The University of Chicago

Evolutionary Response to Selection on Clutch Size in a Long-Term Study of the Mute Swan.
Author(s): Anne Charmantier, Christopher Perrins, Robin H. McCleery, and Ben C. Sheldon
Source: *The American Naturalist*, Vol. 167, No. 3 (March 2006), pp. 453-465
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/499378
Accessed: 07/08/2014 18:08

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist.*

http://www.jstor.org

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

Evolutionary Response to Selection on Clutch Size in a Long-Term Study of the Mute Swan

Anne Charmantier,[*] Christopher Perrins,[†] Robin H. McCleery,[‡] and Ben C. Sheldon[§]

Edward Grey Institute, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom

Submitted April 27, 2005; Accepted October 7, 2005; Electronically published January 9, 2006

Online enhancement: table.

abstract: Life-history traits in wild populations are often regarded as being subject to directional selection, and the existence of substantial variation and microevolutionary stasis of these characters is therefore a problem in need of explanation. Avian clutch size is an archetypal life-history trait in this context, and many studies have sought to test explanations for stasis in clutch size. Surprisingly, there are many fewer studies that used long-term data to ask how selection acts on clutch size, particularly in a multivariate framework. In this article, we report selection, inheritance, and evolution of clutch size over 25 years in a colony of mute swans using a multivariate quantitative genetic framework to control for correlations with breeding time. We show that clutch size is influenced by both additive genetic and permanent environmental effects and that selection acts on clutch size in combination with breeding time. Natural selection on clutch size is strongly directional, favoring larger clutches, and we observe an increase in clutch size of 0.35 standard deviations, consistent with the expected response based on selection and inheritance of clutch size. We hypothesize that these changes result from recent relaxation of food constraints and predation risks experienced by this colony.

Keywords: additive genetic variance, animal model, breeding values, clutch size, microevolution.

Clutch size is a fundamental life-history trait of major importance for individual reproductive success (e.g., Lack 1954). In birds, many studies have shown that clutch size is heritable (typical heritability around 0.2–0.4; Perrins and Jones 1974; van Noordwijk et al. 1981; Boag and van Noordwijk 1987; Sheldon et al. 2003; Postma and van Noordwijk 2005*a*). Some studies point to stabilizing selection on clutch size (van Noordwijk et al. 1981; Sheldon et al. 2003), but a great many long-term bird studies suggest that clutch size is under positive directional selection (e.g., Boyce and Perrins 1987; Rockwell et al. 1987; Gibbs 1988; Cooke et al. 1990; Tinbergen and Sanz 2004). Genetic variation in clutch size, combined with directional selection, predicts an increasing clutch size over time (review in Postma and van Noordwijk 2005*b*). Nevertheless, most of the studies with a temporal component have failed to find evidence for an increase of clutch size over time (e.g., Boyce and Perrins 1987), and there were similar results from studies of selection on breeding time (e.g., Price et al. 1988; Sheldon et al. 2003). This has led to an extensive debate in the literature, which was first focused on the question, Why does a population's average clutch size differ from the most productive clutch size (e.g., Lack 1966)? Gradually, the debate switched to an evolutionary point of view with a second, related question, Why is clutch size not evolving, despite significant heritability and directional selection (e.g., Price and Liou 1989; Cooke et al. 1990)?

One explanation found in the literature for the common absence of evolution in clutch size is that an environmental factor is correlated with both clutch size and fitness (Cooke et al. 1990). In particular, evolution of clutch size is suggested to be constrained by correlations with traits that are mainly environmentally determined, such as the female's nutritional state or her ability to acquire nutrients (Price and Liou 1989). To assess this explanation, one needs to, first, investigate trait genetic changes and not only phenotypic changes; second, gather large amounts of data on a long-term basis; and third, control for potentially correlated traits by conducting multivariate analyses. Surprisingly, although the debate on life-history evolution of clutch size in birds has been vigorous and ongoing for more than 50 years, rather few such studies have been conducted. The majority of the investigations of clutch

[*] Corresponding author; e-mail: anne.charmantier@zoo.ox.ac.uk.

[†] E-mail: chris.perrins@zoo.ox.ac.uk.

[‡] E-mail: robin.mccleery@zoo.ox.ac.uk.

[§] E-mail: ben.sheldon@zoo.ox.ac.uk.

Am. Nat. 2006. Vol. 167, pp. 453–465. © 2006 by The University of Chicago. 0003-0147/2006/16703-41048$15.00. All rights reserved.

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

Table 1: Studies of unmanipulated natural bird populations reporting selection on clutch size, measured over more than 1 year, published since the 1983 publication of Lande and Arnold's method to estimate natural selection on correlated traits

		Measures of selection reported				
Species	No. years	Linear selection	Nonlinear selection	Multivariate selection	Correlational selection	Reference
Parus major	23	Yes	Yes	Yes	No	Boyce and Perrins 1987
Anser caerulescens caerulescens	11	Yes	Yes	No	No	Rockwell et al. 1987
Geospiza fortis	6	Yes	Yes	No	No	Gibbs 1988
Ficedula albicollis	7	Yes	No	No	No	Gustafsson and Sutherland 1988
Empidonax minimus	3	Yes	No	No	No	Briskie and Sealy 1989
Parus major	14	Yes	Yes	Yes	No	Tinbergen and Daan 1990
Parus major	5	Yes	Yes	Yes	Yes	Hõrak et al. 1997
Parus caeruleus	3	Yes	Yes	Yes	No	Svensson 1997
Petrochelidon pyrrhonota	3	Yes	No	No	No	Brown and Brown 1999
Ficedula albicollis	19	Yes	Yes	Yes	Yes	Sheldon et al. 2003
Parus major	16 + 21	Yes	No	No	No	Postma and van Noordwijk 2005*a*

Note: We considered as multivariate analyses those studies employing multiple regression but also studies using residuals of clutch size correcting for a correlated trait (e.g., Boyce and Perrins 1987). We included here some experimental studies (Boyce and Perrins 1987; Gustafsson and Sutherland 1988; Briskie and Sealy 1989; Brown and Brown 1999) in which selection in unmanipulated nests was analyzed separately from manipulated broods.

size evolution to date rely on brood size manipulation experiments before or after hatching (e.g., Pettifor et al. 1988; Moreno et al. 1991; Tinbergen and Sanz 2004) to test whether parents lay the optimal clutch size that maximizes recruitment or the sum of parental and offspring fitness (Perrins 1964). However, interpretation of these experiments is hampered by their underestimation of costs of reproduction, such as the energy expenditure for egg laying and/or egg incubation, which undoubtedly influence the overall selection for clutch size (Monaghan and Nager 1997; Visser and Lessells 2001). Also, even if clutch size is individually optimized, this does not provide a complete explanation of why individuals laying larger clutches do not come to predominate in natural populations. Hence, although these experiments are a useful way to test for a phenotypic trade-off between clutch size and offspring survival, a complementary approach is necessary to reach conclusions relevant to genetic changes while controlling for correlated traits. Purely analytical approaches have their drawbacks as well, but they can be invaluable in identifying the key experimental manipulations that need to be conducted.

Recently, both data and methods have become available that make it possible to investigate genetic changes in clutch size over time while controlling for correlations with other traits. First, with the use of complex pedigrees obtained from long-term population monitoring, restricted maximum likelihood (REML) procedures (Meyer 1989; Knott et al. 1995) allow us to predict individual breeding values. These are based on the phenotypic observations of the individual itself as well as on the performances of all related individuals while controlling for various environmental factors. The predicted breeding value will be a measure of the additive effects of an individual's genes, that is, the expected effect of its genes passed on to its offspring (Lynch and Walsh 1998). Studying changes in predicted breeding values allows us to check whether changes of phenotypes over time are merely the result of a plastic response to changes in environmental conditions or whether there is a true underlying genotypic change (Hendry and Kinnison 1999). Second, we can perform multivariate quantitative genetic and selection analyses to control for the occurrence of genetic correlations between the focal trait and other traits under selection (Lynch and Walsh 1998). Multivariate regressions can disentangle the direct and indirect effects of selection and allow an estimation of selection gradients on all correlated characters (Lande 1979; Lande and Arnold 1983). The extent to which the genetic correlations can be accounted for depends on the number and the nature of the correlated traits and how easily they can be measured. Surprisingly, the publication of Lande and Arnold's (1983) approach for the estimation of the magnitude of selection on correlated characters has been followed by very few multivariate studies investigating selection on clutch size over multiple years in natural bird populations (table 1); there are only five, to our knowledge (Boyce and Perrins 1987; Tinbergen and Daan 1990; Hõrak et al. 1997; Svensson 1997; Sheldon et

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

al. 2003). Also, although a phenotypic correlation between laying date and clutch size has been well documented (review in Merilä and Sheldon 2001), hardly any estimates of genetic correlations exist (but see Sheldon et al. 2003). Thus, despite the status of avian clutch size as a model trait for understanding phenotypic variation in the wild (Fox et al. 2001; Bennet and Owens 2002), there have actually been remarkably few comprehensive studies of natural selection on this trait. Consequently, our understanding of evolutionary dynamics of this trait is meager.

Here we present a study investigating selection on, and microevolution of, clutch size in a mute swan (*Cygnus olor*) colony. Many of the studies of selection on clutch size have been performed on small passerines with relatively "fast" life histories, and one motivation for this analysis was a wish to explore the behavior of this character in a bird with a relatively "slower" life history. Combining multivariate quantitative genetic and selection analyses controlling for potential genetic correlations with laying date and for indirect selection, we show that this population has displayed a clear microevolutionary change in clutch size that is consistent with patterns of natural selection on this character.

Methods

Study Site and Data Collection

Historical records show that the mute swan colony at Abbotsbury, Dorset (on the south coast of England at 50°39′N, 2°36′W), has existed since at least the mid-fourteenth century, although detailed population records do not exist before the 1960s. Monitoring of individually marked birds started in 1976. The study site at the Abbotsbury Swannery is described in detail by Perrins and Ogilvie (1981) and Perrins et al. (1994). Since the early 1970s, when the number of breeding pairs in the colony was around 20, the numbers have slowly built up and since 1991 have exceeded 100 pairs in all but 2 years, with a peak of 163 pairs in 2001. By 1990, none of the adults breeding in 1976 were still alive. Hence, from 1990 on, virtually all the breeders had been ringed as cygnets in the colony and so were of known age (some 10% of the breeding males and 5% of the females are immigrants of unknown origin and age).

During the breeding season, most of the swans' nests are located in an area of about 1 ha, with some nests as little as 2 to 3 m apart. Nests are visited daily, and date of first egg (laying date), clutch size, and hatching dates are recorded for all nests. Females were considered to have died if they were not recorded breeding for two successive years and had not been caught in the roundups that occur in July of alternate years. In late September or early October, when the cygnets are almost fully grown, they are ringed with a unique metal British Trust for Ornithology ring and a large numbered plastic (Darvic) ring that can be read in the field without having to recapture the bird. It was usually possible to identify the parents of each cygnet, but because the cygnets can switch broods, a small number of them may have been assigned to the wrong parents. After 1989, this problem was eliminated by web-tagging all cygnets within 2 days of hatching, before the brood left the nest. Of the 4,012 cygnets web-tagged between 1989 and 1998, 446 (11.1%) have recruited as breeders in the population.

Records of mute swans sighted in the United Kingdom as well as the rest of Europe show that 2.5% of cygnets ringed in Abbotsbury between 1976 and 2003 were seen outside the colony area. This order of magnitude for cygnet dispersal was considered insignificant for the following analyses.

It must be stressed that the population is not entirely natural. The two most unnatural management procedures relate to the amount of food provided to the swans and the use of rearing pens. First, the swans currently are provided with supplementary food throughout the year, including during the run-up to the breeding season, and the growing cygnets are also fed. This food supplementation began in 1975–1976 when a new warden took charge in the Swannery. Second, some of the cygnets are placed in rearing pens, either with their parents or with other families. In the pens, in addition to receiving supplementary food, the cygnets are protected from aggression from breeding adults and are somewhat safer from predators. As a consequence, their survival to fledging is considerably increased compared with cygnets reared outside pens (Perrins and Ogilvie 1981). Although overall standard general linear models showed no effect of pen rearing on either laying date or clutch size (laying date: $F = 0$, df $= 1, 1{,}796$, $P = .993$; clutch size: $F = 0.78$, df $= 1, 1{,}796$, $P = .377$), this factor was included as a fixed effect in our quantitative genetic analyses to account for possible interactions with other independent variables. Notwithstanding these two points, the population is free ranging and not subject to any other form of intervention.

In the following analyses, we consider the breeding attempts recorded between 1979 and 2003; 101 attempts when females abandoned their nest after laying one or two eggs have been omitted, leaving 2,141 records for which a precise laying date and clutch size are known. In 70% of these attempts, the female's mother was known and was herself recorded as a breeder, which allowed us to control for maternal effects on reproductive traits. Out of 502 breeding females, 132 (26.3%) had more than one male partner during their reproductive lifetime. The pedigree of breeding individuals used in the quantitative genetics

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

analyses included a total of 960 individuals, with 209 fathers of recruited individuals and 189 mothers in the pedigree. The longest family branch included six successive generations.

Laying Date and Clutch Size as Sex-Limited Traits

Although usually considered to be female-restricted phenotypes, laying date and clutch size may be subject to the male partner's influence. For example, females may allocate resources differentially depending on male attractiveness, or they may be influenced by other male characteristics such as territory quality (Kirkpatrick et al. 1990; Sheldon 2000). To test for an influence of males on both traits, we performed generalized linear mixed models (GLMMs) with ASReml software (Gilmour et al. 2002), using female and male identity as random effects. Standard linear models showed that year of breeding, year of birth of the female, and age of the female, fitted as categorical variables, all had highly significant effects on laying date and clutch size (all $P < .0001$). Hence, these three factors were fitted as fixed effects in the GLMM. This model included 510 pairs of swans, with 431 males and 387 females having bred more than once. Laying date seemed to be influenced by both male and female identities (t-tests on variance components, both $P < .001$), whereas clutch size was influenced by female identity (variance component, 0.49 ± 0.08, $t = 5.84$, $P < .001$) but not significantly by male identity (variance component, 0.10 ± 0.06, $t = 1.67$, $P = .095$). In the absence of positive evidence for male effects on clutch size, we will consider clutch size as a sex-limited trait when estimating its heritability and its evolutionary response. Because almost 75% of females had only one male breeding partner during their reproductive life, the male effect on the laying date will be included mainly within the permanent environment effect fitted in the quantitative genetic analyses, which accounts for repeated environmental conditions (see next section).

Quantitative Genetic Analyses

Variance components for laying date and clutch size were estimated using a multivariate restricted maximum likelihood procedure with the software ASReml, release 1.1 (Gilmour et al. 2002). An individual "animal model" (Lynch and Walsh 1998; Kruuk 2004) was fitted using the pedigree of breeding swans and the phenotypic values of all breeders. The animal model is a form of mixed model with fixed and random effects that partitions the variance in phenotypic values for a quantitative character into different components (see recent applications in Réale and Festa-Bianchet 2000; Merilä et al. 2001; Garant et al. 2004; review in Kruuk 2004):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e}. \tag{1}$$

In the above matrix form of the animal model, $\mathbf{y}$ is the vector of phenotypic observations, $\mathbf{b}$ and $\mathbf{a}$ are the vectors of fixed and random effects, $\mathbf{e}$ is the vector of residual errors, and $\mathbf{X}$ and $\mathbf{Z}$ are the design matrices relating the fixed and random effects to each individual record. The ASReml software uses all the pedigree information combined with the phenotypic records to estimate the variance components using restricted maximum likelihood. ASReml also estimates the best linear unbiased estimates (BLUEs) and the best linear unbiased predictors (BLUPs) for the fixed effects and the random effects, respectively (Gilmour et al. 2002). The BLUPs of the additive genetic effect are predictors of the individuals' breeding values (Lynch and Walsh 1998) or, in other words, the expected effect of their genes passed on to their offspring.

Similarly to the GLMMs described above to test sex limitation, year of breeding, year of birth of the female, and age of the female were fitted as categorical fixed effects along with a bimodal factor indicating whether the female was brought up in a pen. However, because they are not the focus of this study, these fixed effects will not be reported in detail. The data set included 2,141 records on 502 breeding females, of which 388 (77.3%) had bred more than once. There were on average 4.3 (SD = 3.3) records per female, and the maximum number of breeding attempts by a single female was 16. Repeated records on individuals throughout their lifetimes allowed us to account for and estimate the variance caused by persistent differences between individuals that were not already attributed to the additive genetic variance. These effects include nonadditive genetic effects as well as conditions in the environment that explain persistent individual differences over time. They will hereafter be called the permanent environment effects and were fitted in the model as a random effect. Mother identity was also fitted as an additional random effect, in order to estimate the maternal environmental effect. Maternal effects occur when the phenotype of the mother affects the phenotype of her offspring, triggering higher resemblance between them (Falconer and Mackay 1996). In accordance with the GLMMs testing for sex limitation, an additional male identity random effect accounted for a significant proportion of the variance in laying date (but not clutch size), reducing the part of the variance attributed to permanent environment effect. Because all other variance components were unchanged, details of this model are not presented. One potential drawback of the animal model compared to traditional techniques is its increased computational complexity, where model overspecification can hamper the interpretation of the results; we therefore aimed to reduce model complexity where possible.

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

The total phenotypic variance (V_P) was partitioned as

$$V_P = V_A + V_M + V_{PE} + V_R, \quad (2)$$

where V_A is the additive genetic variance, V_M is the maternal effect variance, V_{PE} is the permanent environment effect variance, and V_R is the residual variance.

The narrow-sense heritability, which describes the degree to which offspring can be expected to resemble their parents, is defined as $h^2 = V_A/V_P$. Standard errors for all variance components and for their ratio over the total phenotypic variance were computed with ASReml. Statistical significance of variance components and of variance ratios was assessed by z scores tested against a standard normal distribution. To account for possible genetic correlation between the two traits studied, the animal models fitted were multivariate, including both laying date and clutch size as dependent variables.

Because the pedigree links used in the quantitative genetic analyses rely on observed pairings rather than genetic parentage, extrapair paternity (EPP) could result in underestimated heritability. Although rates of EPP have not been estimated in the mute swan, we expect typical rates of 10%–20% extrapair cygnets (e.g., 15% were recorded in the black swan *Cygnus atratus*; Kraaijeveld et al. 2004). However, according to a simulation study conducted by Charmantier and Réale (2005), our high sample size (960 breeding birds in the pedigree) will result in inconsequential biases on heritability estimation caused by EPP, especially for traits with rather low heritability such as clutch size and laying date.

Lifetime Selection Analysis

We measured natural selection on both reproductive traits using standard techniques relating fitness measures to trait values (Arnold and Wade 1984). For all analyses, characters were standardized (zero mean, unit variance) within the subset of data on which the analysis was performed (Hereford et al. 2004). Individual fitness was also converted to relative fitness by dividing by the mean fitness of all individuals within the subset of data. All analyses of selection were performed using the software SAS (SAS Institute 1992).

Lifetime fitness was estimated by the total number of offspring recruiting as breeders in the Abbotsbury population from an individual female. This estimation of lifetime reproductive success can be accurate only after a female has died and after sufficient time has elapsed for all offspring to recruit. Hence, we kept for this analysis the 377 females that did not breed after 1998 and were not alive in 2003, which still provided a relatively high power to detect selection (Hersch and Phillips 2004). Standardized directional (S') and stabilizing (c') selection differentials were estimated using univariate linear and second-order polynomial regressions, respectively (Arnold and Wade 1984). Subsequently, multivariate regressions were conducted to provide estimates of standardized directional (β') and stabilizing (γ') selection gradients, accounting for the possible correlation between the two characters (Lande and Arnold 1983). We also estimated correlational selection, which occurs when a trait's relation to fitness depends on its interaction with another trait (Phillips and Arnold 1989; Schluter and Nychka 1994; Sinervo and Svensson 2002). We estimated the standardized nonlinear selection gradient (γ'_{ij}) measuring the selection acting on the covariance between laying date and clutch size by fitting the cross product in the multivariate analysis (Lande and Arnold 1983). The fitness surface was visualized using a cubic spline fitting procedure with the software STATISTICA (StatSoft 1999), with a stiffness of 0.15 and a high fit line resolution.

Annual Selection Analysis

We performed analyses of selection separately for each year using the same type of univariate and bivariate regressions to estimate standardized selection differentials and gradients on female laying date and clutch size. Annual measures of fitness were number of hatchlings (estimated for 1979–2003), female survival to the next breeding season (1979–2001), and number of recruits (1979–1998; 82% of the females breed for the first time at 5 years or younger). Statistical significance of the standardized selection differentials and the selection gradients was assessed using regressions with normal errors for the lifetime number of recruits, the number of hatchlings, and the number of recruits and binomial errors for female survival (see Sheldon et al. 2003).

Response to Selection

Using the breeders' equation (Falconer and Mackay 1996), one can theoretically predict the evolutionary response of a trait: $R = h^2S$, where h^2 is the heritability of the trait based on univariate analyses and S is the nonstandardized directional selection differential. However, if two characters are correlated genetically, the expected response in one of the traits depends not only on the direct selection acting on it but also on the genetic correlation between the traits and the selection acting on the correlated trait. The response of trait 1 is in that case given by the equation

$$R = h_1^2\beta_1 + r_g h_1 h_2 \beta_2, \quad (4)$$

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

Table 2: Components of phenotypic variances and standard errors for laying date (March 1 = 1) and clutch size in Abbotsbury's mute swans, estimated using a multivariate animal model on 2,141 observations from 502 breeding females over 25 years

	March laying date		Clutch size	
	Variance ± SE	% of total ± SE	Variance ± SE	% of total ± SE
V_R	65.03 ± 2.71***	64.5 ± 3.2***	1.39 ± .06***	66.5 ± 3.3***
V_A	0	0	.41 ± .13**	19.5 ± 5.8***
V_M	9.11 ± 3.60*	9.0 ± 3.4**	0	0
V_{PE}	26.7 ± 4.42***	26.5 ± 3.8***	.29 ± .11**	14.0 ± 5.2**
Trait mean (±SD)	47 ± 11		5.5 ± 1.5	
Phenotypic correlation	−.50 ± .02***			

Note: V_R = residual variance, V_A = additive genetic variance, V_M = variance due to common mother environment, V_{PE} = variance due to permanent individual environment. Year of breeding, year of birth, age of females, and pen rearing were fitted as categorical fixed effects.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

where h_1^2 is the heritability of trait 1, β_1 is its standardized selection gradient, r_g is the genetic correlation coefficient, and h_2^2 and β_2 are the standardized selection gradient and genetic correlation coefficient of trait 2, respectively. In the case of a sex-limited trait, the expected response is halved because only one sex is under selection.

We predicted the expected rate of change of clutch size in the Abbotsbury swan population using this equation, with the selection gradients calculated from the analysis of selection on females for the lifetime number of recruited offspring. The value of R was compared with the actual rate of change of phenotypes and breeding values over the study period (1979–2003), which were calculated using linear regressions of annual means over time, weighting for the number of observations per year and including laying date as a covariate.

Accuracy of the Breeding Value Prediction

Although the accuracy of a quantitative genetic analysis determines how well evolution can be understood or predicted, very few studies give an indication of their own reliability. The accuracy of the predicted breeding values is measured by their variance ($V_{\hat{A}}$) compared with the additive genetic variance (Cameron 1997):

$$r_{A\hat{A}} = \sqrt{\frac{V_{\hat{A}}}{V_A}}. \tag{5}$$

The effective number of records is an indication of the mean number of records per female, provided by repeated measures on the same female, as well as pedigree links with other measured individuals. It is defined as (Cameron 1997)

$$n_e = \frac{\lambda}{1 - r_{A\hat{A}}^2} - \lambda, \tag{6}$$

with

$$\lambda = \frac{1 - h^2}{h^2}.$$

In our study, $r_{A\hat{A}} = 0.65$ and $n_e = 3.9$. For comparison, using one mean value per female instead of repeated values would have led to $r_{A\hat{A}} = 0.57$ and $n_e = 1.3$.

Results

Quantitative Genetic Analyses

The multivariate animal model using repeated measures on 502 females showed no additive genetic variance for laying date but significant V_A for clutch size, translating into a significant heritability of 0.195 ± 0.058 ($z = 3.35$, $P < .001$; table 2). Phenotypes for laying date and clutch size were highly significantly negatively correlated (table 2). We did not investigate genetic correlation between the two traits or predict breeding values for laying date because this trait, analyzed in this way, did not display any additive genetic variance (however, see Charmantier et al., forthcoming, for evidence of age-specific genetic variance for laying date).

Maternal environment effects estimated through the animal model explained a significant portion of the variance in laying date but not in clutch size (table 2). The permanent environment component was significant for both traits, indicating that persistent differences in local environment between females explained an important part of the variation in both laying date and clutch size. For clutch size, this effect was of roughly the same magnitude as

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

additive genetic effects, while for laying date the permanent environment effect accounted for 27% of the total trait variance (table 2).

Selection Analyses

The total number of offspring a female recruited into the population was negatively associated with her laying date, averaged over her lifetime (table 3). Hence, females laying earlier had more cygnets breeding in later years than females laying late. This was true even after correcting for the correlated selection acting on clutch size ($\beta' = -0.313 \pm 0.107$, $t = -2.92$, df $= 1,374$, $P = .004$). Clutch size was significantly positively selected, also after correction for indirect selection ($\beta' = 0.519 \pm 0.107$, $t = 4.84$, df $= 1,374$, $P < .001$). The selection surface had a characteristic ridgelike aspect (fig. 1; Sinervo and Svensson 2002), which illustrates the significant negative bivariate nonlinear selection gradient (table 3): females are selected for one main adaptive peak with early laying dates and large clutches. This evidence for consistent correlational selection acting on laying date and clutch size over the study period is in accordance with the negative phenotypic correlation observed between the two traits (table 2; Brodie 1992; Sinervo and Svensson 2002).

Annual selection gradients showed consistent negative selection on laying date via number of hatchlings, female survival, and number of recruits (for details, see table A1 in the online edition of the *American Naturalist*). Clutch size was very strongly positively selected via number of hatchlings (all selection gradients were positive, and 24 out of 25 were significant) as well as number of recruits (all selection gradients positive, and eight out of 21 were significant). However, there was no evidence for an association between clutch size and subsequent female survival (table A1). No selection gradient showed temporal dependence (weighted GLMs, $F_{1,24}$, $F_{1,21}$, $F_{1,19}$ for selection on number of hatchlings, female survival, and number of recruits, respectively, all $P > .1$), with the exception of the selection on laying date via female survival, which became weaker over time ($F = 7.02$, df $= 1,21$, $P = .015$).

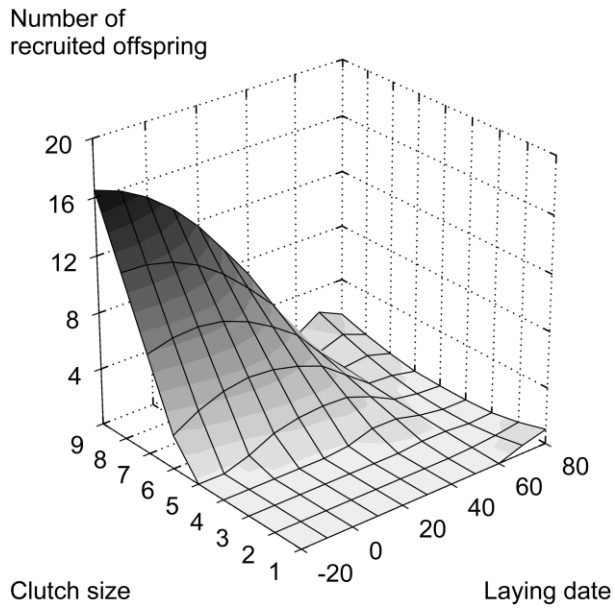

Figure 1: Fitness surface for laying date and clutch size visualized using a cubic spline smoothing procedure. Fitness is estimated as the total number of offspring recruited in a female mute swan's lifetime. For laying date, March 1 = 1.

Response to Selection

According to the breeders' equation, with heritability of laying date being null, the trait is not expected to evolve over time, whether subject to direct selection or indirect selection via a correlated trait. In accordance with this expectation, phenotypic values of laying date did not change significantly over time (fig. 2 *top*). The directional positive selection on clutch size, combined with an estimated heritability of 0.19, and accounting for sex limitation, leads to a predicted rate of change of 0.078 eggs/swan generation. Average generation time as calculated following Charlesworth (1994) was 7.2 years. Hence, the predicted rate was $R = 0.011$ eggs/year. Over the study period, clutch size increased both at the phenotypic (fig. 2 *bottom*) and genetic (fig. 3) level. The slope of the phe-

Table 3: Selection on laying date and clutch size of female mute swans for lifetime number of offspring recruited

Trait under selection	N	S'_i (SE)	c'_i (SE)	β'_i(SE)	γ'_i (SE)	γ'_{ij} (SE)
Laying date	377	−.550 (.098)***	−0.058 (.038)	−.313 (.107)**	−.072 (.040)	
Correlated coefficient						−.339 (.113)**
Clutch size	377	.662 (.096)***	.127 (.068)	.519 (.107)***	.009 (.078)	

Note: Standardized selection differentials (S' = linear models for directional selection; c' = quadratic models for stabilizing/disruptive selection) and selection gradients (β' = linear; γ' = quadratic) were calculated using univariate and bivariate regression models, respectively. The analysis included 377 females, which all died before 2003.

** $P < .01$.

*** $P < .001$ after Bonferroni sequential correction.

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

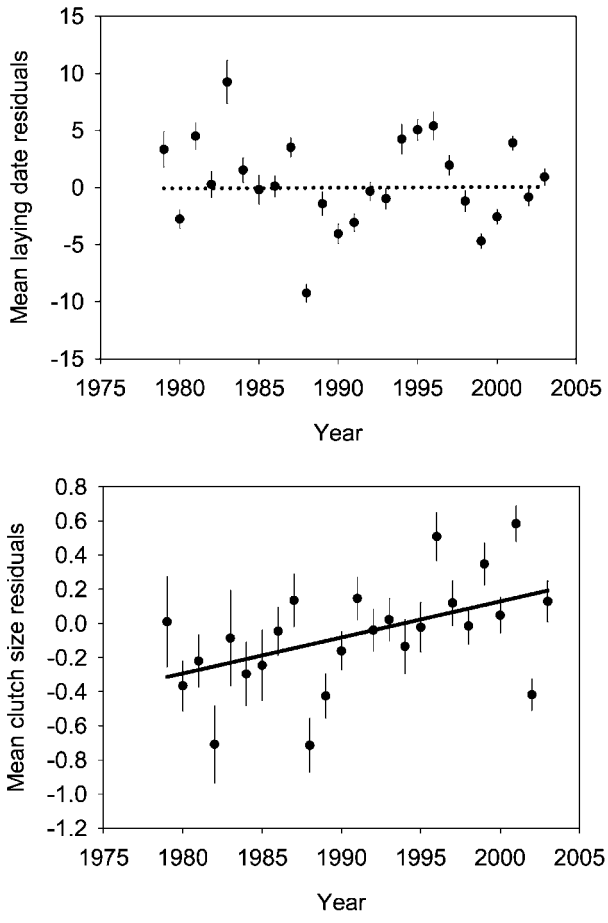

Figure 2: Trends over time for mean residuals of laying date after controlling for the correlated clutch size (*top*) and residuals of clutch size after controlling for laying date (*bottom*), in the Abbotsbury swan population (1979–2003). Bars represent 1 SEM. There is no trend of laying date over time (weighted linear regression with clutch size as covariate: $b = 0.129 \pm 0.104$, $t = 1.25$, df $= 24$, $P = .226$); in contrast, clutch size increases significantly over time (weighted linear regression with laying date as covariate: $b = 0.022 \pm 0.009$, $t = 2.52$, df $= 24$, $P = .019$). Dotted lines illustrate nonsignificant regressions.

notypic change over time was not different from the expected response to selection ($n = 25$ years [1979–2003]; $b = 0.022 \pm 0.009$; comparison with R, $z = 1.27$, $P = .205$). Similarly, the significant increase in clutch size breeding values over female birth years fitted with the expected response to selection ($n = 26$ years [1974–1999]; $b = 0.009 \pm 0.002$; comparison with R, $z = 1.10$, $P = .271$).

The increase of clutch size over time could be the result of a plastic change within the population, without any underlying genetic change, or an improvement in the quality of the environment. The change in predicted breeding values over time is, however, a powerful indication of real genetic changes rather than a phenotypically plastic response of clutch size in the population. Data from long-lived species offer an opportunity to test whether animals with similar genes show different phenotypes at different periods over a longitudinal study. Cooke et al. (1990) suggested that a comparison of the phenotypes of daughters born to the same mother separated in time by many years would be an effective way to test the relative roles of genetic and environmental change in phenotypic evolution. If the population's ability to exploit the environment had improved over a period of time, than the phenotype of daughters from the same mother would differ in accordance with the population change. A general linear model, including age of the breeding daughter and year as fixed effects, did not show any significant dependence of the daughter's clutch size on the age of the mother when the daughter was born, although there was a positive trend (fig. 4). This confirms that phenotypic plasticity cannot fully explain the changes observed in clutch size.

Discussion

Studies showing evolutionary responses over a small temporal scale have rarely been reported (but see, e.g., Losos et al. 1997; Rethink et al. 1997; Garant et al. 2005), especially so in wild populations (review in Hendry and Kinnison 1999). The reason for this scarcity is probably in part that explaining the evolutionary dynamics of quantitative traits in the wild requires exceptional long-term data sets, with information on both phenotypes and relatedness over many generations. Hence, apart from a small number of well-known studies, such as the evolution

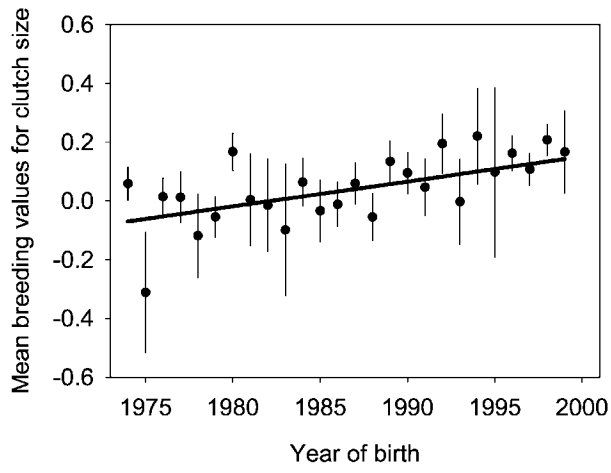

Figure 3: Increase of mean clutch size breeding values for females over their year of birth (1974–1999, $b = 0.009 \pm 0.002$, $t = 3.98$, df $= 25$, $P < .001$). Bars represent 1 SEM.

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

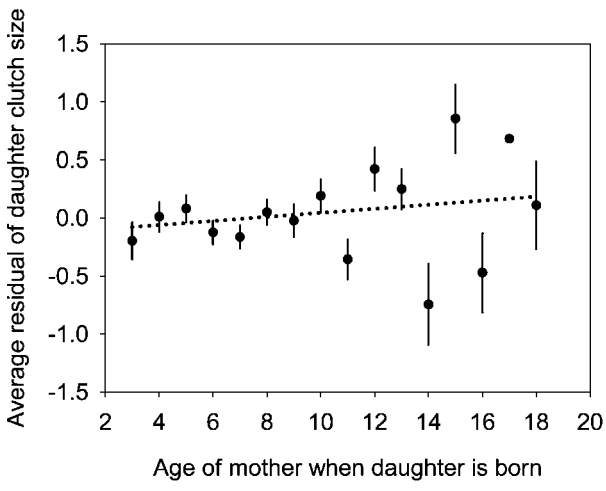

Figure 4: Average clutch size of daughters, standardized for their year of breeding and their age, does not increase significantly with their mother's age when they were born (weighted linear regression: $b = 0.017 \pm 0.017$, $t = 1.02$, df = 15, $P = .3252$). Bars represent 1 SEM.

of Darwin's finches' beak morphometry on the Galápagos Islands that is related to episodic selection (see, e.g., Grant and Grant 1993, 1995, 2002), clear evidence for microevolutionary change in natural populations is very limited in contrast to the number of laboratory studies that give support for the ability of quantitative genetic theory to predict evolutionary response (Falconer and Mackay 1996). Here we have shown that a heritable life-history trait under strong positive directional selection, namely, clutch size in a mute swan population, increased by 0.35 standard deviations over 25 years. This result contrasts with the many studies on bird clutch size that suggest that this trait is at evolutionary equilibrium (Gibbs 1988; Pettifor et al. 1988; Coach et al. 1989; Cooke et al. 1990; Dhondt et al. 1990; Sheldon et al. 2003; Tinbergen and Sanz 2004).

Traditionally, one of the main explanations proposed for this absence of evolution is the correlation between clutch size and traits that are environmentally determined, such as female nutritional state. Although detailed data on food abundance in the colony is lacking, we suggest that the evolution of clutch size in Abbotsbury swans may in fact have been facilitated by the food supplementation scheme that started in 1975–1976. This change in the environment could thus have relaxed food constraints, allowing for a rapid evolution of clutch size. Below, we discuss explanations for the striking results in this study.

No Genetic Variance for Laying Date

One surprising result of this study is the estimated zero additive genetic variance for laying date (table 2), which to our knowledge is the first such published with reasonable sample size for analysis. In the literature, laying date heritability is typically between 0.15 and 0.5 and thus well within the range usually attributed to life-history traits (Merilä and Sheldon 2001). However, in the first attempt to estimate heritabilities of laying date and clutch size simultaneously using an animal model, Sheldon et al.'s (2003) study on the collared flycatcher (*Ficedula albicollis*) showed a low level of additive genetic variance for laying date compared with mother-daughter regressions. Although surprising, our result is likely to be robust given the high power of our animal model, as shown by the significant heritability in clutch size and the accuracy of our predicted breeding values. Additive genetic variance expressed for laying date in the mute swan is in fact a complex factor dependent on age-specific effects, as we show in a complementary article (Charmantier et al., forthcoming).

The Importance of Permanent Environment: Valuable Repeated Measures

This study illustrates the importance of controlling for environmental effects such as the permanent environment or maternal effects. In our analysis, permanent between-individuals differences, which are most commonly not included in other studies (but see Réale et al. 1999; Coltman et al. 2001), accounted for 27% of the variance in laying date and 14% of the variance in clutch size. This suggests that environmental effects that are persistent for a female swan between years (beyond additive genetic effects), and that differ from the conditions experienced by other females, are important in determining both how many eggs she will lay and the date at which she will lay them (see also van der Jeugd and McCleery 2002). The origin of these persistent differences could be long-term effects of conditions early in life (Lindström 1999), other constant environmental conditions such as a female's breeding site or her pairing with a specific male if such effects are constant over most of the life of an individual, or finally, nonadditive genetic effects that are also individual specific and permanent. More studies are needed to identify which environmental factors determine these consistent permanent conditions, as well as to assess whether certain species (such as swans) may be predisposed to permanent environmental conditions, as a result, for example, of their long-lasting pair bonds or extreme site fidelity. Unfortunately, measuring this environment component of variance requires repeated observations across years on the same individuals. Collecting sufficient longitudinal data on the same individuals is really feasible only in long-lived mammals and birds. In most long-term studies of passerines (e.g., Sheldon et al. 2003; Møller and Szep 2005), the mean

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

number of repeated observations per individual is not adequate to control for permanent environment effects, leading to the use of an average or a unique record (but see Postma and van Noordwijk 2005*a*).

The increased accuracy in heritability estimation in our study because we control for permanent environment effects may explain why our estimation of clutch size heritability (0.19) is toward the low end of the range of estimates found in other studies. The advantage of repeated measures is also reflected in the increased accuracy of estimated variance components and predicted breeding values when using all measures ($r_{A\hat{A}} = 0.65$) as opposed to using an average value ($r_{A\hat{A}} = 0.57$). The precision with which the breeding values are predicted is a key factor minimizing the bias in the predictions of the trait's evolution.

Lifetime Selection for Clutch Size

As commonly found in studies of birds, clutch size and laying date were negatively correlated (table 2). Several studies have failed to show independent direct selection on clutch size once this correlation was accounted for (e.g., Boyce and Perrins 1987; Hõrak et al. 1997; Sheldon et al. 2003). However, our analyses show that laying date and clutch size in this mute swan population are both subject to independent selection (table 3). The estimated directional selection differential for clutch size (0.662 ± 0.096) is well within the upper range of the values found in the literature (e.g., $S = 0.33$ in lesser snow geese *Anser caerulescens caerulescens*; Rockwell et al. 1987), particularly given the large sample size. Lack of positive directional selection on clutch size has previously been commonly attributed to life-history trade-offs (although as we have stressed, there have been few comprehensive studies of multivariate selection). First, although larger clutches confer higher annual reproductive success, they may be correlated with subsequent reduced female survival, resulting in a lifetime reproductive success no higher than the average (Price and Liou 1989). Such a phenotypic trade-off is not obviously present in mute swans because clutch size is positively selected both annually and over a female's lifetime, with no evidence for consistent negative survival selection (table A1). Another common suggestion is that individual females lay the "optimal" clutch size (Pettifor et al. 1988), with a trade-off between clutch size and offspring quality. The individual optimization hypothesis has especially been tested in brood size experiments on nidicolous birds, showing highest recruitment rates for parents rearing clutches of size equal to their original ones (Pettifor et al. 2001). Once again, our results do not support any such trade-off in this population because our annual selection gradients show strong positive selection on clutch size for both the number of recruited chicks and the number of hatchlings (table A1), although a clear test would demand experimental brood size manipulation (e.g., Lessells 1986). Hence, we have here evidence for strong directional positive selection on clutch size, which, combined with significant heritability, is predicted to result in evolutionary changes over time.

Changes in Clutch Size over Time: Plasticity or Evolution?

Our phenotypic analyses show a significant increase in clutch size over time, even after correcting for the strong negative correlation with laying date (fig. 2*B*). However, these phenotypic changes need not have underlying genetic changes. In particular, if the environment changes over time, the breeders' equation's assumptions are violated, and the response we observe may be because of plasticity in response to these changes (Hendry and Kinnison 1999). Indeed, changes in clutch size within an individual's lifetime have been revealed in this mute swan population (Perrins et al. 1994). However, we have several reasons for believing that the change in clutch size over time is the result of microevolution (i.e., genetic change) and not simply a plastic response. First, annual selection gradients (table A1) show that the selection intensity and direction on clutch size do not fluctuate over time. Additionally, one way to test for phenotypic plasticity within a population in response to changes in the environment is to compare the phenotypes of daughters within a mother's lifetime (Cooke et al. 1990). In our population, daughters' clutch size was found to be independent of their mothers' age when they were born, suggesting that performances of daughters did not improve significantly because of phenotypic plasticity within the population (fig. 4). Hence, the environmental component does not seem to change consistently over the study period (1979–2003), which justifies our use of the breeders' equation. Finally, the complex pedigree and the use of the animal model methodology allowed us to predict individual breeding values, providing a powerful test for genetic changes over time. As we discussed, the complex structure of the swan pedigree used confers high accuracy to our prediction of breeding values, which should consequently not be solely dependent on an individual phenotype but more so on the performances of its relatives. This is confirmed by the correspondence between predicted and estimated genetic response to selection, providing evidence for a genetic change over time at a relatively small timescale (Falconer and Mackay 1996).

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

Past and Future Evolution of Clutch Size

In this study population, clutch size shows a response to selection, providing us with a clear illustration of microevolutionary process at a small timescale. Two questions remaining are, Why has clutch size been evolving since the early 1980s? and What happened before that? The answer to these questions may lie in changes in the environment of the colony a few years before clutch size started to increase. In nidifugous species, clutch size has been suggested to be limited by nutrient acquisition during laying (Lack 1954) or alternatively by predation (Safriel 1975). The food constraint in particular might explain why colonial swans found in Denmark and England generally have lower mean clutches (4.7–5.2) than noncolonial swans (common range: 5.5–6.1 but up to 6.7; Wieloch et al. 2004) because increased population density will probably lead to increased competition for food. This possibility seems corroborated by the fact that at Abbotsbury, mute swans have been reported to be lighter than elsewhere (Perrins and Ogilvie 1981). However, after the arrival of a new warden at Abbotsbury Swannery in 1975, both constraints were relaxed. The new management started a feeding regime to ensure the breeding swans were given additional food at the nest (D. Wheeler, personal communication). Additionally, in the mid-1980s, a secure fence was built around the colony to reduce the damage and disturbance caused by foxes (*Vulpes vulpes*) at nesting time, and security was reinforced by an electric fence in 2001. Hence, we hypothesize that in the past 25 years, we have witnessed ongoing evolution, following a change in the environment, and that the clutch size has been evolving toward a novel optimum for the new conditions of low predation and high food abundance.

This leads on to the question of how clutch size may continue to evolve in the future. The correlational selection detected between laying date and clutch size is in accordance with the negative phenotypic correlation observed and suggests that the two traits should evolve together: natural selection favors the combination of large and early clutches (fig. 1). Yet at this point, the prediction of changes in both traits is limited by the difficulty of predicting the effect of age-specific heritabilities of laying date on microevolution, which needs further exploration using a modeling approach. If the expression of genetic variance for laying date in early and late life (Charmantier et al., forthcoming) allows for a response to selection on this trait, then laying date is predicted to evolve along the adaptive ridge toward earlier values and clutch size toward higher values. We can hypothesize that if conditions remain the same (high food abundance and low predation risk), clutch size should reach a mean of nine eggs in fewer than 200 years. However, such a large mean clutch size is well above the averages observed in natural mute swan populations (between 4.7–6.7 in the west Paleartic; Wieloch et al. 2004). Hence, new environmental constraints are likely to arise before this optimum is reached.

Acknowledgments

We are extremely grateful to Mrs. C. Townshend for permission to study the swans. We thank the Swannery staff, especially D. Wheeler and the researchers who participated in the long-term monitoring over the years. E. Postma provided useful discussions on clutch size selection. Thank you to J. Tinbergen and one anonymous reviewer for comments that greatly improved the manuscript. A.C. was supported by a Marie Curie Intra-European Fellowship. B.C.S. was supported by a Royal Society University Research Fellowship.

Literature Cited

Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. Evolution 38:709–719.

Bennet, P. M., and I. P. F. Owens. 2002. Evolutionary ecology of birds: life histories, mating systems, and extinction. Oxford University Press, New York.

Boag, P. T., and A. J. van Noordwijk. 1987. Quantitative genetics. Pages 45–78 *in* F. Cooke and P. A. Buckley, eds. Avian genetics. Academic Press, New York.

Boyce, M. S., and C. M. Perrins. 1987. Optimizing great tit clutch size in a fluctuating environment. Ecology 68:142–153.

Briskie, J. V., and S. G. Sealy. 1989. Determination of clutch size in the least flycatcher. Auk 106:269–278.

Brodie, E. D., III. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. Evolution 46:1284–1298.

Brown, C. R., and M. B. Brown. 1999. Fitness components associated with clutch size in cliff swallows. Auk 116:467–486.

Cameron, N. D. 1997. Selection indices and prediction of genetic merit in animal breeding. CAB, Wallingford.

Charlesworth, B. 1994. Evolution in age-structured populations. 2nd ed. Cambridge University Press, Cambridge.

Charmantier, A., and D. Réale. 2005. How do misassigned paternities affect the estimation of heritability in the wild? Molecular Ecology 14:2839–2850.

Charmantier, A., C. Perrins, R. H. McCleery, and B. C. Sheldon. Forthcoming. Age-dependent genetic variance in a life-history trait in the mute swan. Proceedings of the Royal Society of London B.

Coltman, D. W., J. Pilkington, L. E. B. Kruuk, K. Wilson, and J. M. Pemberton. 2001. Positive genetic correlation between parasite resistance and body size in free-living ungulate population. Evolution 55:2116–2125.

Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke. 1989. Long-term decline in fecundity in a snow goose population: evidence for density dependence. Journal of Animal Ecology 58:711–726.

Cooke, F., P. D. Taylor, C. M. Francis, and R. F. Rockwell. 1990. Directional selection and clutch size in birds. American Naturalist 136:261–267.

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

Dhondt, A. A., F. Adriaensen, E. Matthysen, and B. Kempenaers. 1990. Nonadaptive clutch sizes in tits. Nature 348:723–725.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Longman, Essex.

Fox, C. W., D. A. Roff, and D. J. Fairbairn. 2001. Evolutionary ecology, concepts and case studies. Oxford University Press, New York.

Garant, D., B. C. Sheldon, and L. Gustafsson. 2004. Climatic and temporal effects on the expression of secondary sexual characters: genetic and environmental components. Evolution 58:634–644.

Garant, D., L. E. B. Kruuk, T. A. Wilkin, R. McCleery, and B. C. Sheldon. 2005. Evolution driven by differential dispersal within a wild bird population. Nature 433:60–65.

Gibbs, H. L. 1988. Heritability and selection on clutch size in Darwin's medium ground finches (*Geospiza fortis*). Evolution 42:750–762.

Gilmour, A. R., B. J. Gogel, B. R. Cullis, S. J. Welham, and R. Thompson. 2002. ASReml user guide, release 1.0. VSN, Hemel Hempstead.

Grant, B. R., and P. R. Grant. 1993. Evolution of Darwin's finches caused by a rare climatic event. Proceedings of the Royal Society of London B 251:111–117.

———. 1995. Predicting microevolutionary responses to directional selection on heritable variation. Evolution 49:241–251.

Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707–711.

Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335:813–815.

Hendry, A. P., and M. T. Kinnison. 1999. The pace of modern life: measuring rates of contemporary microevolution. Evolution 53: 1637–1653.

Hereford, J., T. F. Hansen, and D. Houle. 2004. Comparing strengths of directional selection: how strong is strong? Evolution 58:2133–2143.

Hersch, E. I., and P. C. Phillips. 2004. Power and potential bias in field studies of natural selection. Evolution 58:479–485.

Hõrak, P., R. Mänd, and I. Ots. 1997. Identifying targets of selection: a multivariate analysis of reproductive traits in the great tit. Oikos 78:592–600.

Kirkpatrick, M., T. Price, and S. J. Arnold. 1990. The Darwin-Fisher theory of sexual selection in monogamous birds. Evolution 44: 180–193.

Knott, S. A., R. M. Sibly, R. H. Smith, and H. Møller. 1995. Maximum likelihood estimation of genetic parameters in life-history studies using the "animal model." Functional Ecology 9:122–126.

Kraaijeveld, K., P. J. Carew, T. Billing, G. J. Adcock, and R. A. Mulder. 2004. Extra-pair paternity does not result in differential sexual selection in the mutually ornamented black swan (*Cygnus atratus*). Molecular Ecology 13:1625–1633.

Kruuk, L. E. B. 2004. Estimating genetic parameters in wild populations using the "animal model." Philosophical Transactions of the Royal Society of London B 359:873–890.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford.

———. 1966. Population studies of birds. Oxford University Press, London.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. Evolution 33:402–416.

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

Lessells, C. M. 1986. Brood size in Canada geese: a manipulation experiment. Journal of Animal Ecology 55:669–689.

Lindström, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology & Evolution 14:343–348.

Losos, J. B., K. I. Warheit, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387:70–73.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland, MA.

Merilä, J., and B. C. Sheldon. 2001. Avian quantitative genetics. Current Ornithology 16:179–255.

Merilä, J., L. E. B. Kruuk, and B. C. Sheldon. 2001. Cryptic evolution in a wild bird population. Nature 412:76–79.

Meyer, K. 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. Genetique, Selection, Evolution 21: 317–340.

Møller, A. P., and T. Szep. 2005. Rapid evolutionary change in a secondary sexual character linked to climatic change. Journal of Evolutionary Biology 18:481–495.

Monaghan, P., and R. G. Nager. 1997. Why don't birds lay more eggs? Trends in Ecology & Evolution 12:270–274.

Moreno, J., L. Gustafsson, A. Carlson, and T. Part. 1991. The cost of incubation in relation to clutch-size in the collared flycatcher *Ficedula albicollis*. Ibis 133:186–193.

Perrins, C. M. 1964. Survival of young swifts in relation to brood size. Nature 201:1147–1148.

Perrins, C. M., and P. J. Jones. 1974. The inheritance of clutch size in the great tit (*Parus major*). Condor 76:225–228.

Perrins, C. M., and M. A. Ogilvie. 1981. A study of the Abbotsbury mute swans. Wildfowl 32:35–45.

Perrins, C. M., R. H. McCleery, and M. A. Ogilvie. 1994. A study of the breeding mute swans *Cygnus olor* at Abbotsbury. Wildfowl 45: 1–14.

Pettifor, R. A., C. M. Perrins, and R. H. McCleery. 1988. Individual optimization of clutch size in great tits. Nature 336:160–162.

———. 2001. The individual optimization of fitness: variation in reproductive output, including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of great tits *Parus major*. Journal of Animal Ecology 70:62–79.

Phillips, P. C., and S. J. Arnold. 1989. Visualizing multivariate selection. Evolution 43:1209–1222.

Postma, E., and A. J. van Noordwijk. 2005*a*. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. Nature 433:65–68.

———. 2005*b*. Genetic variation for clutch size in natural populations of birds from a reaction norm perspective. Ecology 86:2344–2357.

Price, T., and L. Liou. 1989. Selection on clutch size in birds. American Naturalist 134:950–959.

Price, T. D., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science 240: 798–799.

Réale, D., and M. Festa-Bianchet. 2000. Quantitative genetics of life-history traits in a long-lived wild mammal. Heredity 85:593–603.

Réale, D., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Heritability of body mass varies with age and season in wild bighorn sheep. Heredity 83:526–532.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997.

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions

Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934–1937.

Rockwell, R. F., C. S. Findlay, and F. Cooke. 1987. Is there an optimal clutch size in snow geese? American Naturalist 130:839–863.

Safriel, U. N. 1975. On the significance of clutch size in nidifugous birds. Ecology 56:703–708.

SAS Institute. 1992. SAS user's guide. SAS Institute, Cary, NC.

Schluter, D., and D. Nychka. 1994. Exploring fitness surfaces. American Naturalist 143:597–616.

Sheldon, B. C. 2000. Differential allocation: tests, mechanisms and implications. Trends in Ecology & Evolution 15:397–402.

Sheldon, B. C., L. E. B. Kruuk, and J. Merilä. 2003. Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. Evolution 57:406–420.

Sinervo, B., and E. Svensson. 2002. Correlational selection and the evolution of genomic architecture. Heredity 89:329–338.

StatSoft. 1999. STATISTICA for Windows. StatSoft, Tulsa, OK.

Svensson, E. 1997. Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. Evolution 51:1276–1283.

Tinbergen, J. M., and S. Daan. 1990. Family planning in the great tit (*Parus major*): optimal clutch size as integration of parent and offspring fitness. Behaviour 114:161–190.

Tinbergen, J. M., and J. J. Sanz. 2004. Strong evidence for selection for larger brood size in a great tit population. Behavioral Ecology 15:525–533.

van der Jeugd, H. P., and R. McCleery. 2002. Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. Journal of Evolutionary Biology 15:380–387.

van Noordwijk, A. J., J. H. Vanbalen, and W. Scharloo. 1981. Genetic and environmental variation in clutch size of the great tit (*Parus major*). Netherlands Journal of Zoology 31:342–372.

Visser, M. E., and C. M. Lessells. 2001. The costs of egg production and incubation in great tits (*Parus major*). Proceedings of the Royal Society of London B 268:1271–1277.

Wieloch, M., R. Wlodarczyk, and A. Czapulak. 2004. *Cygnus olor* mute swan. BWP Update 6:1–38.

Associate Editor: Robert Montgomerie
Editor: Jonathan B. Losos

A pair of mute swans *Cygnus olor* with eggs and hatchlings in Abbotsbury colony, Dorset, United Kingdom.

This content downloaded from 158.135.136.72 on Thu, 7 Aug 2014 18:08:08 PM
All use subject to JSTOR Terms and Conditions