There is currently considerable controversy in evolutionary ecology revolving around whether social familiarity brings attraction when a female chooses a mate. The topic of familiarity is significant because by avoiding or preferring familiar individuals as mates, the potential for local adaptation may be reduced or favoured. The topic becomes even more interesting if we simultaneously analyse preferences for familiarity and sexual ornaments, because when familiarity influences female mating preferences, this could very significantly affect the strength of sexual selection on male ornamentation. Here, we have used mate-choice experiments in siskins Carduelis spinus to analyse how familiarity and patterns of ornamentation (i.e. the size of wing patches) interact to influence mating success. Our results show that females clearly prefer familiar individuals when choosing between familiar and unfamiliar males with similar-sized wing patches. Furthermore, when females were given the choice between a highly ornamented unfamiliar male and a less ornamented familiar male, half of the females still preferred the socially familiar birds as mates. Our finding suggests that male familiarity may be as important as sexual ornaments in affecting female behaviour in mate choice. Given that the potential for local adaptation may be favoured by preferring familiar individuals as mates, social familiarity as a mate-choice criterion may become a potential area of fruitful research on sympatric speciation processes.

1. Introduction

Sexual selection was proposed by Darwin [1] as a general selective process to explain the paradoxical evolution of exaggerated male traits that are detrimental to survival. A main characteristic of this process is that the males developing these extravagant secondary sexual traits are generally preferred by all the choosing females of the population over males with smaller ornaments. As a consequence, the evolution of such ornamental traits underlies directional selection (i.e. additive genetic variance) [2]. The Darwinian sexual selection paradigm of mate choice has been a landmark in science, and has guided hundreds of theoretical and empirical studies [3]. There is, however, increasing evidence that mate choice may also be based on non-additive genetic variance criteria [4]. This may be the case when individuals select for genetic compatibility, so that one male may not be good for all females [5,6]. Recent work has found, for instance, that mating preferences may be linked to compatibility of the major histocompatibility-complex system [7,8], personality [9–11], size [12] or familiarity [13].

The topic of familiarity has repeatedly attracted the interest of researchers. Familiarity within the pair, the territory or the neighbours has been shown to increase breeding success in several species [14–17]. The study of preferences for local song dialects versus novel songs is also a way to study preference for familiarity [18].

The way in which social familiarity could act as a criterion for non-additive genetic variance in mate choice is nevertheless controversial. Traditionally, it had been assumed that social familiarity should not breed attraction when a female chooses a mate [19–22]. Preference for unfamiliar mates was thought
to be favoured because it avoids inbreeding and increases gene flow [23]. However, recent work and some earlier papers show that familiarity and close relatedness may also bring attraction in mate choice [13,24–33].

The interplay between mating preferences for genetic compatibility and ornamental traits may cause individuals to face a conflict between these two preferences [33,34]. This is also the case of social familiarity, because when familiarity influences female mate preferences, the strength of sexual selection on male ornamentation could be altered; it could, for instance, cause females to mate with males of lower genetic quality [5,6,35]. Mate choice for—or against—familiar individuals is particularly interesting and goes beyond the subject of mating systems, because by avoiding or preferring familiar individuals as mates, the potential for local adaptation and even speciation may be reduced or favoured [18,36]. To date, however, only a handful of studies have investigated the interaction between familiarity and ornamentation [8,33], and several of them have been conducted in species that either avoid familiarity or in which familiarity does not facilitate social courtship interactions [35,37,38].

Here, we used the siskin (Carduelis spinus), a small monogamous cardueline finch, to analyse how familiarity and patterns of ornamentation interact to influence mating success. The siskin is a highly social species flocking all year round in social units of about five to 15 individuals [39,40]. Pairing takes place in early spring, when the birds are still at the wintering areas [41]. The siskin has a yellow stripe on its wings, and the size of this stripe is tightly correlated to an individual’s ability to find food [42,43]. In previous work, we documented that, in mate-choice trials with unfamiliar males, females showed a marked preference for males with larger wing patches [44]. For this work, we tested whether females preferred familiar or unfamiliar mates when choosing between males with similar-sized wing patches (i.e. ornaments). Having found that familiar males were preferred, we then determined the relative importance of familiarity versus ornamentation by confronting females with the choice between a highly ornamented unfamiliar male and a less ornamented familiar male.

2. Material and methods

Siskins used in the experiments were captured in the suburban area of Barcelona (Catalonia, northeast Spain) in the autumn and winter of 2007–2008. We used only transient birds to avoid any bias related to residence, and because transients are far more abundant in an area than residents [45]. Upon capture, we measured the length of the yellow stripe on primary six, from the distal edge of primary covert four to the distal end of the yellow stripe, according to Senar & Escobar [43]. This measure on primary six correlates highly with the size of the whole yellow patch and was thus used to estimate its size [43]. Age was assessed according to Svensson [46] and Martin [47], distinguishing yearlings (birds in their first winter) from adults. Except during experiments, the birds were kept in indoor cages (100 × 40 × 40 cm) with natural light, in flocks of one female and two males. One of the males had a large (L) yellow wing patch, whereas the other had a small (S) yellow wing patch (average patch for L = 7.1 mm; S = 3.8 mm; average difference between the two individuals within the ‘group’ ± s.d. = 3.3 ± 1.0 mm; paired t-test = 12.7, p < 0.001). To ensure familiarity between the three birds, they were retained in their same groups for at least two months over the winter, before starting the mate-choice experiments. Previous studies have determined that familiarity in siskins is attained after 20 days of cohabiting in the same cage [48]. Our period of at least two months is therefore more than sufficient time for the three birds to become familiar.

Mate-choice trials were conducted in the spring of 2008 (when females were ready to mate, spring being the breeding season), following the experimental set-up of Hill [49]. We used a mate-choice box that consisted of a central chamber measuring 100 × 100 × 100 cm (cage C). The box had two side compartments measuring 20 × 20 × 30 cm (cages A and B). A Plexiglas window was attached to an exterior cage at the end of each side compartment. During each trial, the two exterior cages each contained one stimulus male bird and the main chamber housed the test female. The test female could view only one stimulus male at a time. To do so, the female had to hop under one of the two doorways (10 cm high) that led to a side compartment (A and B) and jump up on to a perch (for details see [44,49,50]). Females were released into the central chamber between 14.00 and 15.00 h on the day before the experiment. Passing the night in the experimental cage allowed them to become accustomed to the cage well in advance of the experiment.

Both the central (C) and the side (A and B) compartments contained infrared detectors connected to a computer. The computer automatically recorded the time that the female stayed in each compartment. Trials lasted 4 h, timed from the moment the computerized system detected that the female had visited both stimulus males. All trials were conducted from 9.00 h, when males were introduced into the side cages. Whether a given male was housed in compartment A or B was chosen at random, thereby eliminating positioning effects. No observers were present in the experimental room during trials.

The time that the females spent in association with each of the two stimulus males was used to measure mate preference, as this is known to be a good indicator of mating behaviour in captive birds [51–53]. The method has been used as a proxy for mate preference in many laboratory studies in several taxa [24,52,54–58] (see below).

We conducted two separate experiments. In experiment 1, we analysed the relationship between female preference and familiarity (n = 15 trials). In this experiment, females had to choose between a familiar and an unfamiliar male, both ornamented with a large yellow wing stripe. We analysed the time spent by females in association with each of the males with repeated-measures ANOVA. The results obtained were the same when using either parametric or non-parametric (i.e. ranked) data [59]. Hence, we show results only from parametric analyses. We used different females for each trial (n = 15 females), and a different pair of males (no male was repeated) for each female tested (n = 30 males), thus ensuring independence. Females used in the different trials were randomly chosen. The sets of two males were also chosen at random, but under the restriction that the difference in size of the yellow wing stripe between the two stimulus birds should be less than 0.5 mm.

In experiment 2, we analysed the interaction between familiarity and ornamentation (n = 15 trials). Females had to choose between a poorly ornamented familiar male (small yellow wing patch) and a more ornamented unfamiliar male (large yellow wing patch). We analysed again the time spent by females in association with each of the males with repeated-measures ANOVA. We used different females for each trial (n = 15 females) and a different pair of males (no male was repeated) for each female tested (n = 30 males). The birds were the same as those used in experiment 1, but we ensured that they were confront with different males to those used in experiment 1. Females used in each trial were chosen at random. The sets of two males were also chosen at random, but this time under the restriction that the difference in size of the yellow wing stripe between the two stimulus birds should be at least 2 mm, as this had previously proved sufficient to detect a preference by the females [44].
It should be noted that experiments 1 and 2 were not carried out sequentially; the order of each experiment for each female was chosen at random. We did not perform a control experiment, because the experimental design was identical to that used in a previous study [44].

In order to validate, within our experimental set-up, that the time a female spends in front of a male really measures her mate preference, in the spring of 2013 we carried out an additional experiment. This was based on 14 females and 28 males captured in the winter 2013 in two areas around Barcelona. In the first part of the experiment, we measured the time a female spent in front of each of two males during a standard binary choice situation. In the second part of the experiment, the female was housed for 4 days in a large cage (1 × 1 × 1 m) where she could fully interact with the two males. This time we measured female mate preference by quantifying bouts of courtship feeding with a male and her wing-quivering solicitation displays. Both are typical sexual behaviours of cardueline finches [60]. A male was scored as sexually preferred by a female when she engaged with that male in courtship feeding and/or she showed wing quivering in front of him. We then compared the relative time (%) spent by females in front of sexually preferred and non-preferred males. The observer was naive to the status of the male (preferred or non-preferred) in the previous association experiment. Females showed a clear sexual preference engaging in courtship with just one of the males. Only in one dyad, the female briefly engaged in courtship with the second male, but the duration was negligible. In five cases, females showed no sexual preference for any of the two males. Four of these females showed a similar lack of preference in the association experiment. Concordance between showing or not showing a preference in the two experimental set-ups was high (Spearman rank \( r = 0.85, p < 0.001 \); Yates’s chi-square \( = 6.54, d.f. = 1, p = 0.01; n = 14 \) dyads).

Females spent more time in front of the sexually preferred males than in front of the non-preferred males (median preferred: 99%, non-preferred: 1%; Wilcoxon matched pairs test, \( z = 2.7, p < 0.01; n = 9 \) dyads in which the female showed a sexual preference). This result, similar to that obtained by Witte [53], validates our experimental design, showing that the time spent by a female in front of a male represents a true sexual mating preference.

Data supporting our paper are made available in the electronic supplementary material.

3. Results

In experiment 1, where we presented siskin females with two males that were equally ornamented (i.e. with long yellow wing stripes) but different in social familiarity, females showed a significant preference for the familiar males (repeated-measures ANOVA: \( F_{1,14} = 15.5, p < 0.01, n = 15 \) trials; figures 1 and 2).

In experiment 2, females had to choose between a poorly ornamented familiar male (small yellow wing patch) and an ornamented unfamiliar male (large yellow wing patch). In this experiment, the difference was not significant (repeated-measures ANOVA: \( F_{1,14} = 0.1, p = 0.82; n = 15 \) trials; figures 1 and 2), which was due to about half of the females choosing familiar males and others choosing well-ornamented males (table 1).

The interaction between the time spent by females with the stimulus males (familiar versus unfamiliar) between the two experiments was significant (repeated-measures ANOVA interaction: \( F_{1,28} = 4.1, p = 0.05 \); figure 1). Time spent by females with the unfamiliar males was different according to whether familiar males were highly or poorly ornamented (\( F_{1,28} = 5.1, p = 0.03 \); figure 1). Altogether, this suggests that male ornament and familiarity interactively affect female mate choice.

4. Discussion

Although there is currently general agreement that mate choice may be based on either additive or non-additive genetic variance criteria [4,5,34,61], the interplay of ornamental and compatibility mate-choice criteria has only recently attracted the interest of evolutionary ecologists [33]. Of the
Table 1. Results from the second experiment in which females had to choose between a poorly ornamented familiar male (small yellow wing patch) and an ornamented unfamiliar male (large yellow wing patch). According to binomial tests, we found that seven out of 15 females (47%) chose the familiar male, five chose the unfamiliar male and three showed no preference.

<table>
<thead>
<tr>
<th>% time with familiar</th>
<th>z</th>
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<tbody>
<tr>
<td>94</td>
<td>8.7</td>
<td>&lt;0.001</td>
<td>poorly ornamented</td>
</tr>
<tr>
<td>99</td>
<td>9.7</td>
<td>&lt;0.001</td>
<td>familiar</td>
</tr>
<tr>
<td>45</td>
<td>0.9</td>
<td>0.36</td>
<td>no choice</td>
</tr>
<tr>
<td>99</td>
<td>9.9</td>
<td>&lt;0.001</td>
<td>poorly ornamented</td>
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<tr>
<td>20</td>
<td>5.9</td>
<td>&lt;0.001</td>
<td>ornamented</td>
</tr>
<tr>
<td>90</td>
<td>7.9</td>
<td>&lt;0.001</td>
<td>poorly ornamented</td>
</tr>
<tr>
<td>98</td>
<td>9.5</td>
<td>&lt;0.001</td>
<td>poorly ornamented</td>
</tr>
<tr>
<td>43</td>
<td>1.3</td>
<td>0.19</td>
<td>no choice</td>
</tr>
<tr>
<td>91</td>
<td>8.1</td>
<td>&lt;0.001</td>
<td>poorly ornamented</td>
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<td>19</td>
<td>6.1</td>
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<td>ornamented</td>
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<tr>
<td>54</td>
<td>0.7</td>
<td>0.48</td>
<td>no choice</td>
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<tr>
<td>87</td>
<td>7.3</td>
<td>&lt;0.001</td>
<td>poorly ornamented</td>
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<td>10</td>
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<td>24</td>
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<tr>
<td>0</td>
<td>9.9</td>
<td>&lt;0.001</td>
<td>ornamented</td>
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Different forms of compatibility, social familiarity is a topic of great interest because it can speed up or slow down processes of local adaptation and speciation [18,36]. Our data from a visual ornament are conceptually similar to the body of research on studies of preferences for local song dialects versus novel songs, which have also found that a mating preference for familiar songs can lead to local adaptation and speciation [18].

Most previous studies analysing the interaction between male attractiveness and social familiarity in mate choice found familiarity to affect mate choice negatively, and that attractiveness was more important than familiarity when choosing a mate [35,37,38,62,63]. These results were confirmatory of the general view that animals should avoid inbreeding [36]. However, a few recent studies, including one in cichlid fish *Pelvicachromis taeniatus* [33] and our study in siskins, support a different view, in that attractiveness alone in these species is not enough and that social familiarity adds to attraction.

An alternative interpretation of our results could be that females were simply showing preferences to forage with flock mates rather than mating preferences. We have to point out that as our experiment was carried out during the mating season and food was present only in the central neutral chamber, foraging preference is less probable than a mating preference. Several previous works have already shown, in similar experiments, that measures of proximity by females to a potential male, in captive experimental conditions, are correlated to frequency of courtship displays and a shorter time to mating [53,64], validating the use of time spent with a male as a good indicator of female mate preference. Our additional experiment carried out in 2013 (see Methods) agrees and supports this view. Additionally, even if we were simply measuring affinity for association, then this could lead to assortative mating between groups if females prefer to associate with males of their own familiar flock [51,65].

Our results from experiment 1 could also be interpreted as a by-product of pair-bonds with the attractive familiar male already being formed even before the trials were started. Under this scenario, we would expect females to show reduced interest in other males in experiment 2. However, this was clearly not the case, because half of the females showed a significant interest either for non-attractive familiar males or attractive new males. This rules out that previously established pair-bonds could distort our results, and strengthens the role of familiarity in mate choice.

Similar to the mate-choice trade-off between good genes and compatible genes [4], the relationship between familiarity and ornamental mate-choice criteria could result in two scenarios: in the first one, some females would choose only well-ornamented males, and others would choose only familiar males. In the second scenario, all females would have no preference for either of the males, because both males would be similarly attractive as mates. Our current results on siskins seem to support the first scenario, although we are currently unable to discern whether the significant variation among females in interest for different males was due to variation in individual preferences, or alternatively was due to chance, such that females might choose one male arbitrarily because both were similarly ‘attractive’.

The familiarity factor may help us to understand patterns of sympatric local adaptation and divergent ecological selection, providing a simple framework to explain why inbreeding, and hence local adaptation, is more common in nature than was previously recognized [36]. The familiarity factor may be especially important in species in which different sub-populations cohabit during the mating period, because this cohabitation would otherwise provide ample opportunities for gene flow [66,67]. In the siskin, two different sub-populations, residents and transients, have been described [45]. These two sub-populations intermix and cohabit during the winter pairing period [41,45], but sub-populations consistently differ in morphometrics [68,69]. Crossbills *Loxia* spp. are considered another typical example; studies have shown that different cryptic species may cohabit in the same geographical areas but that they seem to mate assortatively [52,65,70–75]. The citril finch *Serinus citrinella* is a third example. Different sub-populations, known to adapt locally and to differ in morphometrics and genetic structure [76,77], are allopatric during the breeding season, but intermix in the shared...
wintering areas where pairing takes place [78,79]. Citril finch subpopulations, however, remain differentiated [76,77].

Subpopulations remain differentiated in siskins, crossbills and citril finches, even though cohabitation of the different subpopulations during the pairing period would provide ample opportunities for intermixing, resulting in gene flow, and ultimately in homogenization [27,79]. One possible explanation is that the mating preference for socially familiar individuals (i.e. for the individuals of their own flock), which could explain the maintenance of these instances of local differentiation. In this way, as individuals flock assortatively according to their origin or characteristics (i.e. residents with residents, transients with transients, birds from one area with birds from the same area), a preference to pair with familiar individuals would cause, by definition, a high reduction in the probability of intermixing.

Interspecific variation in the role of familiarity in mate choice has been mainly attributed to the probability of inbreeding [13]. This view would explain why, in species with a high probability of inbreeding, as for instance in promiscuous species, females generally avoid males that are familiar to them, as a mechanism to avoid the costs of inbreeding [13]. Forest cardueline finches in general, and siskins in particular, are socially monogamous species [80], and low rates of extra-pair paternity have been found in these species [81]. Avoidance of familiar individuals is therefore not expected in these species.

We do, however, think that interspecific variation in the role of familiarity in mate choice could also be related to interspecific variation in the degree of stability in the composition of groups, which is in fact a prerequisite for social familiarity. Cardueline finches, like siskins, crossbills and citril finches, breed in semicolonies that have high social interaction among their members [80,82]. The high social costs of flock switching enhance membership stability [48,83–86], and data on siskins and other finches suggest that flocks formed in the original breeding localities probably remain together in the wintering grounds [86]. In this scenario, if birds develop a mating preference for familiar birds, flock structure would favour pairing with individuals from the same breeding subpopulation, thereby reducing gene flow and allowing local adaptation.

To summarize, our results obtained with siskins suggest that social familiarity can add to attractiveness. As a preference for mating with familiar individuals could favour local adaptation [18,25,30,36], the study of social familiarity as a mate-choice criterion may become an area of fruitful future research on sympatric speciation processes.

Birds were handled under permission of the Catalan Ringing Office (ICO) and the Department of Environment and Housing (Medi Ambient) of the Generalitat de Catalunya (Catalan Government). Experiments comply with the current laws of the Catalan Government. At the end of the experiments, all individuals were released in healthy condition at the location of capture.

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