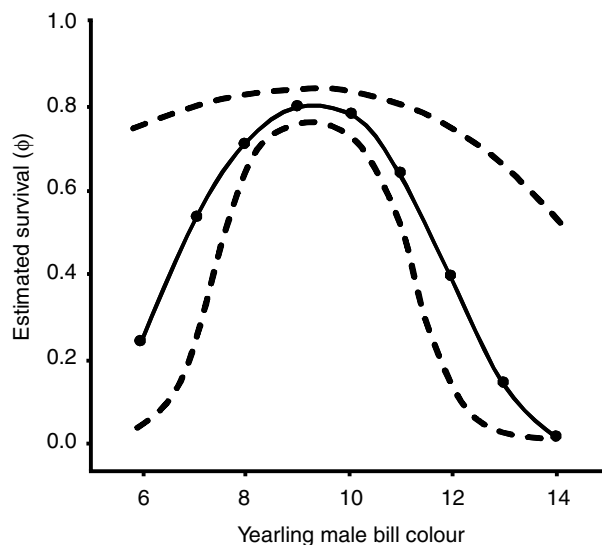

Fig. 1 Survival according to bill colour in yearling blackbirds. The plotted line represents estimated survival probabilities (Φ) of yearling male blackbirds with respect to bill colouration, produced by the retained final model ($\Phi_{\text{Billcolour,billcolour}^2}$; *p.*). Solid line indicates means and dotted lines 95% confidence interval.
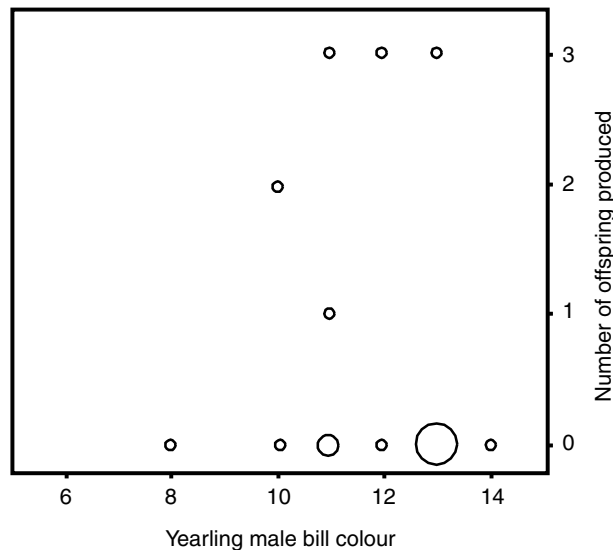

Fig. 2 Reproductive output according to bill colour in yearling blackbirds. The size of open circles is proportional to the number of individuals ($n = 15$).

Discussion

Our results suggest strong stabilizing natural selection on bill colour, a secondary sexual trait, when it develops in male blackbirds. Functional explanations may be

advanced for the extremes of the survival curve in relation to bill colour (Fig. 1) indicating stabilizing selection. Because of the suggested condition-dependence of carotenoid-based traits (Lozano, 1994), dull bill colour may reflect lower foraging ability or poor immunocompetence, accounting for the lower survival rate of less ornamented yearlings. In addition, these individuals showing low quality signal may be out competed by other males for space or resources acquirement.

However, the lower survival rate of more ornamented males may result from a trade-off between survival and reproductive investment, as investment in sexual traits is known to be negatively correlated with reduced male lifespan (Cords & Partridge, 1996). Here, we did not obtain any relationship between the reproductive success of a yearling male and its bill colour, suggesting that the males possessing an intense bill colour do not benefit from an increased reproductive success. However, this result has to be taken with caution because it is based on a small sample size, and zeros predominate in the dataset. Therefore, it is difficult to exclude a direct cost of reproduction. In addition, the parameter evaluated here does not correspond to the true reproductive success. Indeed, an important source of variance in the reproductive success between males corresponds to extra pair paternities (EPP) that may occur in Blackbird populations (Creighton, 2000). Then, males with a orange bill could benefit from more EPP, increasing their reproductive success. In addition, we cannot exclude that orange-billed yearling males that survive may experience a higher breeding success in the following years. Unfortunately, our small sample size is too low to assess this point.

A direct toxic effect of carotenoids is unlikely to explain the lower survival of males with intense bill colour (Olson & Owens, 1998). The costs associated with intraspecific competition or predation may actually select against the most ornamented yearlings. Snow (1958) explained that males of European blackbirds frequently engaged in fights for territory defence. Occasionally, injuries may lead to the death of one of the fighting males (Snow, 1958). Recently, Bright & Waas (2002) have shown that resident males reacted more to orange-billed than to yellow-billed stuffed adult males presented as intruders, and stated that orange-billed males were perceived as more of a threat to territory ownership. As new breeders, yearling males have to systematically acquire a breeding territory by competing with other males. Consequently, they have an intruder status. Even if we cannot exclude a direct cost of reproduction, this could explain the low survival of yearling males with an intense bill colour.

Overall, our study strongly suggests that apparent lack of selection on secondary sexual traits in adulthood does not necessarily mean lack of selection on these traits, as the selection might have occurred already at early life stages. Detection of such a selection may be difficult due to logistic constraints posed by many model systems. However, CMR methods might provide more power to detect such effects as compared with traditional ways of measuring selection because they allowed less biased estimates of survival. Studies exploring short and long-term costs and benefits associated with the expression of secondary sexual traits in different life stages, particularly in early life stages regarding to the precocity of trait development, are required to see how general the results presented in this paper are.

Acknowledgments

References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: *International Symposium on Information Theory Akadémiai Kiadi* (B. N. Petran & F. Czàki eds), pp. 267–281. Budapest, Hungary.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.

Bright, A. & Waas, J.R. 2002. Effects of bill pigmentation and UV reflectance during territory establishment in blackbirds. *Anim. Behav.* **64**: 207–213.

Brodie, E.D., Moore, A.J. & Janzen, F.J. 1995. Visualizing and quantifying natural selection. *Trends Ecol. Evol.* **10**: 313–318.

Burnham, K.P. & Anderson, D.R. 1998. *Model Selection and Inference. A Practical Information-Theoretic Approach*. Springer, New York.

Choquet, R., Reboulet, A.-M., Pradel, R. & Lebreton, J.-D. 2000. *U-CARE: User's Guide*. CEFE-CNRS, ftp://ftp.cefe.cnrs-mop.fr/pub/biom/soft-CR2000Montpellier.

Cords, R. & Partridge, L. 1996. Courtship reduces longevity of male *Drosophila melanogaster*. *Anim. Behav.* **52**: 269–278.

Creighton, E. 2000. *Reproductive Strategies in the European Blackbird, Turdus merula*. PhD thesis. The Open University, Milton Keynes.

Faivre, B., Préault, M., Théry, M., Secondi, J., Patris, B. & Cézilly, F. 2001. Breeding strategies and morphological characters in an urban population of blackbirds, *Turdus merula*. *Anim. Behav.* **61**: 969–974.

Faivre, B., Grégoire, A., Préault, M., Cézilly, F. & Sorci, G. 2003. Immune activation rapidly mirrored in a secondary sexual trait. *Science* **300**: 103.

Harvey, P.H. & Bradbury, J.W. 1991. Sexual Selection. In: *Behavioural Ecology*, 3rd edn. (J. R. Krebs & N. B. Davies, eds), pp. 203–233. Oxford, Blackwell.

Hatchwell, B.J., Wood, M.J., Anwar, A.M., Chamberlain, D.E. & Perrins, C.M. 2001. The haematozoan parasites of Common

Blackbirds *Turdus merula*: associations with host condition. *Ibis* **143**: 420–426.

Jennions, M.D., Møller, A.P. & Petrie, M. 2001. Sexually selected traits and adult survival: a meta-analysis. *Q. Rev. Biol.* **76**: 3–36.

Kingsolver, J.G. & Smith, S.G. 1995. Estimating selection on quantitative traits using capture-recapture data. *Evolution* **49**: 384–388.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gibert, P. & Beerli, P. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* **157**: 245–261.

Lande, R. & Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.

Lebreton, J. D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**: 67–118.

Lozano, G.A. 1994. Carotenoids, parasites, and sexual selection. *Oikos* **70**: 309–311.

Olson, V.A. & Owens, I.P.F. 1998. Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol. Evol.* **13**: 510–514.

Owens, I.P.F. & Bennett, P.M. 1994. Mortality costs of parental care and sexual dimorphism in birds. *Proc. R. Soc. Lond. B* **257**: 1–8.

Préault, M. 2003. *Sélection sexuelle et qualité individuelle chez le Merle noir (Turdus merula)*. PhD thesis, Université de Paris 6, France.

Rohwer, S., Fretwell, S.D. & Niles, D.M. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Am. Nat.* **115**: 400–437.

Snow, D.W. 1958. *A Study of Blackbirds*. British Museum, London.

Van Tienderen, P.H. 2000. Elasticities and the link between demographic and evolutionary dynamics. *Ecology* **81**: 666–679.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (Suppl.): 120–138.