



Divergent sexual selection on birdsong: a reply to Byers

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Byers (2011) raises several issues in his critique of our paper on 'Migration strategy and divergent sexual selection on bird song' (Collins et al. 2009). Our paper focused on the issue of whether migratory populations were under stronger sexual selection pressure than resident populations, investigating the effects of inter- and intrasexual selection independently using the blackcap, *Sylvia atricapilla*, as a model species. However, most of Byers's critique appears to be focused on the hypothesis that female preference drives the evolution of more complex songs. This is surprising, as whether females across species prefer more complex songs is not a central issue of our paper. Byers also criticizes some aspects of our data analysis and our justification for concluding that two parts of the blackcap song have different functions. In our response below, we first address the issue of the evolution of song complexity, as it appears that the main focus of our paper has been misrepresented

in the critique, and then we reply to the specific criticisms of our study.

A number of authors have suggested that migratory populations of birds are under stronger sexual selection pressure than resident populations because of the limited time for breeding and territory formation (Catchpole 1982; Mountjoy & Leger 2001; Friedman et al. 2009). This hypothesis predicts that sexually selected traits (e.g. size, colour, or some acoustic measure) will be more extreme in migratory populations, both within and between species. However, the hypothesis assumes that both intra- and intersexual selection are stronger in migratory populations (e.g. Irwin 2001; Irwin et al. 2008), but this may not be the case (Mahler & Gil 2009). Although the time for breeding is shorter and the environment is possibly more unpredictable for migratory populations (Irwin 2001; Botero et al. 2009), migratory populations may also have a higher food abundance and lower population density than resident populations (e.g. Irwin 2001). This means that the two types of sexual selection pressure do not need to covary in strength. It was this particular question that our study aimed to test: are the two forms of sexual selection both stronger in migratory populations? Therefore, the main focus of Byers's critique in discussing the evidence for female preference for more complex song is not relevant. We could have tested the above hypothesis by comparing any two sexually selected traits, one a focus of male competition

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and one a focus for female choice, in migratory and resident populations. However, previous work has found song differences between resident and migratory populations, specifically that songs are more complex in migratory populations, which has been interpreted as evidence for stronger sexual selection (Read & Weary 1992; Irwin 2001; Mountjoy & Leger 2001; Irwin et al. 2008). Therefore, our original study focused on song differences.

Sexual Selection on Birdsong

The focus on song length and song complexity in our study was driven by the behaviour and ecology of the species in question, the blackcap. We assume that sexual selection focuses on different song traits in different species, analogous to differences found in species for plumage coloration preferences (see references in: Jennions & Petrie 1997; Owens & Hartley 1998; Badyaev & Hill 2000). We would not expect females in all songbird species to show a preference for complex songs (Soma & Garamszegi 2011), nor would we expect all bird species to have a preference for the colour red. However, we think that there is evidence that, in many species, song complexity relates to mating success and that females prefer more complex songs (see references in: Collins 2004; Soma & Garamszegi 2011).

Byers (2011) frequently refers to a review (Byers & Kroodsma 2009) suggesting that female preference for larger repertoires is not common, and on that basis, he concludes that our paper was flawed. We have no issue with the fact that studies do not always find a preference for song complexity. It is true that in our Abstract and Introduction we say that females prefer more complex song. One sentence in the Introduction (Collins et al. 2009, page 585) states 'In all the species studied so far, intersexual selection leads to more complex songs', which we admit was not as precise as we would have liked. A more precise statement would be 'In all the species studies so far, where a significant result was found, females prefer more complex song'. Our original statement was intended to illustrate the fact that it is unlikely that females would prefer less complex song, and we have no disagreement with the fact that, in some cases, there is no preference for song complexity (e.g. Forstmeier et al. 2002).

Byers & Kroodsma (2009) appear to reject the idea that species may differ in whether females prefer complex song. They further argue that the reason for the inconsistency in experimental results is not due to species differences, but due to a bias in laboratory studies compared to field studies. Variation in which traits are used as choice criteria (Jennions & Petrie 1997) is found across species for other acoustic (see references in Collins 2004) and plumage traits (Møller & Pomiankowski 1993), and indeed variation in female preference may be found within a species (e.g. Reid & Weatherhead 1990; Collins & ten Cate 1996; Forstmeier & Leisler 2004). This variability across and within species does not mean that we can conclude that, for example, preference for red plumage does not occur in a specific species, because in some species we find no preference for red (e.g. Yasukawa et al. 2010).

One could also argue that the review by Byers & Kroodsma (2009) is selective in its choice of papers. A recent comprehensive meta-analysis (Soma & Garamszegi 2011) included 15 more papers on field studies than Byers & Kroodsma's (2009) review. Of these 15 papers, 11 showed an effect of song complexity on mating success and four did not (one of which was published after 2009). Soma & Garamszegi (2011) suggested that there is, overall, a weak, but significant, effect of song complexity on female choice in field studies (they excluded laboratory studies). In addition, there were several errors in Byers & Kroodsma's (2009) review. Three papers reported as finding a negative result actually found a positive effect of repertoires on reproductive success (Searcy et al. 1982; Bell et al.

2004; Mennill et al. 2006). Mennill et al. (2006, page 177) reported 'male house finch songs demonstrate an association between elaborate song features and both nest initiation date and clutch size'. Bell et al. (2004) was reported in the text as finding no preference for complex song, whereas Bell et al.'s study found that males with larger repertoires enjoy greater reproductive success even when the authors looked at a short section of the song. (Byers & Kroodsma may have made this mistake because the title of Bell et al.'s paper suggests that females prefer short songs.) A study on the starling *Sturnus vulgaris* (Gentner & Hulse 2000, page 454), which was also cited as a 'rejection' of the hypothesis that females prefer complex song states: 'it is important to reiterate that the influence of repertoire size was not examined explicitly in the present study'.

One final issue is that Byers & Kroodsma (2009) assert that, of 12 species tested multiple times for a relationship between mate choice and complexity, the results are inconsistent in eight. Closer inspection, however, reveals that some of those 'inconsistencies' are not actually inconsistent. In two species there was an effect of song complexity on mate choice for a social partner but not for an extrapair partner, or vice versa (see references in Byers & Kroodsma 2009). Differences in the criteria used to choose extrapair or social partners are common in sexual selection (Owens & Hartley 1998), because different benefits, direct or indirect, are obtained (Andersson 1994; Hasselquist et al. 1996).

The main conclusions from the discussion above are that the strength of the effect of song complexity on female choices varies by species and situation, and that there may be a publication bias (Soma & Garamszegi 2011). There is, however, no reason to conclude that blackcap females do not use song complexity simply because there is no effect of song complexity on female choice in other species. Our assumption was that, in blackcaps, females show a preference for longer warbles (see below). However, to reiterate, the point of our paper was not to present an analysis of the evolution of song complexity, despite that being the main focus of Byers's critique. It was thus never our intention to review the work on female choice for male song repertoires in songbirds.

Byers also takes issue with our 'assertion' that intrasexual selection often leads to short stereotyped songs. However, we are not the first to suggest this idea (Slater 1981), and we did not state that this was true for all species. We stated that male competition 'often' leads to short stereotyped songs, not always. Byers cites several studies in which songbirds used more complex song in competitive encounters (Byers 2011), and we do not disagree that this may occur, as we thought we had made clear in our original paper. However, we did not test whether migration in general leads to the evolution of short stereotyped songs, but whether it is likely that intrasexual selection is stronger in migratory populations using song as an indirect measure of the selection pressure.

Byers (2011, page e2) states, as outlined above, that 'two broad but unsupported assertions about sexual selection on songs form the foundation of [the] analysis'. This shows that Byers is reacting to two minor points mentioned in our paper (Collins et al. 2009) concerning how inter- and intrasexual selection may act on bird-song. However, our study did not rely either on selection through female choice for complex song, or on selection through male competition for more stereotyped song being found across species. Therefore, we fail to see why so much of Byers's critique focuses on addressing this issue, as some of these details were already covered in Byers & Kroodsma's (2009) review. There is evidence that females in some species prefer complex song and that male competition in some species involves short stereotypical songs (see references in: Collins 2004; Catchpole & Slater 2008).

In summary, we think that it is worth making a general point here. The vast majority of empirical studies in behavioural ecology

aim to test hypotheses that might be generally applicable. Nevertheless, empirical studies by definition must be conducted within the confines of a specific study system. It is obvious that a result obtained for one particular study system does not automatically mean that the same result would be obtained in other study systems. Few authors would make this claim, and we did not make this claim for our study on blackcaps. Rather, the usefulness of any hypothesis must be gauged on the balance of evidence accumulated from a range of studies.

We will now address the two specific criticisms that Byers makes about our study. First, whether we have good evidence for the function of the two parts of the blackcap song, and second whether our data are sufficient to test the hypothesis in question.

Blackcap Songs

There is little contention that blackcap song consists of two acoustically different parts, a warble and a whistle (Bergmann & Helb 1982; Shirihai et al. 2001; Collins et al. 2009). Furthermore, there is evidence to suggest that, in blackcaps, long warbles are involved in female choice and short whistles are involved in male competition. In a number of species, female choice selects for long or complex songs and male competition results in short stereotyped songs (e.g. *Acrocephalus* warblers: Catchpole 1980, 1983; dusky warblers, *Phylloscopus fuscatus*: Forstmeier & Balsby 2002). The warble in blackcaps is longer when males sing to attract a female (Johannessen 1998). In addition, blackcap whistles are shorter during competitive encounters (Sauer 1955), and several years of student field projects showed that males often sing only whistles after egg laying has started (S. A. Collins, personal observation). Although it is quite likely that the whistle also functions to attract females to a male's territory, as stated in our original paper, the reduced complexity and length of the whistle during competitive encounters suggests that it is also attended to by male competitors. Byers (2011, page e2) states that 'To me, these three contextual associations do not constitute strong evidence...' (our emphasis). However, Byers does not suggest an alternative explanation for the findings, nor does he provide evidence that repudiates our assumption. It is true that our assumption was based on contextual associations, but many studies have used the timing of song production, and the form of song produced in different situations, as an indicator of a song's function (see Catchpole & Slater 2008).

The Data

Finally, Byers suggests that because we had only two examples of each population type (migratory and resident), we could not conclude that migratory and resident populations differ in song characteristics. Here, we do agree with Byers. Our original findings suggested instead that song in our four blackcap populations differs, not that migratory populations differ from resident populations. In order to test this latter hypothesis, indeed, songs from a larger number of populations would need to be analysed. However, we maintain that the population differences that we found are consistent with the hypothesis that migratory and resident populations differ in song. In particular, we found that our Portuguese resident population, which is more closely related to the two migratory populations in Spain, had song characteristics that were more similar to the second resident population near Gibraltar (Pérez-Tris et al. 2004), showing convergence in song in two sedentary populations of different evolutionary origin.

Many comparable studies examining population song characteristics have used similar numbers of populations. Seddon & Tobias (2007) compared male chestnut-tailed antbirds, *Myrmeciza*

hemimelaena, across three sites; Ruegg et al. (2006) compared five populations of Swainson's thrush, *Catharus ustulatus*, two coastal, two inland, one mixed. Forchler & Kalko (2007) compared three populations of Corsican finches, *Carduelis corsicanus*, and four of citril finches, *C. citronella*, comparing island versus mainland populations within species. This is in no way a criticism of the above studies, simply an observation that the number of populations is not grounds for dismissing the results.

Song and Migration

In the final section, Byers (2011, page e2) again states that our original paper failed 'to provide convincing evidence of a correlation between migratory behaviour and song elaboration'. Yet again this shows a misunderstanding of the purpose of our study. We did not test the general hypothesis that migratory populations have more elaborate song because of stronger sexual selection. We tested whether both inter- and intrasexual selection are stronger in migratory populations (using song characteristics as an indirect measure), which is a different question and is not specific to song elaboration. Interestingly, Mahler & Gil (2009) also suggested that sexual selection resulting from female choice may be stronger in migratory species in *Phylloscopus* warblers, but that male competition may be lower. What we really need are detailed studies of the strength of sexual selection itself, rather than studies using song, colour or other secondary sexual characteristic as a proxy for sexual selection.

To summarize, we think that Byers takes issue with our study because he thinks that it disagrees with his earlier review (Byers & Kroodsmas 2009). However, the 2009 review is not relevant to our study as it addresses mate choice for complex song, not whether there is covariation in intra- and intersexual selection. We agree that our study shows that the four populations differ in song features, rather than explicitly testing migratory versus resident populations. However, we think that the best explanation for the pattern of variation we observed is that the effect of intersexual selection is stronger in migratory populations and that the effect of intrasexual selection is stronger in resident populations.

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