

Our study population, like many in the wild, experienced temporally fluctuating temperatures and rainfall at the breeding site. Variable spring temperatures are known to cause mistiming in the breeding of the birds in relation to peak caterpillar abundance (Nussey *et al.* 2005; Both *et al.* 2006; Charmantier *et al.* 2008), and rainfall is associated with a high general risk that offspring starve or freeze to death (Siikamäki 1996). There is an evidence from some bird populations suggests that highly ornamented males may provide insufficient parental care to successfully raise surviving offspring under some circumstances (Qvarnström 1997; Duckworth 2006), and there may also be context-dependent paternal genetic effects on offspring fitness (Qvarnström & Price 2001). This provides a potential mechanism whereby associations between the ornaments of males chosen as mates and female fitness may change across breeding seasons depending upon the prevailing ecological conditions. Therefore, we examined whether associations between mate choice of male ornamentation and female reproductive fitness (selection on female mate choice) changed across breeding seasons. In most bird species, a female's reproductive output within a given breeding season will also depend upon a number of factors linked to her own phenotype such as her age, her body size, her ability to time her reproduction to match the food availability (laying date), and the quality of the area which she selects to breed (Nilsson & Svensson 1993). Here, we took these factors into account, and estimated the influence of the patch size of her mate on her reproductive output within a given year, thus examining whether selection operating on mate choice based on male forehead patch size varied across the study period. We then extended these models to determine whether environmental factors at a specific period of time could explain variation in selection across breeding seasons.

Temporal variation in the form of selection is a simple intuitive hypothesis to explain evolutionary stasis in natural populations, as selection pressures may only be strong in some circumstances, or may actually average to zero across all conditions. However, selection pressures are only one element required to assess the evolutionary dynamics of phenotypes in natural populations because the response to selection depends upon the heritable genetic basis of the trait upon which it acts (Falconer & Mackay 1996). For example, different genotypes may be favoured across environments because either: (1) selection pressures are constant across environments, but the heritable basis of the trait changes across environments; or (2) selection pressures fluctuate, but the genetic basis of the phenotype remains constant. Therefore, in order to make inference as to how selection influences evolutionary dynamics of female mate choice we also examined individual-level variation, and the quantitative genetic basis of female mate choice across environments. Finally, we also examined individual-level variance of male patch size across environments to ask whether males were repeatable in patch size across environments. Taken together, we investigated the impact of local environmental conditions on the selection on female choice for male ornaments and the potential evolutionary consequences for both trait and preference.

MATERIAL AND METHODS

Study system and environmental variables

Data on pairing patterns, reproductive performance, survival and phenotypic measures were collected using standardised methods as part

of a 25 year (1981–2005) long-term study of a wild collared flycatcher population breeding on the islands of Gotland, Sweden (57°30' N, 18°33' E; Qvarnström 1997; Qvarnström *et al.* 2000, 2006; Sheldon *et al.* 2007; see Supporting Information). Local weather data were available for a 23-year period from 1983 to 2005 (see Supporting Information).

Mate choice of male ornamentation and female fitness across breeding seasons

Annual female reproductive success

We used the total number of offspring that recruited back into the population the following year as a measure of female annual reproductive success, with measures from 4522 females.

As our main aim was to investigate selection on mate choice of male ornamentation, we first converted female reproductive success into relative reproductive success by dividing each individual's observation by the yearly mean. We used general linear models to estimate standardised linear and quadratic selection gradients on the patch size of the female's social partner for each breeding season, whilst controlling for directional selection on lay date (Lande & Arnold 1983). We present these selection gradients in Fig 1.

Second, statistical significance of the relationships shown were estimated by modelling female reproductive success using a generalised linear mixed effects model (GLMM) with a Poisson error structure, implemented within a Bayesian monte carlo markov chain (MCMC) framework, using the R (The R foundation for statistical computing) package MCMCglmm (Hadfield 2010; for fitness measure details and model selection see Supporting Information). Our modelling strategy was to first fit a full model examining direct selection on many different male traits at the same time, whilst also testing for the effects of female characteristics. We did this to assess whether the selection gradients estimated above reflect independent, direct selection on female choice of male patch size, or correlational selection for other male characters. The male traits tested were male body size (tarsus length), male age, and the proportion of white on the primary feathers of the male wing, alongside female characters of female age, female body size. Year effects were also fitted as a factor to control yearly variation in annual recruitment, and we tested for both linear and quadratic selection on all components. We then removed terms in a step-wise manner using model DIC values (Bolker *et al.* 2009). If removing the term improved the model fit then we considered selection not to be acting upon the trait concerned. The full model and all model reduction steps can be found in the Supporting Information.

This resulted in the selection of a final model containing only traits for which there is evidence of an association with annual female reproductive fitness. We then assessed whether selection on each term changed across breeding seasons by including an interaction between the term and year. In this way, we tested for changes in selection on mate choice of ornamentation across breeding seasons, whilst controlling for repeated measures, large-scale spatial differences, differences in reproductive success across years, and because traits are standardised, for differences in trait values across years. The DIC values for the inclusion of each term in the final model are presented in Table 1, the effect estimates from the final model are presented in the Supporting Information, and the model predictions for the

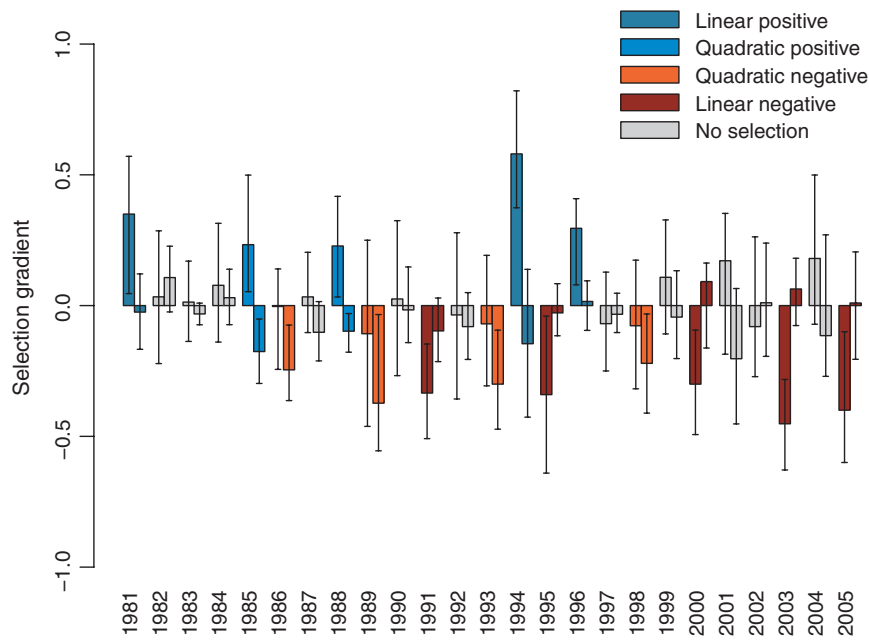


Figure 1 Selection on female mate choice of male ornamentation through relative female annual recruitment success, across years. Two bars are shown for each year (1981–2005) representing linear and then quadratic selection gradients on male ornamentation through relative female annual recruitment. Error bars show the 95% credible interval. Years with red bars are those with negative linear selection and no evidence of quadratic selection; years with orange bars are those with no linear component but a negative quadratic component; years with light blue bars are those with positive linear selection and a negative quadratic term; years with dark blue bars are those with positive linear selection and no quadratic selection; years with grey bars show no evidence of selection.

Table 1 Model of female annual recruitment success that tests for differences in selection on mate choice across years

Model	Δ DIC	Effect included within the model
(i)	8511.53	–
(ii)	–167.96	Year
(iii)	–70.04	Year + lay date
(iv)	–13.67	Year + lay date + social male patch size
(v)	–121.95	Year + lay date + social male patch size + social male patch size ²
(vi)	–71.72	Lay date + social male patch size* year + social male patch size ²
(vii)	9.129	Lay date + social male patch size* year + social male patch size ² * year

All models contained female identity, male identity, and area effects modelled as random to control for repeated measures and local area differences respectively. We present the associated change (Δ) in DIC estimates that occurs when the effect is included within the model. For example, including year reduces the DIC value by 167.96 points as compared to the DIC given for a model containing no fixed effects (i). Year effects were fitted as a factor to estimate yearly variation in recruitment success and interactions (denoted by *) with other covariates. The effect estimates from the model of best fit (vi) are given in the Supporting Information.

relationship between female recruitment success and patch size are presented in Fig. 2a.

Female clutch size

We examined whether mate choice of male ornamentation was associated with female reproductive fitness through female fecundity (clutch size: number of eggs laid). We estimated standardised linear and quadratic selection gradients, using a general linear mixed model

for female clutch size, with female and male identity and area included as random effects. Linear and quadratic terms for lay date and social male patch size were included, alongside female age.

Female survival

We examined whether mate choice of male ornamentation was under selection through female survival (viability selection) to the following breeding season. We first estimated linear and quadratic selection gradients by converting female survival to relative female survival and examining the relationship between this and female mate choice of social male patch size, including both linear and quadratic terms for the patch size of a female's social mate, and her lay date. We then used a GLMM for female survival as a binomial (0/1) variable, with a binomial error structure, female identity and area modelled as random, and linear and quadratic terms for lay date and social male patch size alongside female age modelled as fixed.

Weather variables associated with changing selection on mate choice

Understanding how traits respond to environmental variation is of key interest to both evolutionary biologists and ecologists (Ozgul *et al.* 2009), and thus having described variation in selection on mate choice of male ornamentation across breeding seasons, we then attempted to identify the critical time window during the breeding season where environmental conditions influenced the relationship between mate choice of social mate ornamentation and our proxy measure of fitness. To do this, we used a multiple regression approach to select the appropriate window of environmental variation that influenced the association between our reproductive fitness measure and mate choice (see Supporting Information).

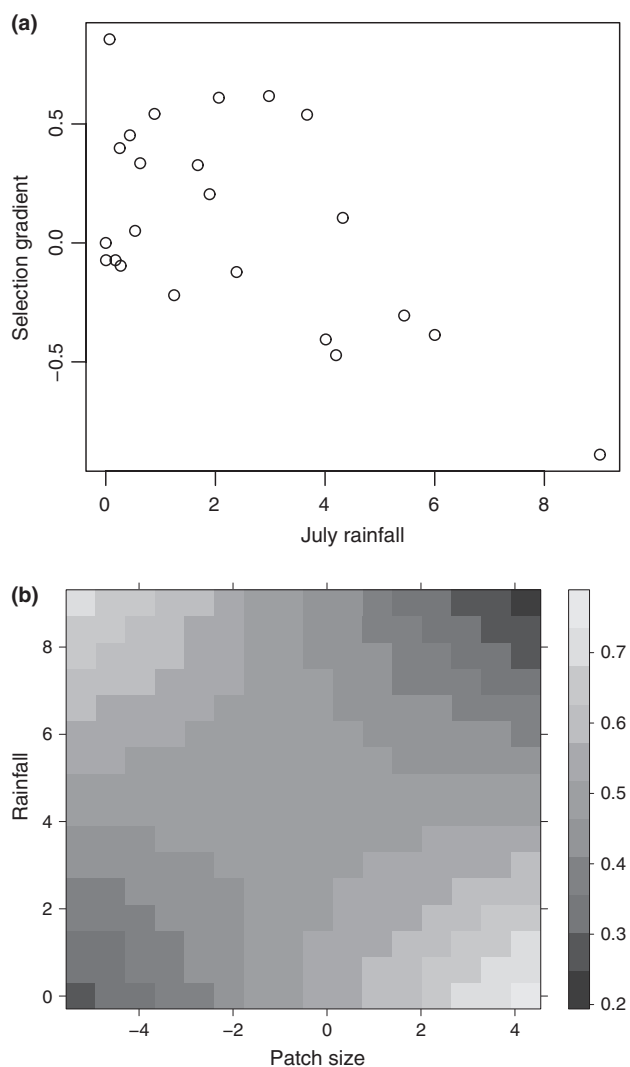


Figure 2 Associations between female annual recruitment and female mate choice of male ornamentation across yearly differences in July rainfall. (a) Predicted patch size-fitness relationships for each year, derived from the model of best fit presented in Table 1, are shown across July rainfall values. Positive values imply more positive linear selection, and negative values imply increasingly negative selection. (b) Contour plot showing predicted female annual recruitment success, derived from the model of best fit presented in Table 2, across ornamentation level of the social male and July rainfall.

In place of the mate choice of male ornamentation-by-year interaction modelled above, we tested for mate choice of male ornamentation-by-environment interaction. We used monthly (North Atlantic Oscillation) NAO values (Hurrell 1995) and local (collected at a nearby weather station) weather variables of rainfall and temperature. We calculated mean temperature and mean rainfall over ten day windows from 1 May to late July, giving nine windows for both temperature and rainfall across the breeding season (see Supporting Information). We simultaneously included these as separate linear fixed effect interactions with both patch size and lay date. We then reduced the model using DIC values to leave a final model containing only the predictors that improved model fit. This model thus infers the environmental variables which best described the mate choice of male ornamentation-by-year interaction which we tested for in the model above.

Heritability, plasticity, and repeatability of mate choice of male ornamentation

Selection pressures are only one element required to assess the evolutionary dynamics of phenotypes in natural populations because the consequences of selection depends upon the heritable genetic basis of the trait upon which it acts. Therefore, we tested for (1) heritable genetic basis of differences between females in their mate choice of male ornamentation; (2) plasticity in mate choice of male ornamentation; (3) individual-level plasticity in mate choice across environments and confirmed our results by testing for repeatability of multiple observations on individuals.

We modelled female mate choice using a linear mixed model, with female identity, area of the study site, and the year of measurement modelled as random, and female age, and lay date effects included as fixed. We included lay date as it has previously been shown that lay date influences a female's choice of mate (Qvarnström *et al.* 2000). We also included monthly May and June NAO values, and the first six windows (pairings are complete by July) of local weather variables of rainfall and temperature calculated above in the year of breeding. This model was conducted on 6431 measures of mate choice recorded from 4909 females. We then reduced the model using DIC values to leave only a final model containing only the predictors that significantly improved model fit.

Having established a model containing only fixed effects that best describe mean differences between females in their choice across breeding seasons, we added additional random effects to the model in a step-wise process (Kruuk 2004; see Supporting Information). First, we attempted to partition individual-level variance into additive genetic and permanent environment components within an animal model framework (see Qvarnström *et al.* 2006 for pedigree details). Second, to test for individual-level plasticity in female choice, we extended the 'animal model' outlined above to test for an interaction between individual-specific effects and the environment ($I \times E$; Nussey *et al.* 2007). In this way, we tested whether individual-level variance (among individual differences) changed as a function of the environmental covariates found to influence the fitness effects of mate choice of male patch size.

Heritability, plasticity, and repeatability of male patch size

We examined whether variation in ornamentation between males, that influences female choice, changed across environments. We used a linear mixed model for male patch size, with male identity, area of the study site, and the year of measurement modelled as random effects (see Supporting Information). We used 4133 measures of forehead patch size recorded from 3098 males. We partitioned individual-level variance into additive genetic and permanent environment components within an animal model framework.

Male moult occurs in the wintering grounds prior to migration and thus we did not test for the effects of environmental descriptors (NAO, local weather) measured at the breeding site. However, we examined the repeatability of male patch size from one year to the next, to ask whether males with a larger than average patch size in year t also displayed larger than average patch size in year $t + 1$. If individuals are consistent in their expression across years then patch size differences between males upon which females are choosing are likely to remain constant across environments. If selection favours

large patch size across both years, then the degree of repeatability is informative.

RESULTS

Mate choice of male ornamentation and female fitness across breeding seasons

We found that the association between the ornamentation of a female's social partner and her reproductive success changed across breeding seasons. Selection gradients through female annual reproductive fitness on mate choice of male ornamentation varied across breeding seasons (Table 1 showing improvement in model fit with social male patch size-by-year interaction), and fluctuated from positive, to stabilising, to negative (Fig. 1). Overall selection was stabilising across years, suggesting that fitness consequences differ between years such that females choosing large patched males would be either favoured or selected against, while choosing a male with medium sized forehead patch would never be strongly selected for or against. Female identity was fitted as random, and we found that the variance accounted for by this term was close to zero (0.017 , CI $4.016e^{-4}$: 0.102), indicating no repeatability for reproductive success across environments.

We have found no evidence for an association between the ornamentation of a female's social partner and the number of eggs laid (effect of mate choice of ornamentation on clutch size, standardised linear selection gradient: -0.011 , CI -0.038 : 0.014 , change in model DIC value -2.91 ; quadratic selection gradient: 0.017 , CI -0.022 : 0.054 , change in model DIC value -0.19 , for the full model estimates see Supporting Information), suggesting that female fecundity was not influenced by her mate choice. Therefore, fluctuations in the relationship between the ornamentation of a female's social partner and her recruitment success must reflect a relationship between offspring survival and mate choice.

We also found no evidence of an association between the ornamentation of a female's social partner and female survival (standardised linear selection gradient: 0.024 , CI -0.003 : 0.043 ; quadratic selection gradient: -0.004 , CI -0.022 : 0.010 ; effect of mate choice of ornamentation on female survival in GLMM: linear term -0.012 , CI -0.055 : 0.031 , change in model DIC value 3.59 ; quadratic term 0.059 , CI -0.015 : 0.134 , change in model DIC value -0.58). Therefore, we found no evidence that mate choice of male ornamentation conveys any direct costs or benefits to female survival.

Weather variables associated with changing sexual selection

Variation in mid-July rainfall (10–20) has shown the greatest association with fluctuations in selection gradients on mate choice of male ornamentation through recruitment success (Table 2 for model estimates, and Supporting Information Table S5 showing that the patch size-by-mid July rainfall interaction was associated with largest improvement in model DIC). It is likely that other weather variables are involved, and not just mid-July rainfall (see Supporting Information where other patch size temperature variables result in a slight improvement in DIC value), however this variable was associated with the greatest change in model DIC. Females who paired with highly ornamented males had lower relative recruitment during breeding seasons of high mid-July

Table 2 Model of female annual recruitment success that tests for differences in selection on mate choice across yearly descriptors of environmental conditions at the breeding site

	Mean	l – 95% CI	u – 95% CI
(Intercept)	–0.754	–0.999	–0.538
Lay date	–0.229	–0.269	–0.186
Social male patch size	0.270	0.018	0.528
Social male patch size ²	–0.035	–0.063	–0.014
July rainfall	–0.091	–0.368	0.127
Patch size × July rainfall	–0.069	–0.133	–0.018

The model contained female identity, male identity, area, and year to control for repeated measures, local area differences, and unexplained yearly variation respectively. Here, we tested for environmental variables which best described the social male patch size-by-year interaction described in Table 1 by simultaneously including them all and then reducing our model using DIC estimates to select the model of best fit, which is presented here. The Supporting Information gives the DIC values of all model reduction steps.

rainfall, but in breeding seasons of lower rainfall females paired with highly ornamented males had high relative recruitment (Fig. 2). This is evidenced by the model predictions for the mate choice–year interaction, which become negative as July rainfall values increase (Fig 2a), and by predicted female reproductive fitness plotted across July temperatures and mate choice of ornamentation (Fig 2b). Variable selection on mate choice creates different mate choice optima across years, and as the association between female choice and her reproductive success depends upon conditions experienced after the choice has been made, it is likely to be unpredictable at the time of mate selection, making optimal mate choice difficult for females.

Heritability, plasticity, and repeatability of mate choice of male ornamentation

Differences among females in their choice of social mate on the basis of male patch size were heritable ($b^2 = 0.146$, CI 0.042 : 0.217). We found evidence for population-level plasticity in mate choice of male ornamentation, with May temperatures (estimate of effect -1.202 , CI: -2.458 : -0.094) and May rainfall (estimate of effect -1.173 , CI: -3.315 : -0.976) at the breeding site influencing the average ornament size chosen across different years (for full model see Supporting Information). Therefore, it appears that on average the patch size of males chosen as social mates may depend upon the environmental conditions experienced by females at the time when the choice was made. We found no evidence for any individual-level plasticity in mate choice across environments (DIC change with the inclusion of female identity-by-May temperature interaction: 1.22 ; and with the inclusion of female identity-by-May rainfall interaction: 1.17). There was no evidence that May temperature (correlation: 0.112 , CI -0.322 : 0.395) or May rainfall (correlation: 0.093 , CI -0.373 : 0.357) were associated with July rainfall. We found that mate choice was moderately repeatable across life ($r_F = 0.206$, $P < 0.001$, $n = 2328$ females with repeated choice). Therefore, the average realised choice varied across yearly environmental conditions, but all females within the population seemed to respond in the same way, and thus mate choice within the population was heritable and there appeared to be consistent individual-level differences (consistent individual-level variance) across environments.

Heritability, plasticity, and repeatability of male patch size

Variation in patch size was heritable ($b^2 = 0.249$, CI 0.095: 0.334) and when we examined only males with repeated measures we found that patch size was significantly repeatable across life ($r_F = 0.576$, $P < 0.001$, $n = 2837$ males with patch size measures) suggesting that males are consistent in the patch size they display relative to the population mean across breeding seasons.

DISCUSSION

Although, female choice of social mate is recognized as an important selective force acting on males (Andersson & Simmons 2006), the evolutionary dynamics of choice itself is often overlooked in studies of sexual selection (Hunt *et al.* 2009; Cornwallis & Uller 2010). We found that there was genetic variation among female collared flycatchers in their tendency to mate with highly ornamented males and that selection on choice varied according to the local environment. There was only a fitness benefit associated with choosing highly ornamented males in terms of an increased relative recruitment success during drier breeding seasons. However, the opposite was true during the wettest breeding seasons. Our results demonstrate that the evolutionary dynamics of mate choice can vary across ecological contexts in a variety of ways, and that this should be an important consideration for studies of sexual selection.

In this study, the fitness consequences of mate choice varied across years, because the environment appears to influence the relationship between female mate choice and offspring survival. These fluctuations may reflect variation in material components (effect of male care), or there may be a possible paternal genetic component (male genes influencing offspring survival) that varies across environments. The scale of these changes (from positive to negative) does not fit with the expectations of most theoretical models on the evolution of mate choice (Zahavi 1975; Lande 1981; Kirkpatrick 1996; Kokko *et al.* 2003). The well-supported pattern of condition-dependent expression of ornaments (Kotiaho *et al.* 2001; Tomkins *et al.* 2004) results in the expectation that male ornamentation provides female with an indication of the genetic or material consequences of choosing particular males. However across most species, ornaments often have a dual role in both mate choice and in male–male aggressive competition over mating (Hunt *et al.* 2009). Allocation of resources to competition over mating (reflected by display traits or weaponry) may trade-off against the allocation of resources to survival (Brooks 2000; Hunt *et al.* 2004; Robinson *et al.* 2008), or as has been suggested in many bird populations, trade-off against a male's ability to provide the parental care necessary to successfully raise surviving offspring (Qvarnström 1997; Qvarnström & Price 2001; Duckworth 2006). The balance between the costs and benefits of being more or less competitive may vary across environmental conditions. Our results imply that large-ornamented male collared flycatchers either compromise their ability to contribute to offspring care during wetter years, or pass on genes that make their offspring more sensitive to such harsh conditions.

In general, among-year fluctuations in the direction of selection create overall (across year) stabilising selection, which is selection against choice of males with extreme forehead patch size. By contrast, our results suggest that a long-term consistent pattern of increased or decreased July rainfall would favour the evolution of mate choice of small patch males or large patched males, respectively. An alternative

evolutionary outcome could be that female flycatchers develop the ability to adjust their choice to the current weather conditions. In other populations, studies have found plasticity in female mate choice across breeding seasons (Lynch *et al.* 2005; Chaine & Lyon 2008). We have previously shown that female flycatchers adjust both their mate choice and clutch size depending on breeding time, which also influences the relationship between male forehead patch size and reproductive performance (Qvarnström *et al.* 2000). While females appear to be able to assess whether they breed early or late in relation to the other females, there may be no reliable cue for July rainfall at the time of pairing in May. We found that female choice of male ornamentation was repeatable across years with consistent heritability and that they do not adjust their clutch size in response to the actual breeding conditions that they later experience (i.e. determined by the combination of male forehead patch size and weather conditions). The fact that the fitness benefits of choosing highly ornamented males are not consistent across years may be one of the underlying reasons why we find no repeatability for female reproductive success. Our findings thus represent a simple intuitive hypothesis to explain evolutionary stasis in this population, and suggest that the availability of reliable cues may influence whether mate choice will act as a selective force that reinforces spatial and temporal variation in the relationship between male ornament size and fitness or as a conservative evolutionary force that reduce the magnitude of such fluctuations.

There are a few limitations of our study, which need to be considered. The first is that we do not assess fitness consequences of extra-pair mating (EPP) since we only use a social pedigree. Most nestlings are sired by the social mate (85%), basically all direct benefits are linked to the choice of the social mate, and they also provide paternal care, thus we assume that the reproductive success of female is mostly determined by her social mate choice. Second, this is an associative study, and thus these processes may be driven not by direct associations of the traits themselves, but through other correlates. We also tested for the effects of age, body size, laying date and large-scale spatial differences (see Supporting Information). Furthermore, there may be some family fidelity in locality, which may influence our estimates of heritability of female choice. Our estimate of heritability for female choice is considerably lesser compared to those made in laboratory environments (reviewed in Bakker 1999; see also Schielzeth *et al.* 2010), which may simply reflect the fact that females have to overcome many obstacles to obtain a preferred male under natural conditions. An interesting next step will be to disentangle the different female traits underlying the process leading to mate choice in nature and then to estimate their relative importance. Such analysis will be able to tell us which of the female traits underlying mate choice that will be most likely to change in response to selection.

One of the main reasons for assuming that sexual selection only leads to speciation under a limited range of conditions is that mate choice is thought to act as a unidirectional selective force (Ritchie 2007). By extension, our results suggest an alternative hypothesis for how sexual selection may drive speciation when populations experience different environmental conditions. When sexual selection is considered across ecological contexts the focus is generally on the costs associated with expressing ornaments or mate choice. Variation in the level of the costs across environmental contexts is expected to lead to different optimal levels of expression of mate choice and ornaments across ecological contexts (Maan & Seehausen 2011). Moreover, given that only locally adapted males are able to develop

large ornaments, females would discriminate against immigrant males without any divergence in choice itself (van Doorn *et al.* 2009). To our knowledge, there is no model on speciation through sexual selection assuming that female mate choice changes in *direction* on the same male trait depending on the ecological context experienced by the population. In this study, if sub-populations experience different environmental conditions, selection would favour divergence in the *direction* of female choice. At present this is speculation, but if similar conditions apply to other species, sexual selection could lead to speciation under a much wider range of conditions that previously realised. This is because divergence in the direction of choice would not only lead to population divergence in allopatry but also to assortative mating during periods of secondary contact. In conclusion, our results suggest that female choice may act both as a divergent micro-evolutionary force between populations experiencing consistently different environments and as a conservative force in populations experiencing fluctuating environments.

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AUTHORSHIP

M.R., L.G. and A.Q. came up with the idea and wrote the manuscript with inputs from S.v.D. M.R. did all the statistical analyses. L.G. organised the long-term study, and all four authors took active part in discussion and commenting on the manuscript. The authors declare no conflict of interest.

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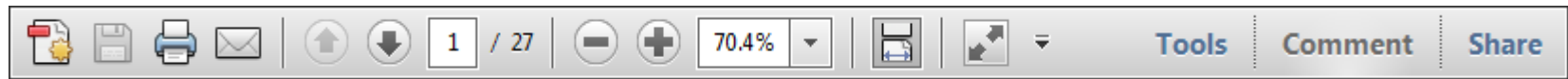
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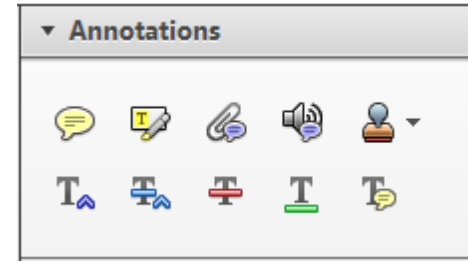
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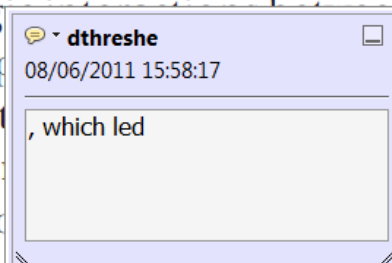


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How to use it

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standard framework for the analysis of microeconomics. Nevertheless, it also led to the emergence of strategic behavior in the number of competitors in the industry. This is that the structure of the industry, which led to the emergence of strategic behavior, are exogenous to the industry. Important works on this by Shirasaka (henceforth) we open the 'black b



2. Strikethrough (Del) Tool – for deleting text.



Strikes a red line through text that is to be deleted.

How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits and the number of competitors are zero and the number of firms (net) values are not determined by Blanchard and ~~Kiyotaki~~ (1987), perfect competition in general equilibrium. The effects of aggregate demand and supply in the classical framework assuming monopoly are an exogenous number of firms

3. Add note to text Tool – for highlighting a section to be changed to bold or italic.



Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

dynamic responses of mark-ups consistent with the VAR evidence

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4. Add sticky note Tool – for making notes at specific points in the text.



Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

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USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

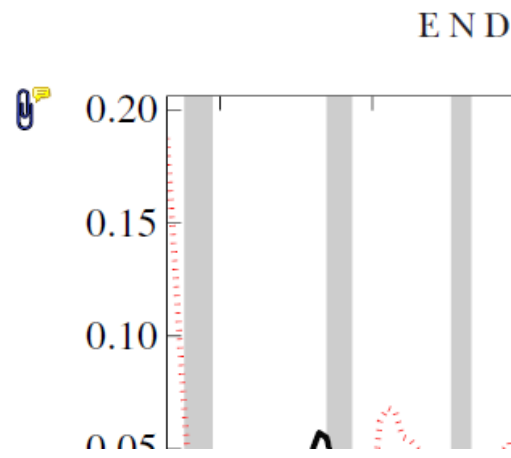
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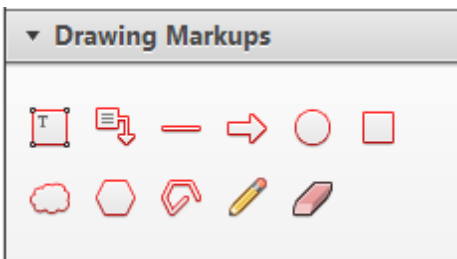


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of the business cycle, starting with the
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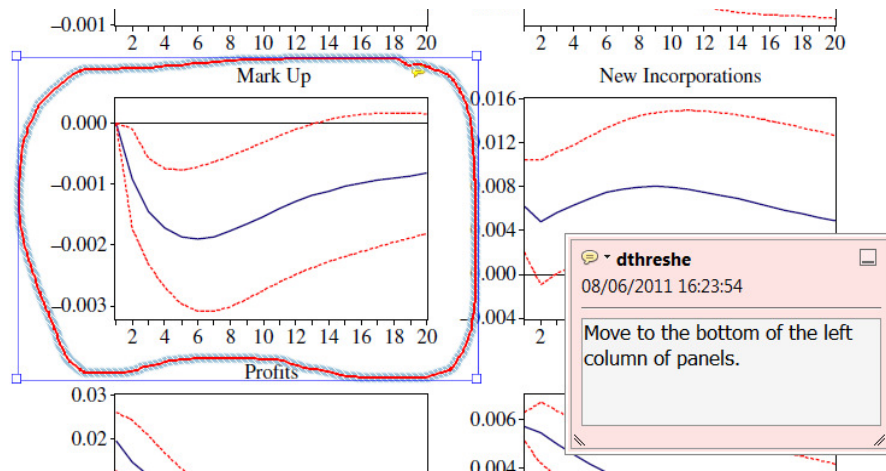


7. Drawing Markups Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks..

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