Ecological crossovers of sexual signalling in a migratory bird

Teerikorpi PE[1], Sirkiä PM[2], Laaksonen T[1]

[1]Section of Ecology, Department of Biology, University of Turku, Finland

[2]Finnish Museum of Natural History, Zoology Unit, University of Helsinki, Finland

* Corresponding author: Pauliina Elisabet Teerikorpi, Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland. Tel.: +358 2 333 5243; Fax: + 358 2 333 6598; Email: peteer@utu.fi

Running title: Ecological crossovers of sexual signals

Author contributions: Original idea P.T., T.L., P.S.; Field work P.T., P.S., T.L.; Statistics P.T.; Writing P.T.; Commenting T.L., P.S.

Data archive location: https://doi.org/10.5061/dryad.s27v5b0

ACKNOWLEDGEMENTS

We would like to thank Markus Ahola, Sara Calhim, Oliver Claque, Jenni Kuismin, Jussi Lampinen, Markus Lampinen, Esa Lehikoinen, Jorma Nurmi, Kalle Rainio, Jenna Ruohonen, Wiebke Schuett, Kirsi Ukkola, Matias Ukkola, Ina-Sabrina Tirri, Emilia Vainio and William Velmala for great help in the field. Funding for the project was provided by the Academy of Finland (grants to T.L. and P.S.), the Ella and Georg Ehrnrooth foundation (to P.J.), the Emil Aaltonen Foundation (to T.L.), the Turku University Foundation (to P.J.) and University of Turku Graduate School (to P.J.). We confirm that this manuscript has not been published elsewhere and is not under consideration by another journal. The authors declare that they have no conflict of interest.

ABSTRACT

Environmental shifts may induce sudden reversals in the relative quality or sexual attractiveness of mates (ecological cross-overs) leading to non-directional sexual selection. Studies on such ecological cross-overs induced by environmental shifts during the non-breeding season are particularly rare. We studied the interactive effects between non-breeding conditions and a male white wing patch on the breeding success of breeding pairs and the local survival of females in a migratory passerine population over a 32-year period. After dry winters, females paired with large-patched males were more likely to survive than those paired with small-patched males, and vice versa after moist winters. Moreover, after dry winters, large-patched males succeeded in attracting females that laid large clutches, while small-patched males bred with females that laid small clutches, and vice versa after moist winters. This phenomenon led to a difference in fledgling numbers only during years with dry winters and high precipitation during the breeding season. The selection on this male trait and its signalling value to females thus depended on a complex interaction between conditions both at the non-breeding and breeding grounds. We show that it is important to consider conditions during the non-breeding season when examining the effects of sexual ornaments on fitness.

Keywords: carry-over effect, climate change, fluctuating selection, mate choice, NAO index, seasonal interactions

INTRODUCTION

Sexual selection is considered responsible for some of the most conspicuous ornamental traits found in animal taxa (Andersson 1994). Sexual selection models assume that the choosy sex (usually females) mates non-randomly with regard to one or more secondary sexual traits, such as colorful patches or long spurs, of the other sex (Darwin 1871, Fisher 1930, Andersson 1994). It was therefore long believed that the choosy sex should always gain by selecting a mate with a conspicuous secondary sexual trait. However, this is not always the case, as sexual selection and trait values can be affected by varying environmental conditions (e.g., Robinson et al. 2012). In addition to natural changes, human-induced changes in environmental conditions (e.g., anthropogenic climate change) evidently affect the dynamics of natural populations (Walther et al. 2002, Peñuelas et al. 2013). Yet, the impacts of such changes on populations are still very difficult to predict as they remain far from being comprehensively studied. Understanding of the effects of such fluctuating environmental conditions on sexual selection (e.g., on its direction and on the expression of secondary sexual traits) is still limited.

Because secondary sexual traits are usually condition-dependent, environmental changes may affect their expression at the population- and individual-levels (e.g., Garant et al. 2004, Saino et al. 2004, Hegyi et al. 2007, Reudink et al. 2015, Järvistö et al. 2016a). Consequently, shifts in environmental conditions might induce sudden reversals in the relative quality or sexual attractiveness of mates (phenomena termed as ‘ecological cross-overs’, Spottiswoode & Saino 2010, Botero & Rubenstein 2012). Studies on ecological cross-overs are scarce, but some evidence exists for cross-overs of the relative quality of mates. Botero and Rubenstein (2012) found that in socially monogamous avian species the partnership stability (a sexual behaviour) interacted with the predictability of temperature cycles affecting the divorce rate. Species with continuous partnerships have higher divorce frequencies in unpredictable environments and species that engage in temporary partnerships have lower divorce frequencies in such environments (Botero & Rubenstein 2012). Thus, species engaging in continuous partnerships appear to divorce to reduce potential negative fitness consequences of unsuitable partnerships under unpredictable environmental conditions. Such environment-dependent quality of mates may lead to the evolution of environment-dependent adaptive plasticity in mate preferences in relation to size or conspicuousness of secondary sexual traits (Qvarnström 2001, Chaine & Lyon 2008). In contrast to a fixed preference such an adaptive plasticity would enable individuals to reverse their mate preference and in this way to have the highest possible fitness in a changing environment (e.g. Botero & Rubenstein 2012). In addition, exaggeration of secondary sexual traits could be reduced by adaptive plasticity in mate preference as the direction of sexual selection would fluctuate (Chaine & Lyon 2008).

Long-distance migratory species are of particular interest when linking environmental conditions to the processes of sexual selection, as their non-breeding and breeding seasons often take place on two separate continents with utterly different environmental processes. The events occurring during the non-breeding season may have carry-over effects on sexual selection during the breeding season (Webster et al. 2002, Norris et al. 2004, Norris & Taylor 2006, Reudink et al. 2009, Robinson et al. 2009). Moreover, such carry-over effects may lead to ecological cross-overs where the signaling function of secondary sexual traits varies across an environmental gradient (Norris & Taylor 2006, Robinson et al. 2009). Therefore, more knowledge of the interplay between an ever-changing environment and sexual selection is essential for comprehensively predicting the consequences of anthropogenic climate change on sexual selection and thereby on population dynamics.

The pied flycatcher (*Ficedula hypoleuca*) is a sexually dimorphic migratory passerine that breeds in most of Europe and western Siberia. The species winters in sub-Saharan Africa, where it undergoes a partial pre-nuptial moult, during which males change into their conspicuous breeding plumage that includes a white wing patch (Lundberg & Alatalo 1992).

The size of this continuous trait varies greatly among males (Lundberg & Alatalo 1992, Laaksonen et al. 2015). Repeatability of the wing patch size is moderate, indicating that this trait is to some extent condition-dependent and heritable as repeatability sets an upper boundary on heritability (Järvistö et al. 2016a). Furthermore, females use patch size as a mate choice cue (Sirkiä & Laaksonen 2009).

We recently found that the white wing patch in the breeding plumage of pied flycatcher males is affected by conditions at the non-breeding grounds through two different pathways: 1) during dry and windy winters (i.e., high NAO winters; the North Atlantic Oscillation index) an individual develops a smaller wing patch size than during moist winters, while 2) the probability of returning to the breeding grounds increases with original wing patch size (i.e., individuals with large wing patches were more likely to return, Järvistö et al. 2016a). We can therefore predict that the information that wing patch size conveys about male quality varies with fluctuating annual non-breeding conditions. Thus, selection would target wing patch size at the breeding grounds through female choice and further through breeding success depending on the non-breeding conditions. The quality and condition of the male can be very important for the fitness of the female because the male is involved in the whole breeding process (Lundberg & Alatalo 1992). The male is guarding the female while she (alone) is building the nest and laying eggs, and feeding her while she is incubating. The male is the main provider for the chicks for the first days after the hatching when they are still brooded by the female. The male continues feeding the chicks until they gain independence a few weeks after fledging. The female is also feeding the chicks when they are older; thus there is also potential for a sexual conflict over parental investment between the male and the female (Laaksonen et al. 2011). The female can be expected to benefit from good condition of the male because this could enable her to reduce her own parental work load without reducing her fitness (Houston et al. 2005; Lessells 2006). It would also be beneficial for the females to have adaptive plasticity in mate preference so that they would be able to choose among alternative male phenotypes according to the environment they experienced during the non-breeding season. This requires that they would be able to perceive and correctly assess variation in two signals: in the male trait and in the non-breeding conditions. In the case the females are capable of reversing their mate preference according to alternating winter NAO, the direction of sexual selection on the males would fluctuate among years.

Environmental conditions during the nestling period may further complicate the selection on wing patch size of male pied flycatchers, as nestlings of large-patched males are more likely to survive during breeding seasons with substantial precipitation than nestlings of small-patched males, and vice versa during breeding seasons with low precipitation (Sirkiä et al. 2010). We can therefore make a further prediction that fitness consequences of selection on patch size measured by breeding success are affected by weather conditions during both non-breeding and breeding seasons.

The detailed mechanisms that link environment with white wing patch size and sexual attractiveness have not been studied and the proximate determination of variation in the size of the white wing patch remains open. The humidity of the environment during molt to breeding plumage has a role in determining the size of the wing patch (Järvistö et al. 2016a), suggesting condition dependence of wing patch size, most likely derived from maintenance costs as the production costs of such nonpigmented plumage traits are questionable (Rohwer, 1982; Pärt & Qvarnström, 1997; Qvarnström, 1997). In addition there are signs of covariation between wing patch size and oxidative stress suggesting that the trait could signal individual quality (Lopez-Arrabe et al. 2014). Moreover, as the white wing patch size is dependent on the lack or presence of melanin coloration around the patch, the melanocortin system (which is under both genetic and environmental regulation) is likely implicated. However, studies on these particular links are very limited (Ducrest et al. 2008, Roulin & Ducrest 2013).

We studied whether interactive effects exist between fluctuating environmental conditions experienced during the non-breeding season in Sub-Saharan Africa (NAO) and male wing patch size on fitness components (laying date, clutch size, fledgling production) in a 32-year data set of a Finnish pied flycatcher population. Additionally, while the breeding outcome is the same for the both the male and female of a pair, it is important to note that males and females may be differentially affected themselves in terms of future survival and reproduction. We therefore examined whether an interaction exists between male partners' wing patch size and non-breeding conditions affecting female return rates. The white wing patch size is assumed to reflect male condition during the breeding season (Järvistö et al. 2016a). Males in good condition should have a positive effect on female fitness, while males in poor condition should have a negative effect. Because large and small wing patch size is suggested to indicate male quality dissimilarly after different winters, we predicted positive fitness consequences (higher female return rates) from pairing with different types of males after different kinds of winters. In addition, to better understand the pathway of the interactive effects between non-breeding conditions and male wing patch size, we tested whether female choice (within females) of male wing patch size is plastic or repeatable. These results add to our understanding of how varying non-breeding conditions carry-over to affect future sexual and natural selection.

METHODS

Study site

We used long term data on breeding and male colouration of pied flycatchers collected in Siuntio (60 °15'N, 24° 18'E) between 1983 and 2007, and on the island of Ruissalo in Turku (60° 26'N, 22° 10'E) between 2007 and 2014 in Finland. One hundred and sixty nest boxes were available for passerines (inner bottom area: 144 cm^2, entrance hole: 32 mm) in Siuntio, and 230 nest boxes in Ruissalo between 2007 and 2010, while 436 nest boxes were available in Ruissalo between 2011 and 2014. Nest boxes were monitored weekly to record laying date (pied flycatchers lay one egg per day), clutch size (median clutch size of the population is seven eggs), hatching date, and brood size at hatching and fledging.

Data collection

Breeding parents were caught with a swing-door trap and ringed with aluminum rings during the nestling feeding period. All individuals were aged as young (one year old) or old (≥ two years old) based on feather characteristics and wear of unmoulted wing coverts (Svensson 1992). In Siuntio the measure of the continuous-sized wing patch size was assessed as the proportion of white in the second tertial feather, which was estimated in 5% intervals (all estimations performed by M.V.). In a previous study (using the same data) Sirkiä et al. (2010) showed that the proportion of white in the second tertial was a good proxy for the size of the whole wing patch ($r_p = 0.54$, $P = 0.0002$, $N = 42$). In Ruissalo, the wing patch was photographed with a millimeter scale in each picture for measuring the actual patch sizes (in mm^2, see Järvistö et al. 2016b). To verify repeatability of the measurements, the wing patch size of 30 males was measured twice from photographs ($r = 0.94$, $F_{1, 29} = 14.80$, $P < 0.0001$). Moreover, to assess the repeatability of measurements via photographing, wing patch sizes were photographed twice during the same capturing bout for 30 males and the repeatability was calculated ($r = 0.84$, $F_{1, 29} = 9.94$ $P < 0.0001$). Returning males were caught again during the next breeding season to collect local survival data and within-individual changes in wing patch sizes. We did not measure wing patch sizes in situations where physical damage was apparent or ongoing moult affected the condition of these traits. To allow the datasets to be combined, we standardized them separately using the following formula: (V – mean) / SD, where V is value, mean is the mean of one data set and SD is the standard deviation of one data set. As a result the wing patch variable in the combined data set has a mean of 0 and a standard deviation of 1.

Environmental data

The non-breeding grounds of pied flycatchers breeding in Finland was identified using ring recoveries from sub-Saharan Africa (N = 3) and available geolocation data revealing locations of wintering pied flycatcher males from our Ruissalo study population (N = 4, Ouwehand et al. 2016). Based on these data, pied flycatchers breeding in Finland winter in West Africa between 5.5° N and 11.5° N, and 6.5° W and 15.5° W (Fig. 1). The peak of the partial pre-nuptial moult of pied flycatchers occurs between mid-February and mid-March (Salewski et al. 2004). We used the North Atlantic Oscillation index (NAO) as a measure of the environmental conditions at the non-breeding grounds. The winter (December–March) NAO index is an indication of large-scale climatic variation (Hurrell 1995). Positive values are related to moist and relatively warm winters, while negative values are related to dry and cold winters in Europe (Hurrell 1995, Osborn 2006). The index has also been shown to describe environmental conditions in North and West Africa (e.g., Moulin et al. 1997, Oba et al. 2001, Evan et al. 2006). In contrast to Europe, positive NAO values correspond to drier winters and negative values to moister winters in Africa (Lamb & Peppler 1987, McHugh & Rogers 2001, Oba et al. 2001). Winter NAO values were derived from http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm.

Statistical analyses

Statistical analyses were conducted using SAS 9.4 with Enterprise Guide 6.1 (SAS Institute Inc., Cary, NC, USA). The potential interactive effects between winter NAO and male wing patch size on the breeding events at the population-level (including all individuals measured and monitored at least once during the 32-year period) were tested using linear mixed models (LMMs). Laying date, clutch size or the number of produced fledglings were used as the response variables, while NAO, the size of the male wing patch and their interaction were entered as fixed effects. Data on each fitness component (laying date, clutch size and number of fledged young) was normalised with respect to the annual average after the following formula (*individual trait value – annual average) / annual average*). When considering fledgling production, in addition to testing all nests (regardless of whether they produced zero or more fledglings), we performed another test that included only those nests that successfully produced one or more fledglings. Female age, male age and laying date (when not as a response variable) were added into these models to control for their possible effects. Moreover, precipitation during the nestling period has an influence on nestling mortality of pied flycatcher males with different sized wing patches (nestlings of large-patched males suffer less from nestling mortality during relatively rainy nestling periods than nestlings of small-patched males, and vice versa during relatively dry nestling periods; Sirkiä et al. 2010). We therefore investigated whether this relationship between precipitation and male wing patch size remains similar after high and low NAO winter, and tested whether a three-way interaction exists among precipitation during nestling period, winter NAO, and male wing patch size affecting the number of produced fledglings.

Out of these three breeding variables, clutch size is seen strongly as a female trait that can be affected by female behaviour (plasticity in female clutch size decisions, e.g., Eggers et al. 2006) or female genotype (clutch size consistent within females, e.g., Merilä & Sheldon 2000). Since an interaction was observed between NAO and wing patch size on the clutch size at the population level (see below), an individual-level analysis (only including females that had been monitored at least twice during the 32-year period) was conducted to distinguish whether the potential effect is due to differences within females (plastic response in clutch size) or among females in relation to clutch size. Thus, the difference between the population- and individual-level analyses is that population-level analysis combines two types of changes – what kind of individuals (in relation to their clutch size) return from the non-breeding grounds and within-individual changes in phenotype (plasticity in clutch size) in those that return. The individual-level analyses reveal only within-individual changes (plasticity in clutch size). To strengthen the interpretation of the individual-level analysis, we tested the repeatability of clutch size (see below) to verify whether it is consistent or plastic within females.

GLMM with binomial error structure was used to examine whether the probability of females surviving and returning to the next breeding season was predicted by the size of the male wing patch in interaction with NAO. Wing patch size in the breeding year_x, NAO (in year_x) and their two-way interaction were entered as fixed effects. The response variable was binary and coded as 1 = "did" or 0 = "did not" return in year $_{x+1}$. Female age, laying date and clutch size were added into this model as covariates to control for their possible effects.

Repeatability of the female preference for male wing patch size was calculated using linear mixed models (LMMs, see Lessells & Boag 1987, Falconer & Mackay 1996). Repeatability (V_I/V_P) captures the trait variance occurring among individuals (V_I) over the total phenotypic variance of the population (V_P). The remaining share ($1-[V_I/V_P]$) describes the amount of within-individual variation (Lessells & Boag 1987, Falconer & Mackay 1996). Following the recommendations of Nakagawa and Schielzeth (2010), females with only one measure (wing patch size of social male) were included in the analyses as well. In addition, female age, laying date and year were controlled for, i.e., adjusted repeatabilities were calculated (Nakagawa & Schielzeth 2010). The variance components (estimated with restricted maximum likelihood) derived from the LMMs were used to calculate repeatability ($R = V_I/V_P$). Likelihood ratio tests of the log-likelihood of models with and without the random effect (individual ID) were used for testing statistical significance of the adjusted repeatability. Following the recommendations of Snijders and Bosker (2012) for determining statistical significance of the repeatability, a mixture distribution was used by comparing the chi-square difference derived from the difference between the two model deviances to a mixture of two critical p-values (Snijders & Bosker 2012). If variance is constrained to be non-negative, the distribution of the chi-square statistic is distributed as an equal mixture of a chi-square with 0 and 1 degrees of freedom (Snijders & Bosker 2012).

Normality of the residuals (laying date, clutch size, number of fledglings) was evaluated by visual examination. The Kenward-Roger's approximation was used for estimating the degrees of freedom of the error terms. The Kenward-Roger is a good method for approximation because it properly takes into account the random effects and adjusts d.f. accordingly. The environmental variable NAO was mean-centered (see Paccagnella 2006). The size of the white wing patch was treated as a continuous variable in the analyses (standardized and combined from the two data sets, see above). In the interpretations of the results we use the terms "large-patched" and "small-patched" individuals to illustrate the directions of the relationships. To take the within-year variation into account (in timing of breeding or other phenological traits), the date of the first laid egg was transformed into a mean-centered running May date (1 = 1st of May, date of first egg - mean date of first egg). The age (young/old) of the female and male were included to control for possible age-dependent effects. Year and individual identity were added as categorical random effects to control for (temporal and individual) clustering of the observations. However, when calculating adjusted repeatability for the female preference and clutch size, year was added as a fixed effect. Confidence intervals were added to Fig. 1 by using the PLM statement in SAS.

RESULTS

Timing of breeding and clutch size

We observed no interaction between male wing patch size and winter NAO on the timing of breeding (Table 1A). Clutch size, however, appeared to depend on male wing patch size differently after different non-breeding conditions (Table 1B). Females paired with large-patched males after high NAO winters tended to lay larger clutches than those paired with small-patched males (0.1 eggs more), while after low NAO winters females paired with large-patched males laid less compared to those paired with small-patched males (0.35 eggs less, Table 1; Fig. 1). To distinguish whether this population-level effect arose from differences within or among female individuals, we conducted an individual-level analysis including only individuals that bred more than once. We found no interaction between male wing patch size and winter NAO on clutch size at the individual level (Table 2), indicating that the interactive effect of NAO and male wing patch size was due to differences between females. Moreover, we tested clutch size repeatability within female individuals, to see whether it supports the interpretation that variation in clutch size is explained more by between- than within-female variation. Clutch size (as a female trait) was rather highly and significantly repeatable ($r = 0.62$, Table 3). The effects of female and male ages and laying date were controlled as appropriate for all the models above (Tables 1-3).

Fledgling production

We observed no interaction between winter NAO and male wing patch size on the number of produced fledglings (Table 1C–D). The models either including or excluding nests with zero fledglings gave similar results (Table 1C–D). The interaction between winter NAO and male wing patch size on clutch size thus did not result in a similar detectable interaction when considering the number of produced fledglings. One explanation for this could be that the effects of weather conditions during the nestling period on the number of nestlings dilute the interactive effects between NAO and male wing patch size on clutch size. Such an effect could even be expected, as a previous study (Sirkiä et al. 2010) showed that nestling mortality is affected by an interaction between male wing patch size and precipitation during the nestling period. We therefore tested whether an interaction occurs between winter NAO and precipitation during the nestling period on how wing patch size is associated with fledgling number. We indeed observed such a three-way interaction, suggesting that the effect of male wing patch size on the number of produced offspring is dependent on the relationship between precipitation during the nestling period and winter NAO (estimate = 0.016 ± 0.0082, $F_{1, 1033}$ = 3.99, P = 0.046, N = 1054, Fig. 2). The model predicts that during moist breeding seasons after high NAO winters males with smallest patches would have on average as much as 7.35 fewer fledglings than males with largest patches (basically ranging from total failure to full fledging success) while after low NAO winters small-patched males have 4.41 more fledglings compared to large-patched males (Fig. 2). During dry breeding seasons the situation is reversed, but the effect is smaller than during moist breeding seasons. After high NAO winters small-patched males have on average 4.66 more fledglings during dry breeding seasons compared to large-patched males, while after low NAO winters large-patched males have on average 2.45 more fledglings compared to small-patched males (Fig. 2). We did not observe any such effects during average breeding seasons (Fig. 2). Laying date was controlled for in this model, as it had an effect on the number of produced fledglings (estimate = -0.060 ± 0.013, $F_{1, 1045}$ = 20.26, P < 0.0001, N = 1054).

Returning probability (females)

The probability of females returning during the next breeding season depended differently on male wing patch size after different non-breeding conditions (Table 4; Fig. 3). Females paired with large-patched males after high NAO winters had a higher probability of surviving to the next breeding season than females that paired with small-patched males after such conditions, and vice versa after low NAO winters (Fig. 3). Female age and laying date were controlled for in the model (Table 4).

Repeatability of female pairing with regards to male wing patch size

We observed no within-individual repeatability of the wing patch size of females' social males; it was zero (Table 5), meaning that the wing patch size of the males that an individual female is paired with during different years varies greatly between years.

DISCUSSION

Despite sexual selection having been intensively studied during the past few decades, the consequences of the interplay between environmental conditions experienced during the non-breeding season and the expression of sexual ornaments on fitness have hardly ever been examined (but see Saino et al. 2004, Järvistö et al. 2016a). Using long-term breeding data on migratory pied flycatchers, we found that the fitness consequences for females from pairing with males expressing a small or large secondary sexual trait (wing patch) depended on non-breeding conditions. Females paired with males with a large wing patch after high NAO winters (i.e., dry non-breeding conditions) were more likely to survive to the next breeding season than those who paired with males with a small wing patch, and vice versa after low NAO winters (i.e., moist winters). Moreover, females paired with large-patched males after high NAO winters laid larger clutches than females paired with small-patched males, and vice versa after low NAO winters. However, this relationship seemed to lead to differences in fledgling numbers only when precipitation was high or low during the breeding season. During average breeding seasons, the differences in fledgling production among males with different sized wing patches after different NAO winters were small compared to that during moist breeding seasons. We also found that females' mate choice was not repeatable between years and thus not fixed, indicating a potential for adaptive plasticity in mate preference. Taken together, these results show that ecological cross-overs in sexual signalling may be more common than previously appreciated, which may partly be due to their complexity and that their effects on traits are confounded.

Fledgling success depends on both non-breeding and breeding conditions

During high NAO winters, male wing patch decreases within individuals and large-patched individuals have a higher return rate than small-patched ones (Järvistö et al. 2016a). This suggests that after such non-breeding conditions wing patch size is a more informative indicator of male quality than during other years. We found that during these high NAO years, female pied flycatchers paired with large-patched males tended to lay larger clutches than those paired with small-patched males. This interaction between non-breeding conditions and wing patch size on clutch size was not influenced by the timing of breeding and was not due to individual females changing their clutch size in response to male wing patch size, as shown by within-female analyses, but was due to males pairing with females laying different clutch sizes (that were highly repeatable). This suggests that large-patched males were able to pair with the most productive females after high NAO winters and vice versa after low NAO winters. However, large-patched males after high NAO winters or small-patched males after low NAO winters do not always appear to benefit from their success in attracting females that lay large clutches, as we observed no similar simple interaction between non-breeding conditions and male phenotype on fledgling production. We therefore examined whether this apparent contradiction could be explained by nestling mortality being further dependent on the interaction between male wing patch size and prevailing weather conditions during the nestling stage (Sirkiä et al. 2010). Indeed, the interactive effect of winter NAO and male wing patch size on fledgling production depended on precipitation during the nestling period. After high NAO winters the fledgling production of large-patched males appeared to increase with increasing precipitation during the nestling period, while the fledgling production of small-patched males seemed to decrease with increasing precipitation. After low NAO winters these relationships were reversed, while in average breeding seasons winter NAO had no effect on the interaction between precipitation and wing patch size. Thus, the interactive effect between male wing patch size and non-breeding conditions on clutch size was diluted by the time of fledging of the chicks, as the outcome was furthermore dependent on the amount of precipitation during the nestling period.

Male sexual ornamentation predicts local female survival

According to a traditional view, choosing a mate with a large and conspicuous sexual ornament should lead to highest possible fitness (Andersson 1994, Greenfield & Rodriguez 2004). On the contrary, we found that the consequences for females of pairing with a male with certain ornamentation are dependent on preceding non-breeding conditions. Females paired with large-patched males after dry and windy non-breeding conditions (high NAO) had a higher probability of returning to the next breeding season than those that chose small-patched males after such conditions, and vice versa after low NAO winters. This relationship was independent of female clutch size and thus not a simple phenotypic correlation of clutch size and return rate. Thus, a more likely explanation is that a large wing patch signals male condition after high NAO winters, while a small wing patch size signals male condition after low NAO as suggested by our earlier results (Järvistö et al. 2016a). Males in good condition may carry out their parental duties or courtship feeding of females more effectively than males in poor condition, and thus females mated with good-condition males may be in better condition or they do not need to compensate or work as hard as those mated with males in poor condition. Indeed, over-stressed pied flycatcher females (i.e., females experiencing brood enlargement) in this population are less likely to survive to the next breeding season than females with decreased brood demand (i.e., females experiencing brood reduction, Järvistö et al. 2016b). Thus, a sexual conflict may occur where females mated with large-patched males after high NAO winters may invest less in parental care than males themselves and have increased future local survival.

Environment-dependent signals of secondary sexual traits

Our previous and current results together suggest that large-patched and small-patched males differ in their adaptation to the non-breeding environment, and thus the signalling function of this secondary sexual trait may vary depending on the environmental context. The wing patch size of selected male partners was not repeatable for individual females that bred two or more times with different males (during different years). Such flexibility in female mate choice in relation to wing patch size may allow individual females to change their preference for male wing patch size according to the non-breeding conditions experienced, which could enable them to maximize their fitness. To reveal such potential adaptive plasticity, manipulative experiments conducted in two or more years with various non-breeding conditions would be needed. In such tests females would be allowed to select their partners from males with manipulated wing patch sizes. Thus, a potential link between differences in the phenotypes of males that were or were not selected and environmental conditions experienced during the non-breeding season would show whether such adaptive plasticity exists.

Context-dependent benefits of mate choice

Sexual selection is a powerful evolutionary force that may lead to rapid changes in population dynamics (Andersson 1994). The choosy sex is traditionally assumed to pair non-randomly with respect to the secondary sexual trait of the other sex, and the choosy sex is also assumed to always benefit from mating with a partner bearing a large sexual ornament either indirectly (the “good genes” model: Zahavi 1975, Hamilton & Zuk 1982) or directly (the “good parent” model: Hoelzer 1989). Nevertheless, several studies have shown that environmental conditions may affect sexual selection (e.g, Robinson et al. 2012, Janicke et al. 2015). Some studies have investigated specifically the effects of non-breeding conditions on sexual selection and fitness (e.g., Saino et al. 2004, Reudink et al. 2009). (e.g., Saino et al. 2004, Reudink et al. 2009). Yet, despite these few examples, our knowledge concerning the effects of the non-breeding environment on sexual selection is still scarce (Bussière et al. 2008, Spottiswoode & Saino 2010). Our results add to the understanding of how environmental changes during the non-breeding season affect signalling value of male secondary sexual traits. Second, such an impact on signaling value further affects females' local survival. Third, reproductive success (measured as the number of fledglings) of males with different-sized secondary sexual traits depends not only on non-breeding conditions but also on conditions experienced during the breeding season. Thus, environmental effects on sexual selection appear complex. Moreover, the signal value of the trait might be affected by the social and/or sexual interactions taking place at the non-breeding grounds (e.g. Reudink et al. 2009). Pied flycatchers are territorial during the non-breeding season (Salewski et al. 2002) but the association between the white wing patch or other ornamental traits in territorial competition is not yet known.

Climate change acting on sexual selection

Current anthropogenic climate change can have major impacts on the honesty and information content of secondary sexual traits, leading to ecological cross-overs (Botero & Rubenstein 2012, Greenfield & Rodriguez 2004, Spottiswoode & Saino 2010). Our current and previous results together suggest that after dry winters (high NAO, Järvistö et al. 2016a), the large wing patch size of pied flycatcher males would signal good male condition, while after moist winters (low NAO) the small wing patch size would signal good male condition. It appears then that, if females chose such as to optimise the condition of their mates, the direction of sexual selection on patch size would then reverse with NAO. We may assume that if the climate at the non-breeding grounds becomes drier small-patched males would be less likely to survive compared to large-patched males (or the remaining individuals would be in poor condition, Järvistö et al. 2016a) and females would gain from choosing large-patched males at the breeding grounds after such conditions. Non-breeding ground climate becoming moister will potentially lead to the survival of large-patched males decreasing compared to small patched males, and females benefitting from pairing with small-patched males. If consecutive years differ greatly from each other in terms of NAO, the net selection will most likely be stabilizing. In case there is adaptive plasticity in female mate choice, in oscillating non-breeding conditions the secondary sexual trait would not change on a long term due to fluctuating sexual selection.

Conclusions

Our study demonstrates that varying environmental conditions during the non-breeding season interact with a male sexual ornament on fitness components in pied flycatchers. This may be caused by shifts in environmental conditions inducing sudden reversals in the relative quality or sexual attractiveness of males. Such ecological cross-overs may have strong effects on sexual selection and population dynamics. Overall our study implies that carry-over effects driven by ecological context should be important consideration for studies of sexual selection.

REFERENCES

Andersson, M. (1994) Sexual selection. Princeton University Press, Princeton

Andersson, M., and Simmons, L. W. 2006. Sexual selection and mate choice. Trends Ecol. Evol. 21:296–302.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15:365–377.

Boake, C. R. 1989. Repeatability: its role in evolutionary studies of mating behavior. Evol. Ecol. 3:173–182.

Botero, C. A., and Rubenstein, D. R. 2012. Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. PLoS ONE 7:e32311.

Bussière, L. F., Hunt, J., Stöting, K. N., Jennions, M. D., and Brooks, R. 2008. Mate choice for genetic quality when environments vary: suggestions for empirical progress. Genetica 134:69–78.

Chaine, A. S., and Lyon, B. E. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. Science 319:459–462.

Cornwallis, C. K., and Uller, T. 2009. Towards an evolutionary ecology of sexual traits. Trends Ecol. Evol. 25:145–152.

Darwin, C. 1871. The descent of man, and selection in relation to sex. John Murray, London.

van Doorn, G. S., Eldaar, P., and Weissing, F. J. 2009. On the origin of species by natural and sexual selection. Science 326:1704–1707.

Ducrest, A.L., Keller, L. & Roulin, A. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. Trends Ecol. Evol. 23: 502–510.

Eeva, T., Lehikoinen, E., Rönkä, M., Lummaa, V., and Currie, D. (2002) Different responses to cold weather in two pied flycatcher populations. Ecography 25:705–713.

Eggers, S., Griesser, M., Nystrand, M., and Ekman, J. 2006. Predation risk induce changes in nest-site selection and clutch size in the Siberian jay. Proc. R. Soc. B. 273:701–706.

Evan, A. T., Heidinger, A. K., and Knippertz, P. 2006. Analysis of winter dust activity off the coast of West Africa using a new 24-year over-water advanced very high resolution radiometer satellite dust climatology. J. Geophys. Res. 111:D12210.

Falconer, D. S., and Mackay, T. F. (1996) Introduction to Quantitative Genetics. Longman, Harlow.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

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

Greenfield, M. D., and Rodriguez, R. L. 2004. Genotype-environment interaction and the reliability of mating signals. Anim. Behav. 68:1461–1468.

Hamilton, W. D., and Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites? Science 218:384–386.

Hegyi, G., Török, J., Garamszegi, L. Z., Rosivall, B., Szöllosi, E., and Hargitai, R. 2007. Dynamics of multiple sexual signals in relation to climatic conditions. Evol. Ecol. Res. 9:905–920.

Hoelzer, G. A. 1989. The good parent process of sexual selection. Anim. Behav. 38:1067–1078.

Houston, A. I., Székely, T., and McNamara, J. M. 2005. Conflict between parents over care. Trends Ecol. Evol. 20:33–38.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269:676–679.

Jang, Y., Collins, R. D., and Greenfield, M. D. 1997. Variation and repeatability of ultrasonic sexual advertisement signals in *Achroia grisella* (Lepidoptera: Pralidae). J. Insect. Behav. 10: 87–98.

Janicke, T., David, P., and Chapuis, E. 2015. Environment-dependent sexual selection: Bateman’s parameters under varying levels of food availability. Am. Nat. 185:756–768.

Järvistö, P. E., Calhim, S., Schuett, W., Sirkiä, P. M., Velmala, W., and Laaksonen, T. 2016a. Carry-over effects of conditions at the wintering grounds on breeding plumage signals in a migratory bird: roles of phenotypic plasticity and selection. J. Evol. Biol. 29:1569–1584.

Järvistö, P. E., Calhim, S., Schuett W., Velmala W., and Laaksonen, T. 2016b Sex-dependent responses to increased parental effort in the pied flycatcher. Behav. Ecol. Sociobiol. 70:157–169.

Laaksonen, T., Adamczyck, F., Ahola, M. P., Möstl, E., Lessells, C(Kate). M. 2011. Yolk androgens and sexual conflict in the pied flycatcher. Behav.l Ecol. Sociobiol. 65: 257–264.

Laaksonen, T., Sirkiä, P. M., Calhim, S., Brommer, J. E., Leskinen, P. K., Primmer, C. R. et al. 2015. Sympatric divergence and clinal variation in multiple coloration traits of *Ficedula* flycatchers. J. Evol. Biol. 28:779–790.

Lamb, P. J., and Peppler, R. A. 1987. North Atlantic Oscillation: concept and an application. B. Am. Meteorol. Soc. 68:1218–1225.

Lessells, C. M., and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Lessells, C. M. 2006 The evolutionary outcome of sexual conflict. Phil. Trans. Roy. Soc. Lond. B 361:301–317.

López-Arrabé, J., Cantarero, A., Pérez-Rodrigues, L., Palma, A., and Moreno, J. 2014. Plumage ornaments and reproductive investment in relation to oxidative status in the Iberian Pied Flycatcher (Ficedula hypoleuca iberiae). Can. J. Zool. 12:1019–1027.

Lundberg, A., and Alatalo, R. V. 1992. The pied flycatcher. T & AD Poyser, London.

McHugh, M. J., and Rogers, J. C. 2001. North Atlantic Oscillation influence on precipitation variability around the Southeast African convergence zone. J. Clim. 14:3631–3642.

Merilä, J., and Sheldon, B. C. 2000. Lifetime reproductive success and heritability in nature. Am. Nat, 155:301–310.

Moulin, C., Lambert, C. E., Dulac, F., and Dayan, Y. 1997. Control of atmospheric export of dust from North Africa by the North Atlantic Oscillation. Nature 387:691–694.

Nakagawa, S., and Schielzeth, H. 2010. Repeatability for Gaussian and non-gaussian data: a practical guide for biologists. Biol. Rev. 85:935–956.

Norris, D.R., Marra, P.P., Montgomerie, R., Kyser, T.K. & Ratcliffe, L.M. 2004. Reproductive effort, molting latitude, and feather color in a migratory songbird. Science 306: 2249–2250.

Norris, D. R., and Taylor, C. M. 2006. Predicting the consequences of carry-over effects for migratory populations. Biol. Lett. 2:148–151.

Oba, G., Post, E., and Stenseth, N. C. 2001. Sub-saharan desertification and productivity are linked to hemispheric climate variability. Glob. Change Biol. 7:241–246.

Osborn, T. J. 2006. Recent variations in the winter North Atlantic Oscillation. Weather 61:353–355.

Ouwehand, J., Ahola, M. P., Ausems, A. N. M. A., Bridge, E.S., Burgess, M., Hahn, S. et al. 2016. Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. J. Avian Biol. 47:69–83.

Paccagnella, O. 2006. Centering or not centering in multilevel models? The role of the group mean and the assessment of group effects. Evaluation Rev. 30:66–85.

Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M. et al. 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. Glob. Change Biol. 19:2303–2338.

Pärt, T. and Qvarnström, A. 1997. Badge size in collared flycatchers predicts outcome of male competition over territories. Anim. Behav. 54:893–899.

Qvarnström, A. 1997. Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. Proc. R. Soc. B doi: 10.1098/rspb.1997.0169

Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M., and Ratcliffe, L.M. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proc. R. Soc. B doi:10.1098/rspb.2008.1452.

Reudink, M. W., McKellar, A. E., Marini, K. L. D. , McArthur, S. L., Marra, P. P., and Ratcliffe, L.M. 2015. Inter-annual variation in American redstart (*Setophaga ruticilla*) plumage colour is associated with rainfall and temperature during moult: an 11-year study. Oecologia 178:161–173.

Robinson, R. A., Crick, H. Q. P., Learmonth, J. A., Maclean, I. M. D., Thomas, C. D., Bairlein, F. et al. 2009. Travelling through a warming world: climate change and migratory species. Endang. Species Res. 7:87–99.

Robinson, R. A., van Doorn, S. G., Gustafsson, L., and Qvarnström, A. 2012. Environment-dependent mate choice in a natural population of birds. Ecol. Lett. 15:611–618.

Rohwer, S. 1982. The evolution of reliable and unreliable badges of fighting ability. Am. Zool. 22:531–546.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and Pounds, J. A. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Roulin, A., and Ducrest, A.-L. 2013. Genetics of colouration in birds. Semin. Cell Dev. Biol. 24: 594–608.

Saino, N., Sz_ep, T., Ambrosini, R., Romano, M. and Møller, A.P. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. Proc. R. Soc. Lond. B. 271: 681–686.

Salewski, V., Bairlein, F., and Leisler, B. 2002. Different wintering strategies of two Palearctic migrants in Wesr Africa – a consequence of foraging strategies? Ibis 144:85–93.

Salewski, V., Altwegg, R., Erni, B., Falk, K. H., Bairlein, F., and Leisler, B. 2004. Moult of three Palaearctic migrants in their West Africa winter quarters. J. Ornithol. 145:109–116.

Sanz, J. J. 2001. Experimentally reduced male attractiveness increases parental care in the pied flycatcher *Ficedula hypoleuca.* Behav. Ecol. 12:171–176.

Siikamäki, P., Haimi, J., Hovi, M., and Rätti, O. 1998. Properties of food loads delivered to nestlings in the pied flycatcher: effects of clutch size manipulation, year and sex. Oecologia 115:579–585.

Sirkiä, P. M., and Laaksonen, T. 2009. Distinguishing between male and territory quality: females choose multiple traits in the pied flycatcher. Anim. Behav. 78:1051–1060.

Sirkiä, P. M., Virolainen, M., and Laaksonen, T. 2010. Melanin coloration has temperature-dependent effects on breeding performance that may maintain phenotypic variation in a passerine bird. J. Evol. Biol. 23:2385–2396.

Snijders, T., and Bosker, R. 2012. Multilevel analysis: An introduction to basic and advanced multilevel modeling, 2nd ed. Thousand Oaks, CA, Sage.

Spottiswoode, C. N., and Saino, N. 2010. Sexual selection and climate change. Effects of Climate Change on Birds, (A.P Møller, W. Fiedler & P. Berthold, eds), pp. 169–189. Oxford University Press, Oxford.

Svensson, L. 1992. Identification Guide to European Passerines. Märsta Press, Stockholm.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S., and Holmes, R. T. 2002. Links between worlds: unraveling migratory connectivity. Trends Ecol. Evol. 17:76–83.

Wilby, R. L. 2001. Seasonal forecasting of river flows in the British isles using North Atlantic pressure patterns. Water Environ. J. 15:56–63.

Wilby, R. L., Wedgbrow, C. S., and Fox, H. R. 2004. Seasonal predictability of summer hydrometeorology of the River Thames, UK. J. Hydrol. 295:1–16.

Zahavi, A. 1975. Mate selection – A selection for a handicap. J. Theor. Biol. 53:205–214.

FIGURE LEGENDS

Fig. 1. Predicted relative clutch size of pied flycatchers as a function of the interaction between male wing patch size and winter North Atlantic Oscillation (winter NAO). Different lines represent model predictions for low -3 (····), average 0 (- - -) and high 3 (—) NAO values (NAO was treated as a continuous variable in the analyses, the three predictions are shown for illustration, Figure was done using PLM statement in SAS).

Fig. 2. Predicted relative number of fledglings for pied flycatcher males that experienced [(a) moist, (b) average, (c) dry breeding seasons] as a function of winter NAO and male wing patch size.

Fig. 3. Probability of females to return to the next breeding season as a function of wing patch size (standardized) of social males for winter NAO with different values (mean centered). Different lines represent model predictions for low -3 (····), average 0 (- - -) and high 3 (—) NAO values, treated as a continuous variable in the analyses.

Table 1. Output of mixed effects models for A) relative laying date (N = 1368), B) relative clutch size (N = 1324), C) relative number of produced fledglings (nests with zero or more fledglings, N = 1106) and D) relative number of produced fledglings (nests with one or more fledglings, N = 1003) at the population-level in relation to winter NAO and wing patch size of social male.

A) Laying date (standardized)

	Estimate ± SE	DF	F	P-value
intercept	0.062 ± 0.019			
female age	-0.050 ± 0.017	1, 617.6	9.20	0.0025
male age	-0.050± 0.016	1, 510.7	9.69	0.0020
wing patch	0.0031 ± 0.0073	1, 445.2	0.18	0.67
NAO	0.015 ± 0.0057	1, 460.3	6.66	0.010
wing patch x NAO	-0.010 ± 0.0057	1, 550.3	3.13	0.08

B) Clutch size (standardized)

	Estimate ± SE	DF	F	P-value
intercept	-0.021 ± 0.0059			
female age	-0.051 ± 0.0062	1, 1221	67.08	<0.0001
male age	-0.012 ± 0.0063	1, 1139	3.84	0.05
laying date	-0.0056 ± 0.00065	1, 1246	73.54	<0.0001
wing patch	0.00099 ± 0.0031	1, 1218	0.10	0.75
NAO	-0.00062 ± 0.0022	1, 1093	0.08	0.78
wing patch x NAO	0.0045 ± 0.024	1, 1210	3.50	0.06

C) Number of fledglings (standardized)

(nests with zero or more fledglings)	Estimate ± SE	DF	F	P-value
intercept	-0.035 ± 0.028			
female age	-0.065 ± 0.030	1, 1064	4.88	0.027
male age	-0.0073 ± 0.031	1, 1082	0.06	0.81
laying date	-0.0095 ± 0.0032	1, 1094	8.87	0.003
wing patch	0.0017 ± 0.015	1, 1039	0.01	0.91
NAO	0.0019± 0.011	1, 1096	0.03	0.87
wing patch x NAO	0.0015 ± 0.012	1, 1087	0.02	0.90

D) Number of fledglings (standardized)

(nests with one or more fledglings)	Estimate ± SE	DF	F	P-value
intercept	0.074 ± 0.037			
female age	0.74 ± 0.023	1, 956	10.78	0.0011

male age	0.0093 ± 0.024	1, 982	0.15	0.70
laying date	-0.0079 ± 0.0024	1, 968	11.28	0.0008
wing patch	-0.0033 ± 0.012	1, 939	0.08	0.78
NAO	0.052 ± 0.024	1, 26.8	4.53	0.043
wing patch x NAO	0.00083 ± 0.0092	1, 975	0.01	0.92

Table 2. Output of mixed effects model for relative clutch size of pied flycatchers in relation to winter NAO and male wing patch size when analysed from data including only individuals with repeated observations (N = 111 individuals and 213 breeding events). Individual identity was fitted as a random effect.

	Estimate ± SE	DF	F	P-value
intercept	-0.047 ± 0.016			
female age	0.071 ± 0.014	1, 146	24.36	<0.0001
male age	-0.0027 ± 0.013	1, 163	0.04	0.84
laying date	-0.0057 ± 0.0013	1, 203	20.60	<0.0001
wing patch	0.015 ± 0.052	1, 178	0.28	0.78
NAO	-0.0083 ± 0.0043	1, 154	3.60	0.060
wing patch x NAO	-0.00062 ± 0.0052	1, 172	0.01	0.91

Table 3. Output of a mixed effects model for calculating adjusted repeatability for clutch size. DF, degrees of freedom, V_I = variance occurring among individuals, V_R = residual variance, R (repeatability) = $V_I / (V_I + V_R)$.

	V_I	V_R	R	DF	F-value	P	N measures	N individuals
Clutch size	0.32	0.20	0.62			<0.0001	1863	1489
Female age				1, 1816	92.54	<0.0001		
Laying date				1, 1757	139.88	<0.0001		
Year				31, 1806	5.59	<0.0001		

Table 4. Output of generalized mixed effects model for probability of females to return in the next breeding season in relation to winter NAO, social male wing patch size and their interaction. N = 1372 female individuals.

	Estimate ± SE	DF	F	P-value
intercept	-1.70 ± 0.86			
female age	0.024 ± 0.21	1, 1365	0.01	0.91
laying date	-0.033 ± 0.022	1, 1365	2.17	0.14
clutch size	-0.13 ± 0.13	1, 1365	0.98	0.32
wing patch	0.12 ± 0.10	1, 1365	1.33	0.25
NAO	-0.047 ± 0.12	1, 24.19	0.17	0.69
wing patch x NAO	0.23 ± 0.076	1, 1365	9.25	0.0024

Table 5. Output of a mixed effects model for calculating adjusted repeatability for female preference for male wing patch size. DF, degrees of freedom, V_I = variance occurring among individuals, V_R = residual variance, R (repeatability) = V_I / (V_I + V_R).

	V_I	V_R	R	DF	F-value	P	N measures	N individuals
Female preference	0.00	0.96	0.00			0.99	1435	1296
Female age				1, 109	2.12	0.15		
Laying date				1, 109	5.74	0.018		
Year				31, 109	1.32	0.15		

Figure 1.

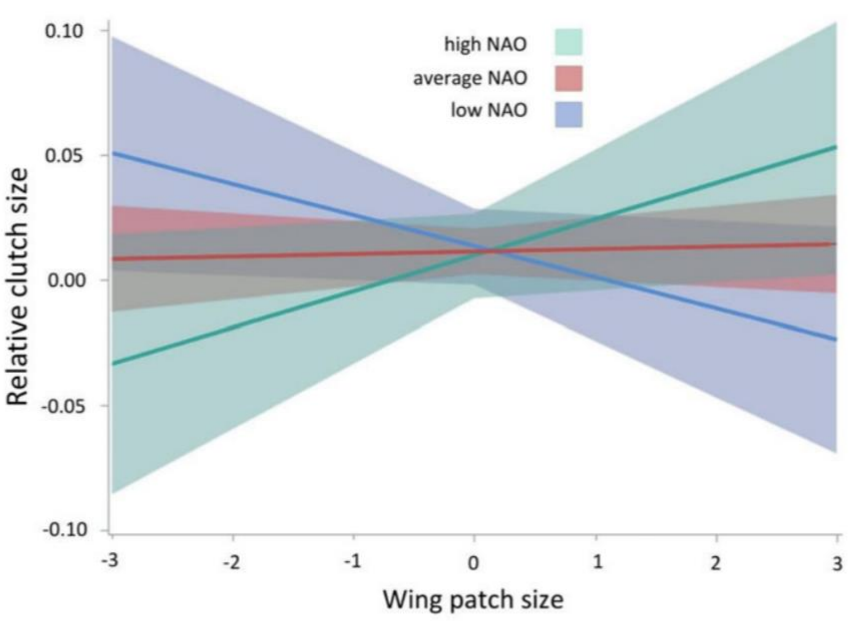

high NAO
average NAO
low NAO
Relative clutch size
0.10
0.05
0.00
-0.05
-0.10
-3
-2
-1
0
1
2
3
Wing patch size

Figure 2.

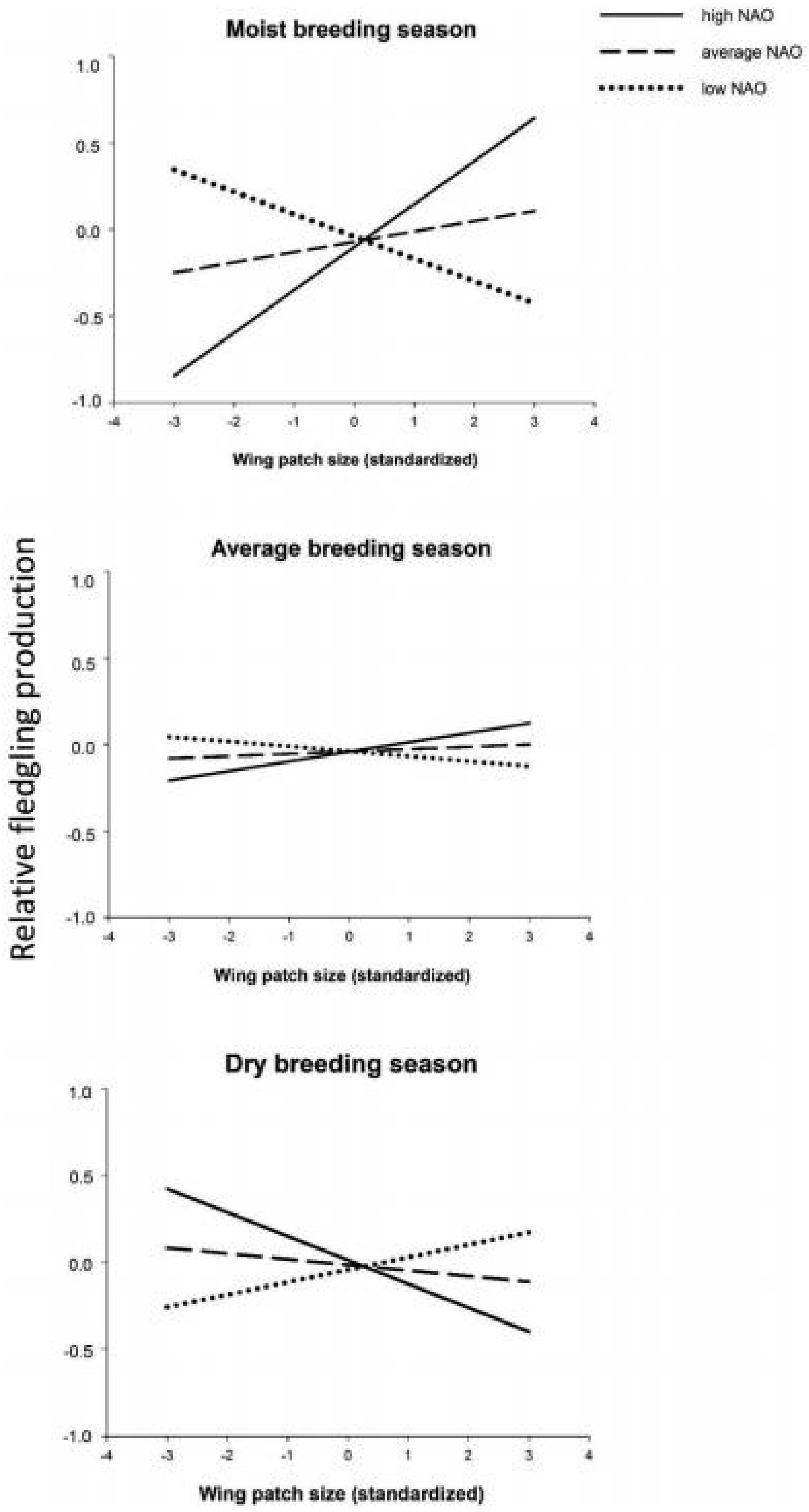
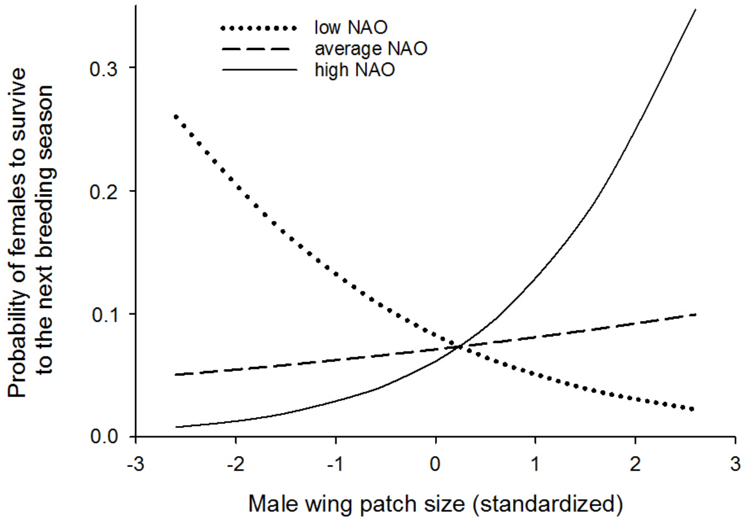

high NAO
average NAO
low NAO
Moist breeding season
Average breeding season
Dry breeding season
Relative fledgling production
1.0
0.5
0.0
-0.5
-1.0
-4
-3
-2
-1
0
1
2
3
4
Wing patch size (standardized)

Figure 3.


low NAO
average NAO
high NAO
Probability of females to survive to the next breeding season
0.0
0.1
0.2
0.3
-3
-2
-1
0
1
2
3
Male wing patch size (standardized)