

Patterns of Fluctuating Selection on Morphological and Reproductive Traits in Female Tree Swallow (*Tachycineta bicolor*)

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Abstract Temporally replicated studies are essential to describe and understand selection in natural populations. Selection patterns can differ among life stages representing different fitness components. Despite the increasing number of long-term studies, yearly estimates of fluctuation in strength and direction are mostly available from studies conducted on a limited number of years. Based on a population of Tree swallows (*Tachycineta bicolor*) monitored over 10,200 km² in Southern Québec, Canada, since 2004, we investigated how patterns of selection may change across breeding stages by dividing the overall selection at the nesting stage (number of fledglings produced) into hatchling (number of hatchlings produced) and fledgling (number of hatchlings having successfully fledged) selection stages. We assessed fluctuation in selection gradients on two morphological (body mass and wing length) and two reproductive (laying date and clutch size) traits in females. We found significant positive selection gradients for body mass and clutch size and negative selection gradients for laying date, though the latter only during the

fledgling selection stage. We also found that selection gradients on reproductive traits significantly fluctuated in direction and/or strength among years but only during the hatchling breeding stage. Our results thus emphasize the need to consider how selection events may be fluctuating in time and among breeding stages and the importance of these patterns for the maintenance of phenotypic variation in wild populations.

Keywords Selection gradients · Fluctuating selection · Laying date · Clutch size · Body mass · Wing length · Birds

Introduction

Understanding the temporal dynamics of phenotypic selection on heritable traits is crucial for a better appreciation of patterns of evolutionary changes in natural environments. Since the publication of the seminal book by Endler (1986) on the effects of natural selection in wild populations, a growing number of studies have shown temporal variation in the overall strength, form and direction of selection on phenotypic traits (reviewed in Siepielski et al. 2009, 2011; Bell 2010; but see also Morrissey and Hadfield 2012). For instance, some studies have shown that temporal variation of selection may be relatively consistent in direction over time (e.g. delay in hibernation emergence of Columbian ground squirrels, *Urocitellus columbianus*; Lane et al. 2012), while others have shown strong and unpredictable variation in direction and/or strength (e.g. fluctuation in beak shape and size of Darwin finches, *Geospiza* spp.; Grant and Grant 2002). In the latter case, fluctuating selection could represent an important mechanism leading to phenotypic variation at the population level (Bell 2010), but could also hinder

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potential population divergence (Ghalambor et al. 2007) and local adaptation (Kawecki and Ebert 2004). Yet, patterns of fluctuating selection found in wild populations remain elusive as the vast majority of studies were conducted on a limited number of years (e.g. median = 3 - years for studies included in the meta-analysis by Siepielski et al. 2009).

Inter-annual fluctuations in biotic and abiotic conditions experienced by natural populations can potentially result in strong variation in selective pressures. Over the last decades, anthropogenic-related changes of the environment due to climate change, species introduction and over-harvesting of natural resources have dramatically increased (Carroll et al. 2007), resulting in stronger variation in direction and strength of selection on a contemporary time scale (e.g. Hendry et al. 2008; Darimont et al. 2009). For example, climate warming has been associated with earlier breeding of passerines from several populations (e.g. Both et al. 2006; Charmantier et al. 2008; reviewed in Gienapp et al. 2008). Describing the dynamics of fluctuating selection in natural populations affected by anthropic activities is thus vital to increase our understanding of the consequences of such changing environments on wild species.

The direction and strength of selection may vary among successive selection stages and thus complicate the interpretation of selection patterns, a phenomenon exacerbated by the fact that selection is estimated based on different proxies of fitness during a given selection stage (Arnold and Wade 1984; Arnold and Duvall 1994; McGlothlin 2010; Pischedda and Rice 2012; Lebigre et al. 2013). Arnold and Wade (1984) developed a framework to emphasize that by estimating selection during successive selection episodes and between life stages, one can estimate the variation in direction and strength of selection among them and their effects on the overall pattern of selection. In birds, reproductive success is often calculated using the number of fledglings produced per year (e.g. Møller and Szép 2002; Yeh and Price 2004; Teplitsky et al. 2011; Tarwater and Beissinger 2013), which is used as a fitness proxy when assessing selection at the nesting stage. However, this proxy of fitness could be further divided into two main components: (1) number of hatchlings produced, which mainly represents fitness related to female fecundity and (2) survival from hatchling to fledgling, which is more representative of parental capacity to raise nestlings until they fledge and corresponds to a combination of parental and nestling fitness. It follows that different traits may be under distinct patterns of selection among these breeding stages. Survival from hatchling to fledgling (more so than hatchling success), for instance, should be directly affected by morphological characters involved in parental capacity to feed nestlings. For example, insectivorous birds with

shorter wings often have higher success at capturing preys, resulting in higher fledgling success (Møller et al. 2006; Møller 2013; Tarka et al. 2014). Therefore, to have a more complete understanding of variation in selection patterns, one should attempt to disentangle the relative effects of several morphological and reproductive traits on different fitness components during successive episodes of selection.

The aims of this study were (a) to assess patterns of selection on two morphological and two reproductive traits over a 10-year period in female Tree swallows (*Tachycineta bicolor*) breeding in Southern Québec, Canada, and (b) to estimate whether selection on different fitness components fluctuate over the study period in an environment affected by anthropic activities. Tree swallows are migratory, aerial insectivorous passerines that breed over most of the USA and Canada. The population breeding in Southern Québec is declining (Rioux Paquette et al. 2014) like most populations breeding in the north-eastern part of the species distribution range (Shutler et al. 2012). In Southern Québec, this decline has been partly associated with anthropic activities, such as agriculture intensification, which may negatively affect insect prey availability (Ghilain and Bélisle 2008; Rioux Paquette et al. 2013) and increase interspecific competition for nest sites (Robillard et al. 2013). Also, individuals from this population showed a temporal decline in average body mass (8 % in females and 2 % in males between 2005 and 2011; Rioux Paquette et al. 2014). Our study will thus contribute to assess critical episodes of selection for this declining population.

Methods

Study System

Since 2004, we monitored breeding activities of Tree swallows in a study system where 400 nest boxes have been distributed equally among 40 farms over an area of 10,200 km² in Southern Québec, Canada. Detailed characteristics of the study system can be found in Ghilain and Bélisle (2008). During the breeding season (from April to August), nest boxes were visited every 2 days. A nest box was considered occupied when at least one egg was laid (as in Ghilain and Bélisle 2008; Robillard et al. 2013). For each female occupying a nest box, the following parameters were noted: laying date of the first egg (in Julian day with 1 corresponding to January 1; LD), clutch size (number of eggs laid; CS), number of hatchlings (number of eggs having successfully hatched) and number of fledglings (number of hatchlings having successfully fledged). Each female was captured at least once during the breeding period and was leg banded with a unique number, weighted (± 0.01 g), and had its wing chord (± 0.5 mm; a

non-flattened measure of wing length, hereafter called wing length) measured. We standardised female body mass by regressing the mass measured on the measurement date (in Julian day) and the time of day at which the bird was weighted (time was treated as a proportion with 0.5 corresponding to midday; see also Rioux Paquette et al. 2014). Standardisation of female body mass was done within each year (correlation between raw and standardised body mass: $r = 0.92$, $P < 0.001$). See Fig. 1 for a representation of mean traits variation among years.

Selection on Fitness Components

We used three different fitness proxies for selection analyses: (1) number of hatchlings (number of eggs having successfully hatched); (2) number of fledglings (number of hatchlings having successfully fledged) and (3) overall nesting selection (number of eggs having successfully fledged). For the number of fledglings, analyses were

restricted to clutches having successfully produced at least one hatchling ($N = 1772$ clutches; Table S1), to effectively assess selection on fledging success independently from hatching success. Because data were missing for a few individuals, sample size may vary among traits thus resulting in a total of 1969 clutches and 1718 broods available for all traits combined in analyses of selection on the number of hatchlings and fledglings, respectively (Table S1). Note that analyses were performed on first clutches for each year ($N = 2043$ clutches between 2004 and 2013; see Table S1 for detailed yearly sample sizes). Only first clutches were considered as Tree swallows lay few second clutches in the system and they are mostly the result of previous clutch failure ($N = 29$ second clutches on average per year; $\sim 12\%$ of clutches).

For each fitness component (number of hatchlings, number of fledglings and overall nesting selection), linear selection differentials for reproductive (LD and CS) and morphological (wing length and body mass) traits were

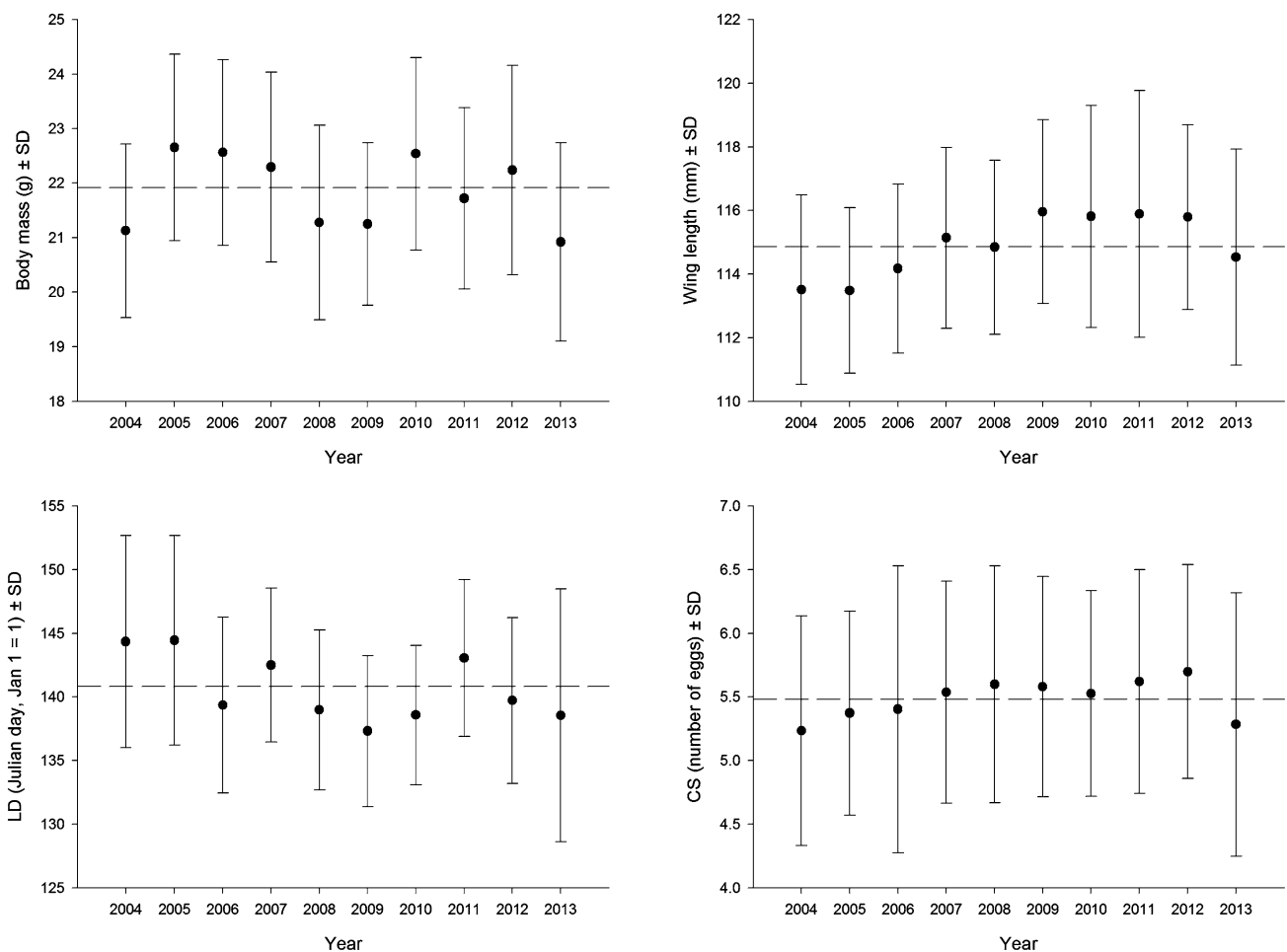


Fig. 1 Yearly mean values (\pm SD) of the morphological (body mass and wing length) and reproductive (laying date, LD, and clutch size, CS) traits from female Tree swallows in Southern Québec, Canada,

between 2004 and 2013. Dashed lines correspond to the overall mean of the trait over the 10-year study period. Sampling sizes for each trait and year are in Table S1

estimated overall and for each year. Linear selection gradients (Lande and Arnold 1983) were also calculated to assess the relative effect of each trait while accounting for the other traits. To obtain standardised selection estimates (e.g. that are comparable among them and with published estimates), each trait was standardised (mean of 0, variance of 1) within each year. Fitness components were transformed to relative fitness by dividing the number of hatchlings (or fledglings) of each female in a given year by the mean number of hatchlings (or fledglings) for the population within the same year.

Statistical Analyses

Estimates (e.g. slopes) of selection differentials and gradients were estimated using general linear models. In brief, selection differentials (S) were obtained by regressing each relative fitness values within each year against standardized values of each trait separately. Selection gradients (β) were estimated from the following multivariate linear model:

$$\omega = \alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \varepsilon$$

where ω = relative fitness, α = intercept, x_1 = laying date, x_2 = clutch size, x_3 = body mass, x_4 = wing length and ε = error term.

Differences in selection gradient slopes among stages for each trait were tested using z-tests. Statistical significance of the covariance between fitness proxies and trait values was, however, assessed by re-running the same fixed model structure as above in generalized linear mixed models that also included farm and female identity as random factors (using Poisson error distribution; see Garant et al. 2007; Porlier et al. 2012 for a similar approach).

Sequential model building (Appendix A in Chenoweth and Blows 2005; see Garant et al. 2007; Porlier et al. 2012 for applications of this method) was used to assess fluctuation in linear selection differentials and selection gradients. For each fitness component (i.e. the dependent variable in the models), we compared a model including all reproductive traits (LD and CS) and morphometric measurements (body mass and wing length) and year (coded as factor) with a full model including all fixed effects as well as the interactions between each trait and year (coded as factor) using a LR deviance test with a χ^2 distribution. If the full model was significant, we successively compared the full model with a model where one of the trait \times year interaction was removed. Such test was performed in order to assess the effect of each interaction independently of the other trait \times year interactions. Each model used was a generalized linear mixed model (with Poisson error distribution) including farm and female identity as random factors. All analyses were performed in R v 3.0.2 (R Development core team 2013). Results are reported with

their standard errors (SEs). Detailed results for selection differentials analyses are presented in the electronic supplementary material (Table S2).

Results

Selection Gradients

Morphological Traits

The linear selection gradient was significantly positive for female body mass in all three breeding stages considered (i.e. overall nesting, hatchling and fledgling stages) and was of similar strength between the hatchling and fledgling selection stages (slope difference z-test: $z = 0.18$, $P = 0.86$; Table 1). In contrast, the linear selection gradient for wing length was not significantly different from zero in all three breeding stages (Table 1) and did not differ in strength between the hatchling and fledgling selection stages (slope difference z-test: $z = 0.30$, $P = 0.76$). Thus heavier females, but not females with larger wings, produced more hatchlings and fledglings.

Reproductive Traits

The linear selection gradient for LD was negative and marginally non-significant for the overall nesting stage (Table 1). The selection gradient on this trait was significantly negative at the fledgling stage but did not significantly differ from zero at the hatchling stage (slope difference z-test: $z = 2.98$, $P = 0.003$; Table 1). The linear selection gradient for CS was significantly positive for the overall nesting stage, as well as for each selection stage (Table 1). Yet, the slope of selection gradient for CS was stronger during the hatchling stage than during the fledgling stage (slope difference z-test: $z = 4.55$, $P < 0.001$; Table 1). Thus, there was selection for earlier breeding only at the fledgling stage and larger clutches produced more hatchlings and fledglings.

Among Years Variation in Selection Patterns

For the overall nesting stage, we found that selection gradients fluctuated significantly among years (Table 2 and S3). However, analyses of trait-specific annual fluctuation during the overall nesting stage revealed that only the LD \times year interaction had a significant effect (Table 2).

We also found differences among selection stages with significant yearly fluctuation at the hatchling stage for both reproductive traits, but not during the fledgling stage (Table 2; Fig. 2). In details, selection gradients on LD at the hatchling stage fluctuated in strength and direction and

Table 1 Selection gradients ($\beta \pm$ SE) for morphological and reproductive traits of female Tree swallows in three selection stages

	Hatchling stage		Fledgling stage		Overall nesting stage	
	β (SE)	<i>P</i>	β (SE)	<i>P</i>	β (SE)	<i>P</i>
Body mass	0.065 (0.010)	<0.001	0.062 (0.013)	<0.001	0.113 (0.016)	<0.001
Wing length	-0.006 (0.010)	0.61	-0.001 (0.013)	0.97	-0.012 (0.016)	0.31
Laying date	0.002 (0.011)	0.86	-0.051 (0.014)	<0.001	-0.031 (0.017)	0.059
Clutch size	0.187 (0.011)	<0.001	0.106 (0.014)	<0.001	0.160 (0.017)	<0.001

Data were collected in Southern Québec, Canada, between 2004 and 2013. Selection gradients were estimated using general linear models and the statistical significance of the covariance between fitness proxies and trait values was assessed using mixed Poisson regressions including farm and female identity as random factors. See Table S1 for sample sizes

Table 2 Assessment of yearly fluctuation of selection gradients for morphological and reproductive traits of female Tree swallows in three selection stages (see Table 1)

		<i>df</i>	Log likelihood	LRT	<i>P</i>
<i>Hatchlings</i>					
A	Without year interaction	16	-4122.9	61.86	0.005
	With year interaction	52	-4092.0		
B	Without year \times wing interaction	43	-4094.6	5.26	0.81
	Without year \times mass interaction	43	-4097.5	10.92	0.28
	Without year \times LD interaction	43	-4102.2	20.37	0.016
	Without year \times CS interaction	43	-4103.8	23.60	0.005
<i>Fledglings</i>					
	Without year interaction	16	-3669.6	42.26	0.22
	With year interaction	52	-3648.5		
<i>Total nest selection</i>					
A	Without year interaction	16	-4350.9	60.22	0.007
	With year interaction	52	-4320.8		
B	Without year \times wing interaction	43	-4323.2	4.90	0.84
	Without year \times mass interaction	43	-4327.1	12.60	0.18
	Without year \times LD interaction	43	-4337.3	33.04	<0.001
	Without year \times CS interaction	43	-4325.7	9.93	0.36

Sequential model building involved testing with likelihood ratio tests (LRTs) (A) the effect of adding two-way interactions between year (coded as factor) and each of all traits and if found significant, then testing (B) the effect of each trait \times year interaction independently of the other interactions

ranged between -0.080 ± 0.035 (in 2012) and 0.124 ± 0.056 (in 2013; Fig. 2; Table S3). For CS, selection gradients at the hatchling stage were always positive but fluctuated between 0.122 ± 0.036 (in 2012) and 0.285 ± 0.031 (in 2006; Fig. 2; Table S3). Neither morphological trait had a significant trait \times year interaction at any stage (Table 2 and S3, Fig. 2).

Discussion

Our analyses of selection patterns on female Tree swallows showed that body mass and clutch size were under positive directional selection during all breeding stages and thus during the overall nesting stage. Laying date was under negative directional selection, though only during the

fledgling stage, and thus only marginally at the overall nesting stage. In contrast, wing length was not under selection at any stage. We also detected that selection varied temporally in strength and direction for laying date only during the hatchling selection stage, while fluctuating selection in strength was detected for clutch size. No fluctuation among years was detected for morphological traits.

Selection Patterns: Overall and Among Selection Episodes

A few long-term studies on passerines have assessed how the strength of selection differs via fecundity on morphological and reproductive traits—using either the number of fledglings or the number of recruits as the proxy of fitness.

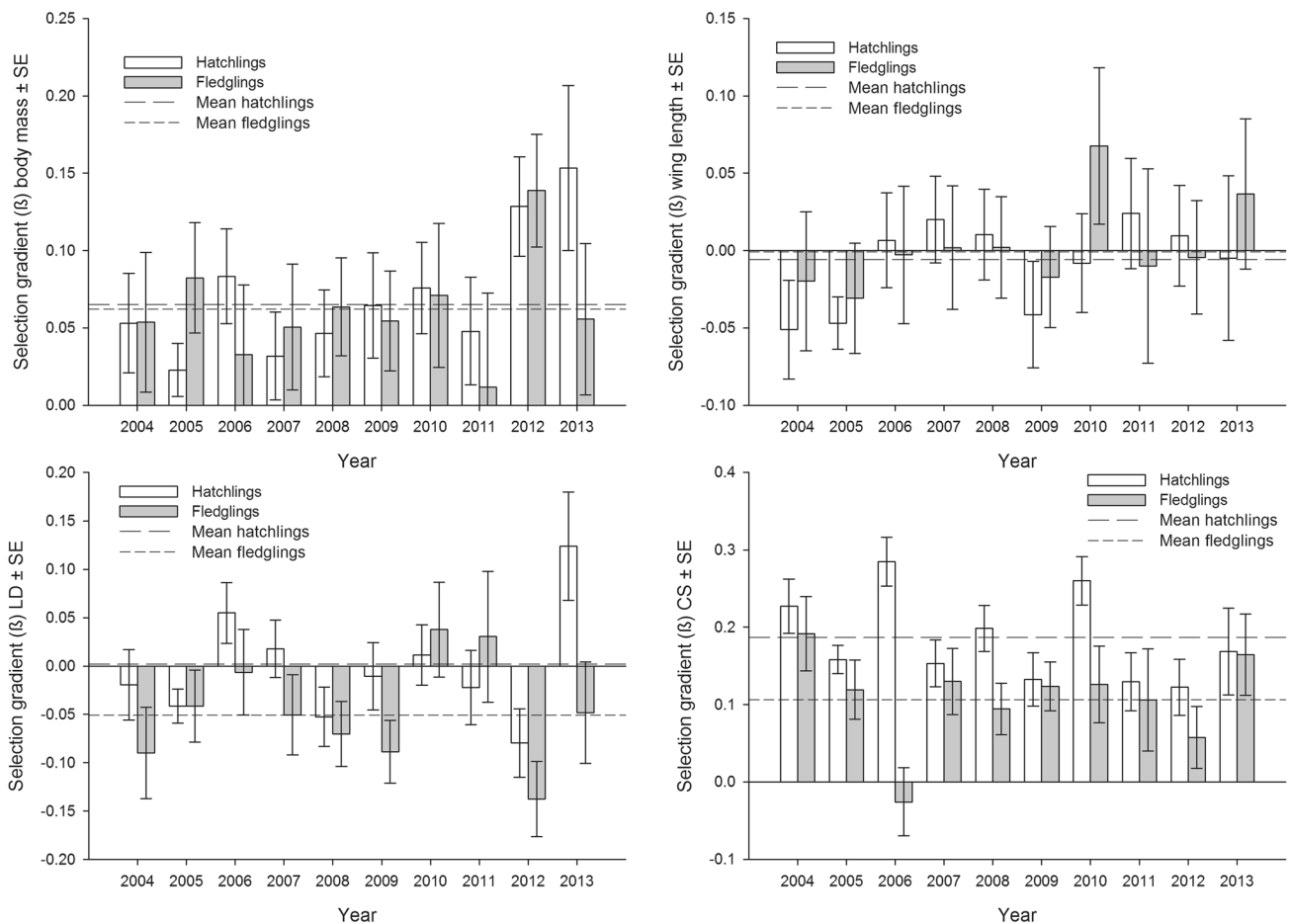


Fig. 2 Yearly linear selection gradients ($\beta \pm SE$) of the morphological (body mass and wing length) and reproductive (laying date, LD, and clutch size, CS) traits of female Tree swallows estimated between 2004 and 2013 in Southern Québec, Canada. Selection gradients were estimated using either the number of hatchlings (white

bars) or the number of hatchlings having successfully fledged (grey bars). Overall mean selection gradients for the hatchling (long dashed line) and fledgling (short dashed line) selection episodes are also provided

Similar to our findings, the majority of these studies reported selection gradients that were negative for laying date, with earlier laying date being favourable, and positive for clutch size, with larger clutches being beneficial (e.g. different populations in Europe : Sheldon et al. 2003; Garant et al. 2007; Husby et al. 2011b; Teplitsky et al. 2011; Porlier et al. 2012). Previous studies of selection on body mass and wing length provided more equivocal results with either positive [body mass in great tits (*Parus major*): Husby et al. 2011a; wing length in collared flycatchers (*Ficedula albicollis*): Przybylo et al. 2000], negative [in great reed warblers (*Acrocephalus arundinaceus*) for body mass, Teplitsky et al. 2014 and wing length, Tarka et al. 2014] or no significant selection (body mass and wing length: several species reviewed in Teplitsky et al. 2014) being reported for these traits depending on the study system and species studied. Interestingly, the patterns of selection we documented here for morphological traits—

selection favours heavier bird, does not affect wing length—are in contrast with the temporal phenotypic trends observed in our study system for females. Indeed, in a previous study in this system, Rioux Paquette et al. (2014) documented both a temporal decrease in body mass and an increase in wing length for females over 7 years. These results suggest that if selection acted on these traits, it should have been overall negative for body mass and positive for wing length. This possible discrepancy among the two studies may stem from a mismatch between individual- and population-level effects on response to selection. At the individual level (e.g. our study), larger female body mass seems steadily and increasingly favoured during the overall nesting stage. At the population-level (e.g. Rioux Paquette et al. 2014), individuals become on average lighter possibly as a result of deteriorating environmental conditions at a larger scale (e.g. wintering and stop-over sites; see Rioux Paquette et al. 2014 for discussion).

Differences between individual- versus population-level responses was also shown in regard to phenological mismatch between the peak of caterpillar availability and the timing of reproduction in a Great tit (*Parus major*) population in the Netherlands (Reed et al. 2013). Reed et al. (2013) reported that climate change-induced mismatch had strong effects on the relative fitness of phenotypes within years (individual-level), but weak effects on mean demographic rates (population-level) across years. Further analyses are on the way in our study system to disentangle individual from population level changes in reproductive and morphological traits (e.g. using the approach proposed by van de Pol and Wright 2009).

Although, earlier laying date typically leads to higher fitness, we only detected directional selection on this trait during the fledgling stage. This contrasting result may be due to selection acting on different life-history aspects at different stage. The hatchling stage is linked to female fecundity and influenced by female condition as the hatchling success will likely be affected by the ability of a mother to invest in egg quality and quantity (Martin and Schwabl 2008). As Tree swallows are income breeders (Bowlin and Winkler 2004; Nooker et al. 2005; Dunn et al. 2011), limited food availability at the beginning of the breeding season will mainly affect the female capacity to lay a large clutch and maintain a large body mass rather than her timing to do so. Thus, at this stage, clutch size and body mass seems the main determinants of the number of hatchling produced, independently of the phenology of reproduction. On the other hand, the fledgling stage is more likely to be affected by selection on the mother and father ability to provide parental care, but also importantly by environmental characteristics as nestlings are dependent upon food availability. Previous studies suggested that egg laying was not timed with the seasonal peak of insect availability in this species (Nooker et al. 2005; Dunn et al. 2011). However, the environmental characteristics of our study system might have affected the selection patterns observed. Indeed, the presence of intensive agricultural areas in our study system results in an early decrease in insect abundance during the breeding season (Rioux Paquette et al. 2013). As a result, selection on nestlings might be stronger for earlier hatching and thus earlier egg laying. Altogether, these results reinforce the suggestion that selection studies should aim at integrating several life stages (Schluter et al. 1991; van Tienderen 2000).

Temporal Fluctuation in Selection

The presence of annual fluctuation—in direction and/or strength—in selection gradients was suggested by previous reviews of temporally replicated studies (reviewed in: Bell

2010; Siepielski et al. 2009, 2011; Kingsolver et al. 2012). Our results revealed yearly fluctuation in selection patterns that differed across traits. During the overall nesting stage, only the selection gradient implying laying date fluctuated across years. Further analyses revealed annual fluctuation of selection gradients only during the hatchling selection stage and only for laying date and clutch size. Morrissey and Hadfield (2012) pointed out that, in several cases, the observed fluctuations in selection result from sampling error (i.e. large standard errors associated with selection gradients) rather than actual fluctuations in selection (i.e. large standard deviation of selection gradients over time). The trends reported here are unlikely to be strongly affected by sampling error as the standard deviations of selection gradients (SD) as a function of their mean standard error (SE) is not significantly different from zero (Fig. S1). Our results also contrast with previous studies on the same traits in other passerine species that found little evidences for significant variation in selection across time for these two traits, for instance in collared flycatchers and blue tits *Cyanistes caeruleus* (Sheldon et al. 2003; Porlier et al. 2012).

A visual inspection of the trends observed for reproductive traits suggests that only selection gradients for laying date show evidences of variation in direction among years (see Fig. 2). The strongest gradients obtained for laying date during the hatchling stage (positive: 2006 and 2013, negative: 2005, 2008 and 2012; Fig. 2; Table S3) corresponded to years where the proportions of successfully hatching eggs were respectively lower and higher than average (see Table S1). These fluctuations may be related to unusual environmental conditions (e.g. temperature) and additional research is needed to identify environmental drivers of selection. The lack of significant temporal fluctuation in selection for laying date during the fledgling stage (negative selection observed in 8 years out of 10) suggest that laying early in spring generally results in increased fledgling survival. As suggested above, laying eggs early may be beneficial due to the environmental characteristics of our study system. The presence of intensive agricultural areas may result in an early decrease in food availability potentially due to pesticides use (Rioux Paquette et al. 2013). This result is also concordant with numerous observations in birds of a decline in reproductive success among individuals breeding later in the season (Perrins 1970; reviewed in Verhulst and Nilsson 2008).

Selection gradients for clutch size showed variation in strength across years at the hatchling stage, but not in direction as they were always positive. The observed fluctuation in strength of selection on clutch size may be associated with the among year differences in environmental conditions, including temperature and early-season food availability. While larger clutches always seem

beneficial, poor conditions (e.g. year 2006) likely increase incubation costs (Heaney and Monaghan 1996; Reid et al. 2000) and thus accentuate the difference in hatching success between individuals able to produce large clutches under such conditions and those unable to do so. Interestingly, the combination of constant positive selection gradients on clutch size and increase in the mean clutch size during the study period (Fig. 1) suggests an adaptive evolutionary response in this Tree swallow population. Clutch size is known to be heritable in other passerine species (e.g. Sheldon et al. 2003; Garant et al. 2008; Teplitsky et al. 2011), but we have yet to assess its genetic basis in our study system.

Finally, we found no yearly variation in body mass or wing length selection patterns. Selection on body mass was always positive and of a relatively similar magnitude across the study period (Fig. 2). This contrasts with a previous study by Husby et al. (2011a) conducted on three populations of Great tits where selection on adult body mass was inconsistent across years, with only 7 (positive) significant yearly selection gradients out of 30 years and important yearly variation in the strength and sign of selection. The lack of variation detected for wing length was probably related to the generally weak selection present for this trait.

Limitations of Our Study

Several non-exclusive factors may have impacted the validity of our findings. First, the use of hatching and fledging success as proxy of fitness, instead of number of recruits to the population, could be questioned. In our study system, recruitment is very low ($\sim 1\%$ of young fledged), which prevented us from using this latter metric. Second, it should be emphasized that traits analysed in our study are not completely independent in their relationships among them and with fitness variables. However, correlations among traits were relatively weak (ranging from $r = -0.34$ for laying date-clutch size to $r = 0.17$ for body mass-clutch size). Also, the use of selection gradients (instead of only selection differentials) should partly control for this non-independence, as this method allows to quantify direct selection acting on a trait while including other traits of interest in the analysis (Lande and Arnold 1983). Third, our results are correlative in nature and thus, we can only speculate about the mechanisms producing the relationships reported here. Ideally, our results should be confirmed using an experimental approach in the future. Fourth, hatching and fledging success do not only depend on a female's contribution, but also on that of the male(s) through genetic fertility and parental care. While we are currently lacking data to quantify care provided by males in our system, a previous

study indicated that a male reproductive success within his nest was partly related to laying date (Lessard et al. 2014). Finally, random environmental variation may have influenced the selection estimates reported here. For example, in our study species, stormy conditions during migration may affect arrival date and breeding condition, which in turn could impact the strength and direction of selection detected. It should however be noted that such variation is arguably present in most studies aiming at detecting fluctuating selection in the wild.

Conclusion

In conclusion, our results highlight that selection patterns can vary across time and differ among successive breeding stages. Such trends may potentially affect the extent of phenotypic variation maintained for traits within the population over time. In doing so, we emphasize the value of long-term studies to identify such important evolutionary processes in the wild. Agricultural intensification within our system may also affect the strength and direction of selection estimates. However, the amount of cultures present around nest boxes for each location sampled is highly stable through time (see Lessard et al. 2014) and thus should have little effect on the temporal variation in selection, which was the main focus of this study. Further work is under way to assess the effect of spatial variation in agricultural intensification on the selection acting on traits in our study system. In combination with the current results, these analyses will allow to assess whether patterns of selection promotes or hinders the decline of this Tree swallow population.

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