

# Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird

Iván de la Hera · Thomas E. Reed · Francisco Pulido · Marcel E. Visser

Received: 1 October 2012 / Accepted: 10 March 2013 / Published online: 22 March 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** In birds, the allocation of resources to plumage production may have important fitness consequences. However, we have only a limited understanding of how plumage traits respond to natural selection, making it difficult to predict how variation in plumage traits may contribute to the adaptation of birds to environmental change. In this study, we collected plumage-related data in a pedigreed population of a long-distance migratory bird (the Pied Flycatcher *Ficedula hypoleuca*) to estimate the heritability of two plumage traits: feather mass (as a proxy of feather quality) and the extent of winter moult. We further explored whether these plumage features were associated with some fitness-related traits. Variation in plumage characteristics could be explained by differences in sex, age and year, which indicates a high degree of plasticity in these traits. After controlling for these effects, however, feather mass and winter moult extent were highly repeatable ( $r = 0.58\text{--}0.82$ ) and heritable ( $h^2 = 0.59\text{--}0.65$ ), suggesting that additive genetic variation accounts for a significant proportion of the residual phenotypic variation of plumage traits in this population. Although the studied characteristics showed evolutionary potential, we did not find any relationship between plumage features and fitness-related traits like spring arrival date, egg-laying date, mating success or mating-time. We conclude that current selection on feather mass and moult extent, if existing, is weak, and that these moult-related traits are currently of minor importance for the adaptation of our study population to global warming.

**Keywords** Coefficient of additive genetic variation · Animal model · Avian migration · MCMCglmm

I. de la Hera · T. E. Reed · F. Pulido · M. E. Visser  
Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50,  
6700 AB Wageningen, The Netherlands

I. de la Hera (✉)  
Department of Zoology and Animal Cell Biology, Universidad del País Vasco (UPV/EHU),  
01006 Vitoria-Gasteiz, Spain  
e-mail: idelahera@bio.ucm.es

F. Pulido  
Department of Zoology and Physical Anthropology, Faculty of Biology, Universidad Complutense de  
Madrid, 28040 Madrid, Spain

## Introduction

Global warming is currently considered one of the most significant threats to biodiversity (King 2004), as it is changing dramatically the phenology and distribution of the food resources on which many organisms rely on for the timing of some crucial life-cycle events (e.g. reproduction). There is mounting evidence that species are modifying the organization of their life-cycles in response to these shifts in ecological conditions (Coppack and Both 2002; Peñuelas et al. 2002; Møller et al. 2010). However, the mechanisms underlying these phenotypic adjustments (i.e. whether they are due to evolutionary change or phenotypic plasticity) are largely unknown (Donnelly et al. 2012). Moreover, it is unclear if these adjustments will be strong and fast enough to ensure the persistence of animal populations (Visser 2008; Reed et al. 2010).

Adaptation to climate change seems to be particularly difficult in migratory animals (Robinson et al. 2009). Although changes in the timing and duration of their main life-history stages are possible, they are expected to be constrained by a tightly scheduled annual cycle. Migratory birds provide some illustrative examples (Møller et al. 2010). In temperate regions, birds are selected to match the phenology of their reproductive season with the peak of food availability, which, in many cases, is advancing progressively as a consequence of increasing spring temperatures. Some avian populations are responding to this ecological alteration by advancing reproduction (Both and Visser 2001; Knudsen et al. 2011). However, most long-distance migratory birds arrive at their summer territories only shortly before the initiation of breeding. As a consequence, the advancement of reproduction may be constrained by the tight time schedule of migratory birds in spring (Coppack and Both 2002), which will eventually lead to a detrimental mismatch between timing of breeding and food availability (Both et al. 2006).

It has been suggested that the inability of long-distance migrants to arrive earlier at their breeding territories is due to the fact that in these species the onset of spring migration is triggered by cues at the wintering grounds that are not affected by climate change, such as the photoperiod (Both and Visser 2001; Pulido 2007; Rubolini et al. 2010). Departure from the wintering grounds might also be determined by the environmental conditions experienced, which may be reflected in the duration, timing and/or extent of the moult that approximately half of the migratory species overwintering in the tropics perform during winter (note that the other half of the species moult during summer at breeding grounds; Jenni and Winkler 1994; Rubolini et al. 2005). In fact, variation in this winter moult, or the lack of it, could explain the observed differences among species and populations of long-distance migrants in the response of their migration phenology to global warming (Jonzen et al. 2006). Although it has been predicted by theoretical approaches that winter moult may constrain the initiation of prenuptial migration (Hedenstrom et al. 2007), few empirical studies have attempted to explore the potential relationship between winter moult performance and timing of spring migration (see, for instance, Møller et al. 2011).

Moult is a life-history stage subjected to time constraints within the annual cycle of migratory birds (de la Hera et al. 2009a, 2010a), but these constraints are likely to be relaxed with climate change (Pulido and Berthold 2004; Pulido and Coppack 2004), particularly in species moulting during summer at breeding grounds (Dawson 2005). Experimental evidence suggests that the advancement of the timing of reproduction promoted by global warming could increase the time available between breeding and autumn migration for moulting (Dawson 2005). Consequently, this may favour the production of heavier feathers with better mechanical properties and quality in summer-moulting species (Dawson et al. 2000; Griggio et al. 2009; de la Hera et al. 2010b). This might have a

positive impact on migration and breeding phenology, suggesting that an early arrival and breeding in spring could be facilitated through an increase in flight feather quality. However, no study has tested yet if variation in feather quality actually affects timing of migration and breeding.

Feather mass and the extent of moult are traits with important implications in the lives of birds. Previous research has shown that feather mass is positively correlated with the mechanical properties and resistance to wear of feathers (Dawson et al. 2000; de la Hera et al. 2010b) suggesting that investment in feather mass can be an important determinant of feather quality. In the case of moult extent, its variation can affect the position in a dominance hierarchy, social interactions, and, probably, mating opportunities (Senar et al. 1998; López et al. 2005). Previous studies obtained contradictory results on the factors affecting the expression of these plumage traits. On the one hand, some authors found that moult extent and feather mass are strongly dependent on the availability of resources during feather production. Thus, under energetic and/or temporal constraints, birds will grow lighter and less-structurally complex feathers (Dawson et al. 2000; Dawson 2004; Butler et al. 2008) and have less extensive moults (Jenni and Winkler 1994; Senar et al. 1998; Hall and Fransson 2001), which can carry over into subsequent stages of the annual cycle. In contrast to these observations, which indicate some degree of plasticity, other studies have recorded high within-individual repeatability in feather mass (de la Hera et al. 2009b) and moult extent (Battley 2006), suggesting that variation in these traits has a large genetic component (Dohm 2002). This is a prerequisite for evolutionary change in these plumage characteristics. Thus, although the phenotypic expression of feather mass and moult extent can highly depend on the environmental conditions (e.g. as a consequence of interannual differences in resource availability for moulting), the relative value of the plumage characteristics of one individual could be maintained when compared to other individuals of the population.

To assess the relative contribution of variation in “genes” and “environment” to variation in these traits, we estimated the heritability of feather mass and winter moult extent in a Pied Flycatcher population (*Ficedula hypoleuca*), for which pedigree information was available. For this purpose, we used an animal model approach to separate the additive genetic and environmental components of variation in these plumage features (Wilson et al. 2009; Postma 2010), which will allow us to assess the degree to which moult extent and feather mass may respond to natural selection. We further explored potential selection on these plumage traits by testing how winter moult extent and feather mass (as a surrogate of feather quality) were associated with fitness-related traits, particularly with the timing of migration and reproduction. The Pied Flycatcher population studied advanced their breeding time in response to recent climate change (Both and Visser 2001; Both et al. 2006), which could be accompanied by changes in moult performance and the expression of plumage traits (Coppack and Both 2002; Pulido and Coppack 2004; Dawson 2005). Specifically, we hypothesized that less extensive winter moults, which allow shorter moult durations, and heavier feathers, which reflect higher feather quality, will facilitate an advancement of spring arrival and breeding. Complementarily, we also explored the relationship between these plumage characteristics and other fitness-related traits (i.e. mating success, time necessary to mate), which could be in conflict with a reduced moult extent favouring an early timing of migration and breeding. This approach could be particularly relevant to shed light on the potential of Pied Flycatchers to adjust their annual cycle to rapid environmental changes by modifications of these plumage characteristics, which could facilitate its adaptation to climate change.

## Materials and methods

### Model species and fieldwork

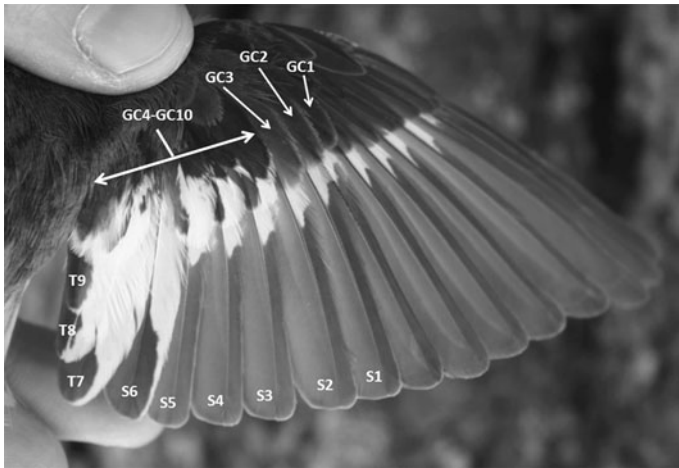
The Pied Flycatcher is a migratory passerine bird species that breeds in the Palaearctic region and winters in tropical Africa. It nests in tree cavities, but readily accepts nest-boxes for breeding (Lundberg and Alatalo 1992). We monitored the Pied Flycatcher population breeding in a wooded area of the Hoge Veluwe National Park (The Netherlands) during four springs (from 2008 to 2011). Pied Flycatchers arrive at our study site from early April, and late-breeding pairs complete reproduction in mid June. Our study area has approximately 400 nest-boxes. During the reproductive season, an average of about 90 nest-boxes are occupied by Pied Flycatchers each year. To determine male arrival date, we carried out daily searches covering the whole study area to document the presence of singing males from the beginning of April. In this population, breeding males had been colour-ringed in the years preceding this study. Thus, individuals could be identified without being trapped by a unique combination of aluminium and colour rings on their legs, the general colour of the body plumage and the shape and size of the forehead patch (Lundberg and Alatalo 1992). We monitored male arrival until the first week of May, when most males have arrived at our study area. Using this data we could infer the exact arrival date of approximately half of the males present in our study area (see Potti 1998 for a similar approach).

Once Pied Flycatcher males were observed at a nest-box, it was checked regularly (every 2–4 days). If males had been able to find a mate, regular nest-box visits allowed us to determine the laying date of the first egg, assuming the production of one egg a day. Most breeding birds were captured inside their nest-boxes when chicks were 7–8 days old. We assumed that adult birds feeding the chicks were the biological parents of the corresponding brood. This assumption is based on preliminary results showing that the incidence of extra-pair paternity in our study population is low (less than 10 %; van der Woude et al. unpublished data), a percentage that also ensures the robustness of heritability estimates (Charmantier and Reale 2005). From the end of the census period until June, males singing in empty nest-boxes were also captured. These males could be unmated males or already mated males trying to attract a second female. The latter was revealed by subsequent recaptures of these males feeding chicks in other nest-boxes. Males that could not be assigned to any brood were considered unmated birds. All Pied Flycatchers were aged, distinguishing between birds in their second calendar-year -SCY- and older, and sexed according to plumage characteristics (Svensson 1992). We also considered the presence or absence of a brood patch to sex some difficult cases (i.e. pale males lacking forehead patch). As age determination is difficult in this species, we also made use of our long-term ringing information to correct for potential errors in ageing, when possible.

We collected one tail feather (one rectrix number three) from each captured bird. In 2009, 2010 and 2011, we also plucked one wing feather (tertial number 7, T7 in Fig. 1) and determined the greater coverts, tertials and secondary feathers replaced during the pre-nuptial winter moult by looking for moult limits in both wings (see Fig. 1 and next section for more details). Collected feathers were stored in paper envelopes until laboratory analyses.

### Moult strategy and plumage characteristics

Pied Flycatchers acquire their first set of true feathers, the juvenile plumage, during the fledging period. Shortly after being independent from their parents and before the initiation



**Fig. 1** Topography of the wing of a Pied Flycatcher indicating the feathers considered to estimate winter moult extent: tertials (T), greater coverts (GC) and secondaries (S). The male of the picture moulted all tertials, 7 greater coverts (GC4–10) and the innermost secondary (S6) in its right wing

of autumn migration, juvenile birds (individuals hatched in the current year) perform a partial moult at their summer grounds, which mostly affects body plumage and lesser and median wing coverts. Simultaneously to the post-juvenile moult of yearlings, adult birds (individuals hatched in earlier years) undergo their annual complete moult (Jenni and Winkler 1994). Immediately after completing the corresponding summer moult, Pied Flycatchers start their autumn migration to tropical Africa, where a partial moult is performed in late winter, just before the initiation of return spring migration to European breeding habitats (Salewski et al. 2004). This winter moult is partial in both adult and juvenile birds (which by now, are considered SCY individuals). It involves the replacement of all body feathers, normally all tertials, and a variable number of greater coverts and secondaries (see Jenni and Winkler 1994). It is important to note that the extent of winter moult in juvenile (or SCY) birds is larger than the partial post-juvenile moult they undergo immediately after fledging, so that all post-juvenile feathers are also replaced in winter and are normally not present during their second year of life in Europe. After the subsequent breeding season, SCY birds are included in the age category of adults while performing their first complete summer moult.

We used our observations on the number of greater coverts, tertials and secondary feathers renewed during winter to estimate winter moult extent for each individual. We only took into account these three groups of feathers because finding moult limits is easier and clearer in these feather tracts than in other feathers moulted in winter (e.g. median and lesser coverts; Fig. 1). Moreover, we also expect variation in the extent of winter moult among different feather tracts to be positively correlated with each other, because we observed a correlation between the number of greater coverts and the number of secondary feathers moulted (Spearman  $r = 0.51$ ,  $t_{629} = 14.9$ ,  $P < 0.001$ ). Since the feathers considered for estimating winter moult extent show large variation in size (e.g. greater coverts are appreciably smaller than secondary feathers), we weighted the contribution of each feather to moult extent by controlling for its mass. For this purpose, we used a Pied Flycatcher found dead in our study area as reference, for which all the feathers susceptible to be replaced during the winter moult were weighed on one wing: the 10 greater coverts,

the 3 tertial feathers and the 6 secondaries. We then calculated the relative mass of each feather in relation to the overall mass of all the feathers weighted (see Table 1). The estimate for moult extent of each individual was obtained from the sum of the standardized mass proportions of the feathers that were renewed in winter. Thus, an individual moulting all greater coverts, tertials and secondaries would show a moult extent of 100 %, while an individual that did not moult any of these feathers would have a score of 0 %. Moult extent scores were calculated for the two wings of each individual separately, but finally the arithmetic mean of these scores (as a fraction of unity) was used as a final estimate.

The two feathers plucked from each individual (see above) were produced in different seasons: the tail feather in summer and the tertial feather in winter. It is also important to note that tertial feathers were produced during a partial winter moult in both adult and SCY birds. However, individuals of different age categories (i.e. SCY and adult birds) had tail feathers produced the previous summer under different ecological and developmental conditions: SCY birds had tail feathers produced during fledging, while tail feathers in adult birds were the result of a complete summer moult (see above).

Feathers were weighed in the laboratory using a high-precision digital balance (Sartorius ME5, resolution 0.001 mg). Feather mass represents the quantity of material invested in feathers by birds and it is correlated with some important properties of the feathers, such as flexural stiffness and resistance to wear (Dawson et al. 2000; de la Hera et al. 2010b). Because of the elongated shape of the feathers considered in this study, we used the overall feather length to control for the among-individual variation in feather mass

**Table 1** Mass of the wing feathers used to estimate winter moult extent, and relative mass of each feather in relation to the overall feather mass

Feather no	Weight (mg)	% Of total weight
<i>Greater coverts</i>		
1 (outermost)	0.78	1.9
2	0.8	1.9
3	0.75	1.8
4	0.72	1.7
5	0.72	1.7
6	0.69	1.6
7	0.66	1.6
8	0.62	1.5
9	0.5	1.2
10 (innermost)	0.32	0.8
<i>Secondaries</i>		
1 (outermost)	5.17	12.3
2	5.1	12.1
3	4.83	11.5
4	4.48	10.7
5	4.12	9.8
6 (innermost)	3.89	9.3
<i>Tertials</i>		
7 (outermost)	3.75	8.9
8	2.69	6.4
9 (innermost)	1.42	3.4
Total	42.01	100

caused by differences in the size of the feathers (the relationship between both variables was significant,  $P < 0.001$ , and Pearson's correlation coefficients were 0.77 and 0.71 for the tail and tertial feathers, respectively). Feather length was measured from the base of the calamus to the feather tip by means of a digital calliper (resolution 0.01 mm). Thus, individuals with heavier feathers, after correcting for their length, will have a more complex feather structure (e.g. wider rachis, and higher density of longer barbs; see de la Hera et al. 2009c) than individuals with lighter feathers. Measurements were taken on feathers that were not visibly damaged or worn. In order to assess the reliability of these variables, we weighed and measured the feathers of 20 randomly selected individuals from each year (in total 80 tail feathers and 60 tertial feathers, note that tertials were not collected in 2008) to obtain repeatability estimates of these measurements, which were extremely high and significant throughout (intraclass correlation coefficients  $r_i$  for tail and tertial feather mass or length were higher than 0.97, and in all cases  $P < 0.001$ ).

### Estimating repeatability

We used linear mixed models to analyse the variation in tail and tertial feather mass and winter moult extent in relation to age, sex and year as fixed effects, and individual identity as a random factor. We also included the corresponding length of each feather in the analyses of tail and tertial feather mass as a covariate. All models were initially run with all possible two-way interactions among fixed effects, but excluding all higher interaction terms. Models were fitted in *R* using the package *lme4*. We used a backwards stepwise model simplification procedure, sequentially removing non-significant terms ( $P > 0.05$ ) using Type III tests starting with interactions, to yield minimum adequate models.  $P$ -values for the  $t$ -tests of the fixed effects were generated through an iterative Markov-Chain-Monte-Carlo sampling procedure, with  $1 \times 10^4$  iterations, implemented in the package *languageR* (Baayen 2008). The goal of this first set of analyses was to determine the fixed effects, among those suspected to be important, that should be included in the animal model in order to obtain unbiased estimates of the additive genetic effects (see next section). They also allowed us to estimate the overall repeatability for each plumage trait, which measures the proportion of remaining phenotypic variation explained by fixed differences among individuals caused by unspecified genetic and non-genetic factors (Wilson et al. 2009). Repeatability was calculated as the ratio  $V_I/(V_I + V_R)$ , where  $V_I$  was the variance component corresponding to the random factor "individual" (not associated with the pedigree structure in this first set of analyses), and  $V_R$  was the residual variance after conditioning on the fixed effects. Feather traits were normally distributed, but winter moult extent had to be arcsine-transformed to ensure an approximate normal distribution of errors.

### Estimating heritability

In a second set of analyses, we used the *MCMCglmm* package in *R* (Hadfield 2010) to fit so-called "animal models", which allowed us to infer the relative contribution of additive genetic and environmental (including potential non-additive genetic) influences to phenotypic variation in feather mass and winter moult extent (Wilson et al. 2009). The animal model is a particular form of linear mixed model in which the breeding value, or "additive genetic merit", of each individual is treated as a random effect, for which an estimate of the variance (i.e. the additive genetic variance  $V_A$ ) can be obtained by combining data on the phenotypic traits of interest with a pedigree. The pedigree gives an expectation of how breeding values should co-vary among individuals of different genetic relatedness, such



that  $V_A$  and other variance components can be solved for algebraically (Kruuk 2004; Wilson et al. 2009). Narrow sense heritability ( $h^2$ ) can then be calculated as the proportion of phenotypic variance ( $V_P$ ) explained by additive genetic variance ( $h^2 = V_A/V_P$ ). For each trait, we included in the corresponding animal model analysis the fixed effects that were significant in the abovementioned linear mixed models. We checked whether the inclusion or removal of these fixed effects in the animal model systematically changed the estimate of  $V_A$  in each case. The inclusion of fixed effects (e.g. age, sex, year) should only affect the estimate of the residual variance, unless the incidence of fixed effects is non-random with respect to the pedigree structure. In all cases, this is what we observed (i.e. a reduction in  $V_R$  but not  $V_A$  as additional fixed effects were added), except for the analysis of tail feather mass, for which the inclusion of sex in the model reduced  $V_A$  by half. This might reflect the fact that with sexually-dimorphic traits, fitting sex as fixed effect reduces the variance attributable to non-genetic between-individual differences (i.e. the permanent environment effect,  $V_{PE}$ ; Wilson et al. 2009), and here we were unable to effectively separate  $V_{PE}$  from  $V_A$  (see below). We therefore exercise some caution in interpreting  $h^2$  values calculated for this trait (see “Discussion”).

*MCMCglmm* is based on the use of Bayesian inference, which requires specification of prior distributions of unknown parameters. We used weakly informative priors for the random effects, each set to  $1/n$  of the phenotypic variance, where  $n$  represents the number of variance components being estimated (e.g. when phenotypic variance was being partitioned as  $V_A + V_R$ , the prior for each was set to  $0.5V_P$ ). We repeated the animal model analyses making substantial changes in the prior distributions, observing that estimates of additive genetic variance were robust to the particular priors used (see tutorial accompanying Wilson et al. 2009). We also tried to separate permanent environment and maternal effects from additive genetic effects, but were not able to obtain reliable results. Permanent environment effects were apparently strongly confounded with additive genetic effects, as evidenced by the fact that their relative estimation was strongly sensitive to priors specifications, most likely due to low sample sizes and a shallow pedigree (phenotypic data usually available for one or two generations, mostly from parent-offspring pairs or siblings). Excluding a permanent environment effects from models with repeated measures on individuals can upwardly bias the estimate of  $V_A$  (Kruuk and Hadfield 2007). To avoid this issue, all animal models were fitted using only one randomly selected record for the individuals with two or more measurements in different years. Maternal/nest effects could not be reliably estimated due to insufficient phenotypic data on offspring sharing the same mother/nest (i.e. we only had 16 cases in which all the plumage characteristics of at least two siblings from the same mother and brood were available).

### Analysis of selection on plumage characteristics

We used the residuals of plumage traits obtained from linear mixed models described (see above), to explore their association with some variables that might contribute to early breeding and fitness (i.e. arrival date, egg-laying date, mating success and mating-time since arrival). We used the *R* packages *lme4* and *languageR* (when necessary to estimate *P* values) to perform these analyses. All these analyses were restricted to the period 2009–2011, because measurements of tertial feather mass and winter moult extent were not obtained in 2008. Analyses of arrival date, mating success and mating-time since arrival were only performed for males. For the analysis of arrival date, we used the standardized arrival dates (actual dates minus the mean arrival date for each particular year, considering the first of April as day 1) as the response variable, and considered age and its interactions with the residuals of plumage characteristics as predictors. We used Generalized Linear



Mixed Models (GLMMs) with a binomial error distribution for the analysis of mating success (considered a binary variable: unmated or mated), where year, age, and the 2-way interactions between them and with plumage characteristics were initially included. The time needed by a Pied Flycatcher male from its arrival to the start of breeding (i.e. mating-time) is expected to be correlated with its ability to attract a female, which could be dependent on plumage characteristics and interfere with the expected selection on plumage characteristics for early migration and breeding phenology. This variable was estimated as the difference between egg-laying date and the arrival date of the male, standardized by the mean mating-time for each year. Standardized mating-time was analyzed in relation to standardized arrival date, residuals of plumage characteristics, and age and its interactions with previous continuous variables. For the analysis of the laying date of the first egg, we considered both sexes in the analyses, using the male and female of each pair as independent data points to simplify the statistical tests. Laying-date is positively correlated with fitness as early broods are larger and their chicks are more likely to be recruited in the population than chicks from late clutches (Both and Visser 2001). The potential effects of plumage characteristics on standardized egg-laying date (i.e. actual date minus the mean for each corresponding year considering first of April as day 1) were analyzed in relation to sex, age, and all two-way interactions among them and plumage characteristics. In all analyses individual was included as a random factor. We also included quadratic effects of plumage characteristics in the models to be able to detect stabilizing selection.

## Results

### Repeatability of plumage characteristics

Feather length was a main determinant of variation in tail feather mass. After controlling for this effect tail feather mass differed among years, and adult birds and males had comparatively heavier feathers than SCY birds and females, respectively (Table 2). Using the remaining variance not explained by all previous effects (see  $V_I$  and  $V_R$  in Table 2), we estimated a repeatability of tail feather mass of 0.65.

Tertial feather mass also differed between years and sexes, but not between age classes ( $t = -0.45$ ,  $P = 0.656$ ), after accounting for its relationship with feather length (Table 2). As observed for tail feathers, males also showed heavier tertial feathers than females. The quotient  $V_I/V_P$  gave rise to a repeatability value of 0.82 for tertial feather mass.

Pied Flycatchers in our study site showed relatively large variation in the number of greater coverts (between 7 and 18 of the 20 feathers, considering both wings) and secondaries moulted during winter (between 0 and 7 of the overall 12 secondary feathers). We also observed that a few individuals retained some unmoulted tertial feathers. The analysis of winter moult extent showed significant differences among years and between age classes. In this case, SCY birds had more extensive moults than adults. We also detected a tendency of males for having less extensive moults than females, but this effect was marginally non-significant. Repeatability of winter moult extent was 0.58, after controlling for fixed effects factors (Table 2).

### Heritability estimates for plumage characteristics

Animal model analyses were performed accounting for the fixed effects that were significant (or marginally non-significant) in the linear mixed models previously shown (see

**Table 2** Results of the linear mixed effects models that analysed plumage characteristics (i.e. tail feather mass, tertial feather mass and winter moult extent) in the Pied Flycatcher

Random effects	Tail feather mass (mg) Variance (observations, individuals)	Tertial feather mass (mg) Variance (observations, individuals)	Winter moult extent Variance (observations, individuals)			
Individual ( $V_I$ )	0.024 (770 obs., 549 id.)	0.014 (632 obs., 477 id.)	0.0029 (631 obs., 476 id.)			
Residual ( $V_R$ )	0.013	0.003	0.0021			
Fixed effects	Estimate $\pm$ SE	$t_1$	$P$	Estimate $\pm$ SE	$t_1$	$P$
Intercept (female, SCY, year*)	-3.055 $\pm$ 0.306			-1.914 $\pm$ 0.214		
Feather length	0.134 $\pm$ 0.006	23.9	<0.001	0.127 $\pm$ 0.005	25.0	<0.001
Sex (male)	0.33 $\pm$ 0.017	18.9	<0.001	0.09 $\pm$ 0.012	7.4	<0.001
Age (older)	0.123 $\pm$ 0.015	8.1	<0.001	Not significant		
Year (2009)	0.02 $\pm$ 0.016	1.3	0.202	Not applicable		
Year (2010)	0.124 $\pm$ 0.017	7.3	<0.001	0.034 $\pm$ 0.008	4.3	<0.001
Year (2011)	0.204 $\pm$ 0.018	11.6	<0.001	0.106 $\pm$ 0.009	12.3	<0.001
				0.667 $\pm$ 0.007		
				Not applicable		
				-0.011 $\pm$ 0.006	-1.9	0.062
				-0.064 $\pm$ 0.006	-10.7	<0.001
				Not applicable		
				-0.0003 $\pm$ 0.006	-0.1	0.947
				0.017 $\pm$ 0.006	2.9	0.004

Year\*: the year of reference in the intercept is 2008 for the analysis of tail feather mass and 2009 for the analysis of tertial feather mass and moult extent

**Table 3** Variance components derived from the animal models estimating additive genetic effects for tail feather mass, tertial feather mass and winter moult extent, after controlling for the fixed effects that were significant in the linear mixed models for each trait (see text)

Variance components	Tail feather mass	Tertial feather mass	Winter moult extent
Additive genetic variance ( $V_A$ )	0.022	0.011	0.0029
Residual variance ( $V_R$ )	0.015	0.006	0.0019
Raw phenotypic variance ( $V_P$ )	0.16	0.043	0.0059
Raw phenotypic mean ( $\mu$ )	4.885	3.575	0.619
Heritability and 95 % CI	0.59 (0.38–0.75)	0.65 (0.46–0.85)	0.60 (0.32–0.84)
Coefficient of additive genetic variation ( $CV_A = V_A^{1/2}/\mu \times 100$ )	3.04	2.93	8.7

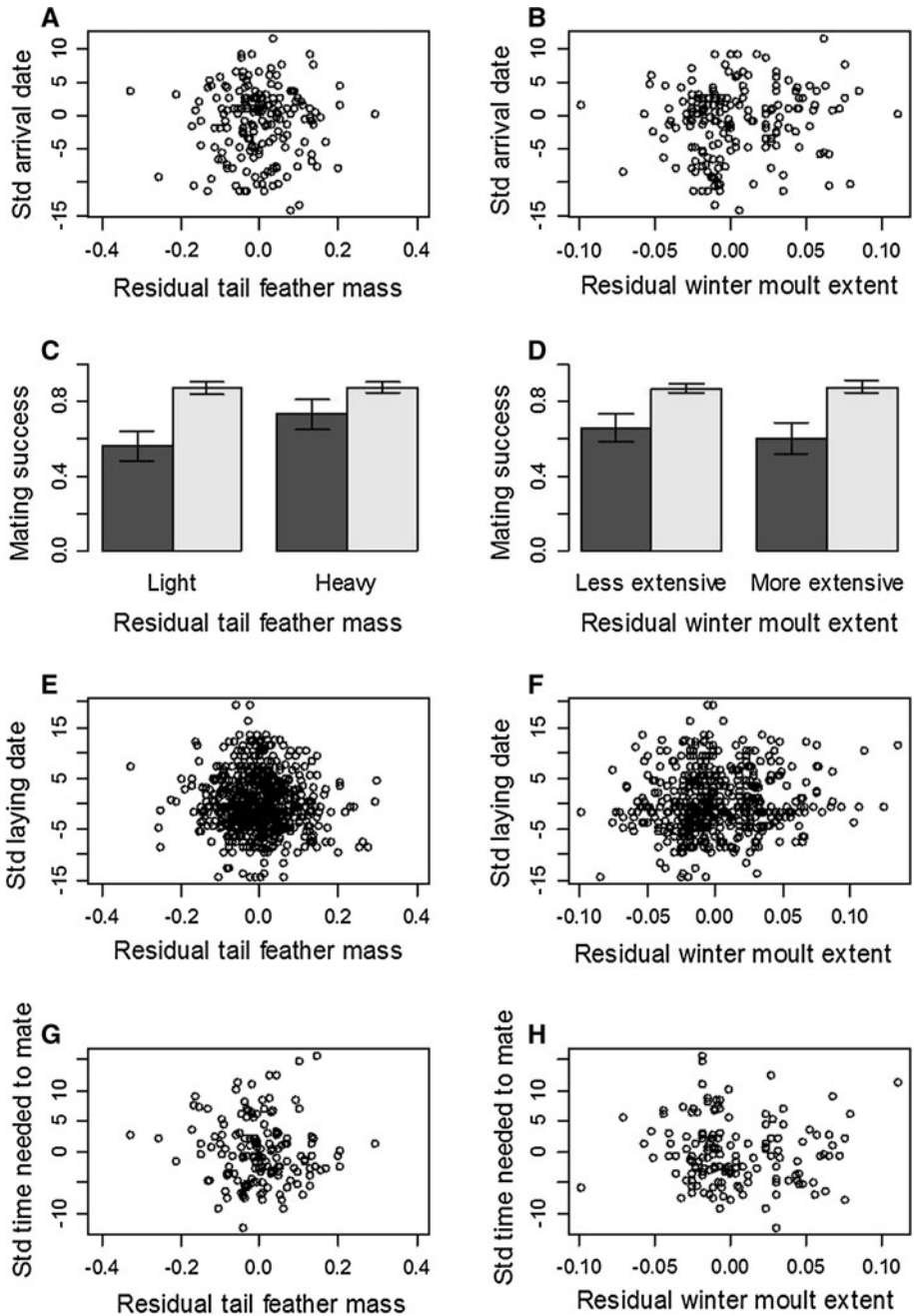
Heritability estimates and confidence intervals (95 %) are also shown. Note that heritability estimates here are conditioned on the fixed effects, i.e.  $h^2 = V_A/(V_A + V_R)$ . Coefficient of additive genetic variation is also shown for each plumage characteristic

Table 2). Heritability estimates for tail feather mass ( $h^2 = 0.59$ ), tertial feather mass ( $h^2 = 0.65$ ) and winter moult extent ( $h^2 = 0.60$ ) were high and statistically different from zero (Table 3). Heritability estimates are model dependent, in the sense that the inclusion of fixed effects reduces  $V_R$  and therefore increases apparent  $h^2$  (Wilson 2008). The coefficient of additive genetic variation ( $CV_A$ ) for each trait is also shown in Table 3. This calculation provides a more standardized estimate of the relative contribution of genetic variation to the phenotypic expression of a trait, which allows a more reliable comparison with other traits and studies (Houle 1992).

#### Analyses of selection on plumage characteristics

In order to simplify the analyses of the relationship between residuals of plumage characteristics and fitness-related traits, we only considered the residuals of tail feather mass and winter moult extent in the analyses. Residual tertial feather mass was not included because this variable was positively correlated with residual tail feather mass (Pearson  $r = 0.3$ ,  $P < 0.001$ ), and yielded similar results. Residual winter moult extent was neither associated with residual mass of tail ( $r = 0.02$ ,  $P = 0.703$ ) or tertial feathers ( $r = 0.02$ ,  $P = 0.543$ ).

Plumage characteristics did not explain variation in arrival date of Pied Flycatcher males (all  $P > 0.05$  for the effects of residuals of tail feather mass and winter moult extent, their quadratic effects or their interactions with the age of the birds; see Fig. 2a, b). The best model for arrival date included only age as a significant effect (for 182 arrivals from 145 individuals: estimate =  $-5.797 \pm 0.967$ ,  $t = -5.99$ ,  $P < 0.001$ ), with adult birds arriving earlier than SCY birds. Plumage features did not explain variance in male mating success ( $P > 0.05$ ). Again, age was the only factor affecting significantly the chances of a male Pied Flycatcher to mate (for 324 records from 235 individuals: estimate =  $1.727 \pm 0.385$ ,  $Z = 4.49$ ,  $P < 0.001$ ), with adult birds having higher probabilities of mating than SCY birds (Fig. 2c, d). Age, and all the effects in which plumage characteristics were involved, did not show significant effects on mating-time (all  $P > 0.05$ ; Fig. 2g, h), estimated from the difference between egg-laying date and arrival date. This interval was only significantly affected by the arrival date of individuals (for 152 observations from 124 individuals: estimate =  $-0.392 \pm 0.08$ ,  $t = -4.91$ ,  $P < 0.001$ ), whereby it was longer in



**Fig. 2** Relationship between tail feather mass and winter moult extent (after controlling for significant fixed effects factors) and arrival date (**a**, **b**), mating success (**c**, **d**), laying date (**e**, **f**) and mating-time (**g**, **h**). For illustrative purposes only, in abscise axes of graphs **c** and **d**, we classified Pied Flycatchers in two categories depending on the scores of the residual values of tail feather mass and winter moult extent (residuals lower than 0: light tail feathers and less extensive moults; residuals higher than 0: heavy feathers and more extensive moults); *dark* and *light* bars represent SCY and adult birds, respectively

early-arriving males than those arriving late. Residuals of tail feather mass did not affect laying-date (Fig. 2e), but we detected a marginally significant effect of winter moult extent (for 541 records from 414 individuals: estimate =  $13.54 \pm 6.76$ ,  $t = 2.00$ ,  $P = 0.046$ ). Thus, individuals with a reduced moult extension tended to lay their eggs earlier than birds with a more extensive moult (Fig. 2f).

## Discussion

Our results indicate that both environmental and genetic factors contribute to phenotypic variation in feather mass and winter moult extent in the Pied Flycatcher. Environmental effects are inferred from the age and the year-to-year variation (i.e. reflecting within individual ontogenetic effects and among individual differences), while the genetic component is supported by the existence of some degree of among-individual consistency in the expression of plumage traits (i.e. high repeatability estimates). In addition, we revealed relatively high heritability values for feather mass and winter moult extent (i.e.  $h^2 \approx 0.6$ ), two traits with potential consequences for fitness for which the relative contribution of genetic and non-genetic factors to phenotypic variation were hitherto unknown. These results imply that these plumage characteristics have high potential for evolutionary change, although the absence of a significant association between these plumage features and some fitness-related traits (i.e. spring arrival phenology, egg-laying date, mating success and mating-time) suggests that they are currently not under directional or stabilizing selection in our study population.

### Environmental and condition effects on variation in plumage traits

Tail feather mass differed among years and between age classes, both in the linear mixed models (which included repeat measures on individuals) and in the animal models (which included only one measure per individual; see “Materials and methods”). These results suggest that the amount of resources invested in these feathers is affected both by general environmental effects experienced by all individuals moulting in the same year and by specific environmental effects inducing phenotypic plasticity within individuals across years. Variation among years can be explained by inter-annual differences in the environmental conditions or productivity in the breeding areas where Pied Flycatchers produce their tail feathers. Differences in feather mass between adults and SCY birds can be attributed to the different conditions under which each plumage type is produced. Tail feathers of SCY birds are produced during the nestling and fledgling period (i.e. fledging period), when the whole plumage is simultaneously grown during a period when other body structures develop (Ginn and Melville 1983). This is expected to constrain the quantity of resources that can be allocated to feather production. Adults, in contrast, produce their tail feathers during a complete moult process, in which plumage is replaced sequentially. This moult pattern minimizes the impact of moult on flight performance and other plumage functions (Jenni and Winkler 1994; Lind 2001). As a consequence, the energetic costs of moult in adults are reduced, which may allow the production of feathers of higher quality (heavier) compared to juveniles. In addition, we also detected significant differences between sexes in tail feather mass, which might be explained as a result of the lower basal metabolic rate of male compared to female Pied Flycatchers (Bushuev et al. 2006). This would allow males to allocate more resources to feather production than females (Lindström et al. 1993; Klaassen 1995).

Tertial feathers, which were produced during winter moult, showed similar patterns to the ones observed for tail feathers. We found between sex and among year effects, yet no age effects on variation in tertial feather mass. This lack of differences between adult and SCY birds for the feathers produced in winter could be explained by the fact that these tertial feathers are the result of a similar moulting event. Unexpectedly, we found a positive but low correlation between the residual mass of these two types of feathers ( $r = 0.3$ ), despite the fact that the production of the collected tail and tertial feathers is widely separated in time (there are more than 5 months between the end of the summer moult and the beginning of winter moult; Salewski et al. 2004). Thus, individuals that grew relatively heavy tail feathers in summer also produced relatively heavy tertial feathers in winter. This pattern might be a consequence of repeatable differences in body condition among individuals, which could be possible, for example, if birds occupying relatively high-quality territories in summer also occupy high-quality territories in winter (Gunnarsson et al. 2005). The same phenomenon would be observed if there were carry-over of effects of condition from one season to the other (Pulido 2007), or if there were genetic differences in phenotypic quality among individuals. However, we think this pattern is more likely to be the result of among-individual variation in a genetic program that controls feather growth. This genetic program would generally determine the size and complexity of the structural components that contribute to the mass of feathers (e.g. rachis width, barb density; de la Hera et al. 2009c, 2010c). Among-individual differences in this program would result in similarity of feathers grown in different body areas under different environmental conditions. This idea is also consistent with the high repeatability and heritability estimates we obtained for the mass of both types of feathers.

The range of variation in the number of greater coverts and secondaries renewed during the winter moult in our Pied Flycatcher population was very similar to the one described by Jenni and Winkler (1994). By using an index of moult extent based on the relative contribution in mass of each replaced feather (see “Materials and methods”), we recorded significant differences among years and between age classes in the extent of the partial winter moult. Again, if we consider winter moult extent a condition-dependent trait (Senar et al. 1998), variation among years is likely to be the result of inter-annual variation in the environmental conditions experienced by Pied Flycatchers in Africa during winter moult. However, we do not believe that differences in body condition can explain the higher moult extent in SCY birds compared to adults. This phenomenon is more likely the result of the allocation of resources to other components of nuptial plumage, which may compromise moult extent in adults. According to our data, a higher investment in the mass of the feathers produced during winter did not mediate the variation in winter moult extent, as can be deduced from the lack of association between moult extent and tertial feather mass within individuals. In contrast, other traits not considered in this study, such as plumage coloration, which also varies between age classes (for example, Pied Flycatcher males produce a less melanised plumage during their second-calendar-year of life than in later years; Dale et al. 1999; Galván and Moreno 2009), could explain some of the observed variation in winter moult extent. Thus, adult males would favour the production of more melanised feathers with a more ultraviolet chroma at the expense of having less extensive moults. SCY males would not be able to afford this because they are costly to maintain due to increased competition (e.g. dark males receive more conspecific aggressions than pale ones; Huhta and Alatalo 1993), and they have a low probability of mating and obtaining a territory.

## Heritability of plumage traits

Our animal model analyses showed a clear association between the pedigree and the phenotypic variation in feather mass and moult extent, suggesting that plumage characteristics are heritable. The heritability estimates we obtained, however, need to be cautiously interpreted, since phenotypic resemblance among relatives may not only be due to genetic resemblance, but may be caused by other factors like maternal or permanent environment effects (Wilson et al. 2009). Our data structure did not allow us to adequately assess whether common environment effects (e.g. related to nest of origin) explained a significant fraction of total phenotypic variance. There is no empirical evidence suggesting that circumstances experienced by birds early in life have long-lasting consequences on the expression of feather mass and winter moult extent and, if they exist, we do not expect such effects to be strong. Nonetheless, further research will be necessary to elucidate the specific role of maternal and environmental effects on the expression of feather mass and winter moult extent.

If common environment and permanent environment effects are indeed unimportant, then the heritability values we found would be relatively high, although it is important to note that heritabilities are not comparable across studies because they strongly depend on the model structure used to estimate them (Wilson 2008). The problem of model-dependent heritability estimates can be avoided, at least to some extent, by scaling the square root of the additive genetic variance of each trait by the mean to obtain the coefficient of additive genetic variation ( $CV_A$ ; see Table 3), which facilitates the comparison with other studies (Houle 1992).  $CV_A$  values for feather mass and moult extent revealed that the evolutionary potential of these traits is actually low and similar to the scores obtained for other life-history and plumage traits of birds showing low genetic variance (see for example, Gienapp and Merila 2010; Husby et al. 2012). Such high  $h^2$  but low  $CV_A$  can be explained by a good knowledge of the fixed effects determining the phenotypic variation in feather mass and moult extent, which drastically reduces  $V_R$  in the models and gives rise to particularly high heritability estimates (Wilson 2008). Correcting for year effects, in particular, can substantially reduce  $V_R$  (and therefore increase  $h^2$ ); however, we would argue that selection acts on the available variation expressed within a given year (or a given selective episode), and therefore that including year in the models is appropriate when the goal is to make inferences about the potential for evolutionary response to selection.

## Selection on plumage characteristics

Although our results suggest the presence of additive genetic variation for feather mass and winter moult extent in our study population, which is a prerequisite for evolutionary change (Falconer and Mackay 1996), we did not find evidence of selection on plumage characteristics, as deduced from the lack of association with some traits correlated with fitness. This result was unexpected, since we predicted selection for these traits in response to recent climate change. For spring arrival date, an event of the annual cycle that may constrain the adaptation of Pied Flycatchers to climate change (Both and Visser 2001), we expected that heavier feathers (i.e. feathers with better mechanical properties; de la Hera et al. 2010b) and less extensive moults could facilitate an earlier arrival to breeding grounds. Although we detected that SCY males, which arrive later than adults (Potti 1998), indeed had lighter feathers and more extensive moults, variation in spring arrival date could not be explained by variation in plumage characteristics after correcting for age effects. Consequently, if moult has long-term consequences on timing of migration and



reproductive prospects in the Pied Flycatcher, as it has been suggested for other species (Nilsson and Svensson 1996; Dawson et al. 2000), such effects do not seem to be mediated by variation in feather mass or winter moult extent, but affected by other characteristics that were not considered in this study (e.g. timing of moult; Møller et al. 2011).

## Conclusion

Our study revealed that feather mass and moult extent are heritable and, hence, able to respond to selection in a Pied Flycatcher population. However, given that these plumage characteristics did not promote earlier reproduction and/or arrival at breeding grounds, we conclude that feather mass and moult extent are currently of minor importance for the adaptation of our study population to global warming. Therefore, the long-term viability of this and other bird populations is likely to rely on adaptive responses that are not related to modifications in these plumage characteristics.

**Acknowledgments** We want to thank all the people that helped during the fieldwork, and particularly to H. Bouwmeester, C. Rueda, N. Turreira and R. Roig. We are also grateful to K. van Oers, P. Gienapp and C.M. Lessells for valuable discussion. This study was funded by the Netherlands Organisation for Scientific Research (VICI grant to M.E.V.), the Department of Education, Universities and Research of the Basque Government (studentship BFI. 09-13 to I.H.), and the Spanish Ministry of Education (MEC; RYC-2007-01861 to F.P.).

## References

- Baayen RH (2008) languageR: data sets and functions with analyzing linguistic data: a practical introduction to statistics. R Package Version 0.953. <http://CRAN.R-project.org/package=languageR>
- Battley PF (2006) Consistent annual schedules in a migratory songbird. *Biol Lett* 2:517–520
- Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411:296–298
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83
- Bushuev AV, Ivankina EV, Kerimov AB (2006) Sex differences in resting metabolic rate in Pied Flycatchers. *J Ornithol* 147:101
- Butler LK, Rohwer S, Speidel MG (2008) Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *J Avian Biol* 39:629–639
- Charmantier A, Reale D (2005) How do misassigned paternities affect the estimation of heritability in the wild? *Mol Ecol* 14:2839–2850
- Coppack T, Both C (2002) Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90:369–378
- Dale S, Slagsvold T, Lampe HM, Sætre GP (1999) Population divergence in sexual ornaments: the white forehead patch of Norwegian Pied Flycatchers is small and unsexy. *Evolution* 53:1235–1246
- Dawson A (2004) The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. *Ibis* 146:493–500
- Dawson A (2005) The effect of temperature on photoperiodically regulated gonadal maturation, regression and moult in starlings—potential consequences of climate change. *Func Ecol* 19:995–1000
- Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L (2000) Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proc R Soc B* 267:2093–2098
- de la Hera I, Díaz JA, Pérez-Tris J, Tellería JL (2009a) A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. *J Avian Biol* 40:461–465
- de la Hera I, Pérez-Tris J, Tellería JL (2009b) Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biol J Lin Soc* 97:98–105
- de la Hera I, Pérez-Tris J, Tellería JL (2009c) Repeatable length and mass but not growth rate of individual feathers between moults in a passerine bird. *Acta Orn* 44:95–99

- de la Hera I, Pérez-Tris J, Tellería JL (2010a) Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. *J Avian Biol* 41:609–614
- de la Hera I, Hedenström A, Pérez-Tris J, Tellería JL (2010b) Variation in the mechanical properties of flight feathers of the blackcap *Sylvia atricapilla* in relation to migration. *J Avian Biol* 41:342–347
- de la Hera I, Hedenström A, Pérez-Tris J, Tellería JL (2010c) Structural and mechanical differences between original and replaced feathers in Blackcaps *Sylvia atricapilla*. *Ardeola* 47:431–436
- Dohm MR (2002) Repeatability estimates do not always set an upper limit to heritability. *Funct Ecol* 16:273–280
- Donnelly A, Caffarra A, Kelleher CT, O'Neill BF, Diskin E, Pletsers A, Proctor H, Stirnemann R, O'Halloran J, Peñuelas J, Hodkinson TR, Sparks TH (2012) Surviving in a warmer world: environmental and genetic responses. *Clim Res* 53:245–262
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics. Longman, Essex
- Galván I, Moreno J (2009) Variation in effects of male plumage ornaments: the case of Iberian Pied Flycatchers. *Ibis* 151:541–546
- Gienapp P, Merila J (2010) Genetic and environmental effects on a condition-dependent trait: feather growth in Siberian jays. *J Evol Biol* 23:715–723
- Ginn HB, Melville DS (1983) Molt in birds. BTO, Tring
- Griggio M, Serra L, Licheri D, Campomori C, Pilastro A (2009) Molt speed affects structural feather ornaments in the Blue Tit. *J Evol Biol* 22:782–792
- Gunnarsson TG, Gill JA, Newton J, Potts PM, Sutherland WJ (2005) Seasonal matching of habitat quality and fitness in a migratory bird. *Proc R Soc B* 272:2319–2323
- Hadfield JD (2010) MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. *J Stat Soft* 33:1–22
- Hall KSS, Fransson T (2001) Wing moult in relation to autumn migration in adult Common Whitethroats *Sylvia communis communis*. *Ibis* 143:580–586
- Hedenstrom A, Barta Z, Helm B, Houston AI, McNamara JM, Jonzen N (2007) Migration speed and scheduling of annual events by migrating birds in relation to climate change. *Clim Res* 35:79–91
- Houle D (1992) Comparing evolvability and variability of quantitative traits. *Genetics* 130:195–204
- Huhta E, Alatalo RV (1993) Plumage colour and male–male interactions in the pied flycatcher. *Anim Behav* 45:511–518
- Husby A, Gustafsson L, Qvarnström A (2012) Low genetic variance in the duration of the incubation period in a Collared Flycatcher (*Ficedula albicollis*) population. *Am Nat* 179:132–136
- Jenni L, Winkler R (1994) Molt and ageing of European passerines. Academic Press, London
- Jonzen N, Linden A, Ergon T, Knudsen E, Vik JO, Rubolini D, Piacentini D, Brinch C, Spina F, Karlsson L, Stervander M, Andersson A, Waldenström J, Lehikoinen A, Edvardsen E, Solvang R, Stenseth NC (2006) Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961
- King DA (2004) Climate change science: adapt, mitigate or ignore? *Science* 303:176–177
- Klaassen M (1995) Molt and basal metabolic costs in males of two subspecies of stonechats: the European *Saxicola torquata rubicula* and the East African *S. t. axillaris*. *Oecologia* 104:424–432
- Knudsen E, Lindén A, Both C, Jonzén N, Pulido F, Saino N, Sutherland WJ, Bach LA, Coppack T, Ergon T, Gienapp P, Gill JA, Gordo O, Hedenström A, Lehikoinen E, Marra PP, Møller AP, Nilsson ALK, Péron G, Ranta E, Rubolini D, Sparks TH, Spina F, Studds CE, Sæther SA, Tryjanowski P, Stenseth NC (2011) Challenging claims in the study of migratory birds and climate change. *Biol Rev* 86: 928–946
- Kruuk LEB (2004) Estimating genetic parameters in natural populations using the animal model. *Phil Trans R Soc B* 359:873–890
- Kruuk LEB, Hadfield JD (2007) How to separate genetic and environmental causes of similarity between relatives. *J Evol Biol* 20:1890–1903
- Lind J (2001) Escape flight in moulting tree sparrows (*Passer montanus*). *Funct Ecol* 15:29–35
- Lindström A, Visser GH, Dann S (1993) The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol Zool* 66:490–510
- López G, Figuerola J, Varo N, Soriguer R (2005) White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* 93:237–244
- Lundberg A, Alatalo RV (1992) The pied flycatcher. T and AD Poyser, London
- Møller AP, Fiedler W, Berthold P (2010) Effects of climate change on birds. Oxford University Press, Oxford
- Møller AP, Nuttall R, Piper SE, Szep T, Vickers EJ (2011) Migration, moult and climate change in barn swallows *Hirundo rustica* in South Africa. *Clim Res* 47:201–205
- Nilsson JA, Svensson E (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc R Soc B* 263:711–714

- Peñuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Glob Chang Biol* 8:531–544
- Postma E (2010) Using animal models to infer and predict the evolutionary consequences of climate change. In: Møller AP, Fiedler W, Berthold P (eds) *Effects of climate change on birds*. Oxford University Press, Oxford, pp 47–55
- Potti J (1998) Arrival time from spring migration in male Pied Flycatchers: individual consistency and familial resemblance. *Condor* 100:702–708
- Pulido F (2007) Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. *Clim Res* 35:5–23
- Pulido F, Berthold P (2004) Microevolutionary response to climate change. *Adv Ecol Res* 35:149–181
- Pulido F, Coppack T (2004) Correlation between timing of juvenile moult and onset of migration in the blackcap, *Sylvia atricapilla*. *Anim Behav* 68:167–173
- Reed TE, Schindler DE, Waples RS (2010) Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Cons Biol* 25:56–63
- Robinson RA, Crick HQP, Learmonth JA et al (2009) Travelling through a warming world: climate change and migratory species. *Endanger Species Res* 7:87–99
- Rubolini D, Spina F, Saino N (2005) Correlates of timing of spring migration in birds: a comparative study of trans-Saharan migrants. *Biol J Linn Soc* 85:199–210
- Rubolini D, Saino N, Moller AP (2010) Migratory behaviour constrains the phenological response of birds to climate change. *Clim Res* 42:45–55
- Salewski V, Altwegg R, Erni B, Falk KH, Bairlein F, Leisler B (2004) Moults of three Palearctic migrants in their West African winter quarters. *J Ornith* 145:109–116
- Senar JC, Copete JL, Martin AJ (1998) Behavioural and morphological correlates of variation in the extent of postjuvenile moult in the Siskin *Carduelis spinus*. *Ibis* 140:661–669
- Svensson L (1992) *Identification guide to European passerines*. L. Svensson, Stockholm
- Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc R Soc B* 275:649–659
- Wilson AJ (2008) Why  $h^2$  does not always equal  $V_A/V_P$ ? *J Evol Biol* 21:647–650
- Wilson AJ, Réale D, Michelle NC, Morrissey MM, Postma E, Walling CA, Kruuk LE, Nussey DH (2009) An ecologist's guide to the animal model. *J Anim Ecol* 79:13–26