



## Geographical variation in male territory defence strategies in an avian ring species



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Interactions between sexual selection and ecology can drive phenotypic divergence between populations. Geographical variation in female preferences has been linked to ecology in several studies, but much less is known about patterns of geographical variation in male competition. I asked whether male aggressive territorial behaviour varied among three breeding populations of a ring species, the greenish warbler, *Phylloscopus trochiloides*. I measured aggressive response to playbacks of conspecific song at multiple time points to determine how territorial behaviour varied throughout the breeding season both within and between populations. Differences in the abundance and timing of resources necessary for raising offspring can shape male competitive strategies, and competition may consequently vary as a function of resource availability. I therefore combined assays of temporal variation in aggressive behaviour with season-long measures of food abundance, population density and parental provisioning rates. I found that the populations differed in intensity of aggressive response, the seasonal pattern of territoriality and the traits used in territorial responses. Overall intensity of aggression was lowest but most prolonged in the population with the lowest food abundance and highest population density, and males responded to playback primarily by singing. By contrast, birds in the two populations that experienced high food abundance and low population density exhibited a burst of aggressive display behaviour only when females were fertile. The results suggest that territorial strategies vary geographically and respond to limited resources, switching in function from season-long food defence where food is scarce to mate guarding where mates are scarce. Interactions between sexual selection and ecology across large geographical scales may ultimately lead to population divergence. The geographical variation in territorial behaviour observed in the greenish warbler implies that male competition may be an important diversifying force in this system.

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Evolution of sexually selected traits has traditionally been attributed to both intersexual (female mate choice) and intrasexual (male competition) selection (Andersson, 1994), with the strength and targets of these processes inextricably shaped by ecology (Maan & Seehausen, 2011; Safran, Scordato, Symes, Rodriguez, & Mendelson, 2013). Geographical variation in female preferences across different habitats can contribute to phenotypic divergence in male sexually selected traits and result in premating barriers to reproduction (Maan & Seehausen, 2011; Panhuis, Butlin, Zuk, & Tregenza, 2001; Scordato, Symes, Mendelson, & Safran, 2014). Although female choice and male competition can vary independently of each other, studies of among-population variation in male

competition lag behind those of female choice (Qvarnström, Vallin, & Rudh, 2012). Male competition has the potential to affect phenotypic divergence if the strategies and traits males use to gain access to females, or to gain access to resources that attract females, vary in different environments (Chuang-Dobbs, Webster, & Holmes, 2001; Forsgren, Kvarnemo, & Lindstrom, 1996; Kolluru, Grether, & Contreras, 2007; Kwiatkowski & Sullivan, 2002; Wong & Candolin, 2005). Although evidence is accumulating that geographical variation in male competition and aggressive behaviour may contribute to phenotypic and population divergence (Lackey & Boughman, 2013; Martin & Mendelson, 2016), quantifying differences in male competition among natural populations remains challenging.

Male competition is typically inferred by assaying male aggressive behaviour in the context of territory and/or mate defence (Catchpole, 1982). Ecological factors shown to affect the intensity of male territorial behaviour in single-population studies

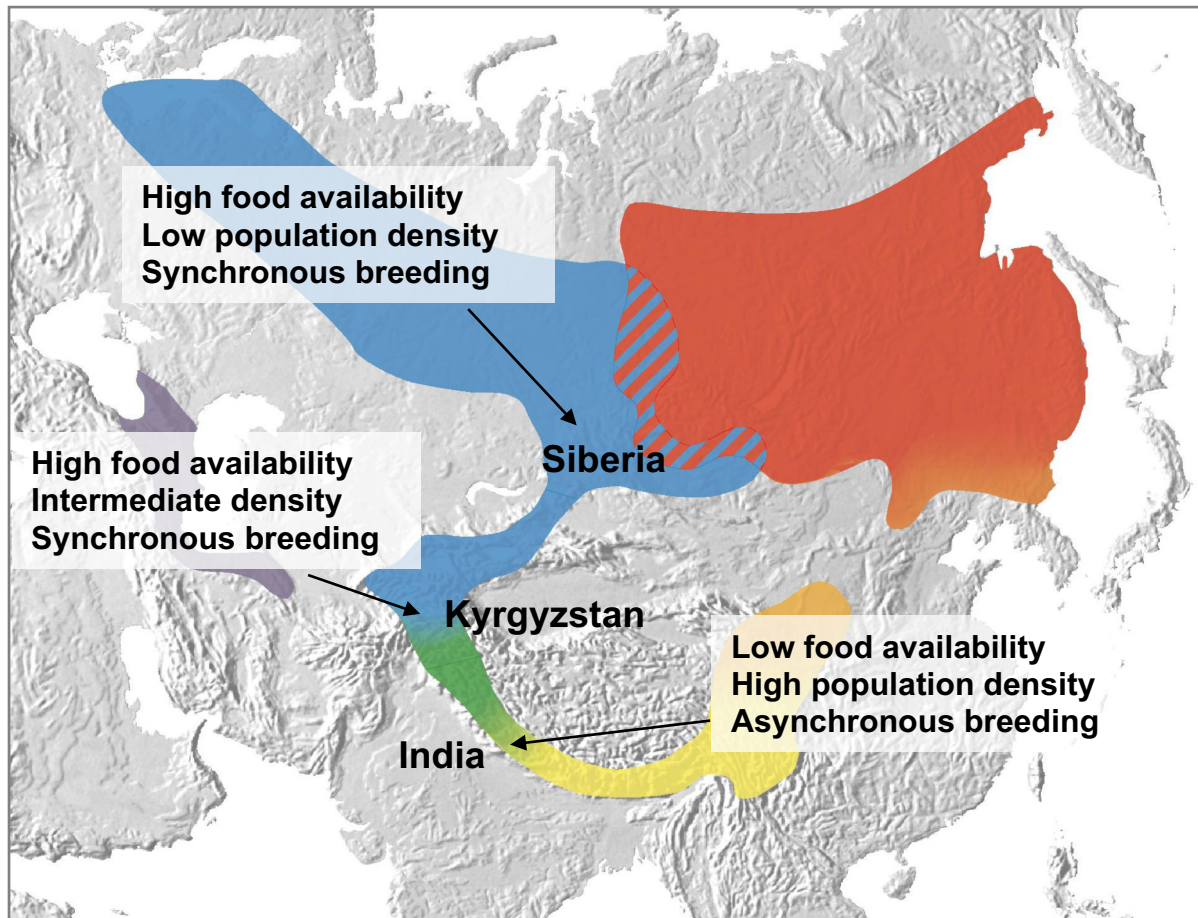
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and experimental studies include the patchiness, abundance and seasonality of resources (Kolluru & Grether, 2005; Reichard, Ondračková, Bryjová, Smith, & Bryja, 2009; Wauters, Bertolino, Adamo, Dongen, & Tosi, 2005), population density (Jirotkul, 1999), sex ratio (Wacker et al., 2013; Weir, Grant, & Hutchings, 2011) and breeding synchrony (Grant, Bryant, & Soos, 1995; Hammers et al., 2009). Moreover, both theoretical and empirical studies indicate that male competitive strategies can be labile and dependent on ecological context, with males defending resources or mates based on whichever is most limited (Hårdling, Kokko, & Elwood, 2004; Harts & Kokko, 2013). However, these predictions have rarely been tested in natural populations experiencing different ecological conditions. For example, competition among males for food resources forms the basis of many hypotheses about the strength and direction of social selection pressures (West-Eberhard, 1983) and has important consequences for life history evolution (Martin, 1987, 1995), but resource distributions have rarely been examined in the context of social competition, especially over an entire season. If resource distributions vary temporally or geographically, then both the intensity of male competition and male competitive strategies may be predicted to vary concomitant with food availability.

In this study, I characterize geographical variation in the intensity and targets of male territorial behaviour in the greenish warbler, *Phylloscopus trochiloides*. The greenish warbler is an excellent system in which to study interactions between sexual selection and ecology at a large geographical scale. It is one of

the few examples of a ring species, wherein two reproductively isolated forms coexist in Siberia but are connected by a chain of genetically and phenotypically intergrading populations around the Tibetan plateau (Alcaide, Scordato, Price, & Irwin, 2014; Irwin, 2005; Irwin, Bensch, & Price, 2001; Fig. 1). Based on short surveys, Irwin (2000) reported latitudinal variation in population density and insect abundance across the *P. trochiloides* breeding range (Fig. 1), implying that competition for food resources may be stronger further south. These patterns of ecological variation set up a natural experiment in which it is possible to assess variation in male competitive strategies between populations in different habitats that remain connected by gene flow. I studied three populations spanning the entire range of ecological differences reported by Irwin (2000). In each population, I measured male response to playbacks of local conspecific song at multiple time points throughout the breeding season to quantify variation in male aggressive behaviour both within and between populations. I also rigorously measured food abundance throughout the breeding season, population density, breeding synchrony and parental provisioning rates. Season-long studies of variation in behaviour and food availability have rarely been conducted in wild populations. By combining temporal measures of variation in male aggressive behaviour within each population with detailed ecological measurements, I was able to evaluate the following three alternative hypotheses about the function and intensity of male aggressive territorial behaviour.



**Figure 1.** Map of the greenish warbler breeding range. Study sites in India, Kyrgyzstan and Siberia are marked with arrows. Ecological characteristics for each site are summarized. Adapted from Irwin et al. (2001).

- (1) Males pursue resource defence strategies in all populations. In this case, aggressive behaviour is predicted to be most intense in the south, because food is comparatively scarce and aggressive behaviour is used to defend resource-based territories.
- (2) Males pursue mate defence strategies in all populations. Aggressive behaviour is predicted to be most intense in the north, where population density is low and food abundance is high. Aggressive behaviour is used to defend comparatively scarce mates.
- (3) Male competition varies across populations according to the limited resource. Males are predicted to guard limited food resources in the south and scarce mates in the north. Peaks in aggressive behaviour correspond to the time points at which mates versus resources are most limited.

Playback experiments simulate a territorial intrusion, and response to playback is a frequently used proxy for both intrasexual competition (Catchpole & Slater, 2008) and competitor recognition (Grether, 2011). To assess the function of male territorial behaviour, I conducted playbacks of songs recorded from local conspecifics to individually marked male birds at multiple time points over the breeding season: (1) when males were establishing territories and attracting mates, (2) when females were incubating and (3) after chicks hatched and both parents were feeding nestlings. By playing local songs at each site, the experimental design tests the strategies males use to respond to conspecific competitors within each population, rather than recognition of competitors versus heterotypics (cf. Irwin, 2000; Seddon & Tobias, 2007; Uy, Moyle, & Filardi, 2009). I therefore consider geographical variation in aggressive response to reflect among-population differences in intrasexual competition and competitive strategies. I predicted that, if the function of aggressive behaviour is to guard food resources necessary for attracting mates and rearing chicks, then males should maintain territory defence behaviour throughout the breeding season, including once chicks have hatched (Golabek, Ridley, & Radford, 2012; Tobias, Gamarra-Toledo, Garcia-Olaechea, Pulgarin, & Seddon, 2011). However, if aggressive behaviour functions to guard mates, response to playbacks should decrease once the period of female fertility is over.

## METHODS

### Study Sites

I studied *P. trochiloides* at three sites along the western part of its breeding range (Fig. 1): Keylong Forest Reserve, India in 2008 (elevation 3300–3650 m; 32°30'3"N, 76°58'42"E), Ala Archa National Park, Kyrgyzstan in 2009 (2230–2600 m; 42°32'48"N, 74°29'17"E) and Tigirek Nature Preserve, Siberia, Russia in 2010 (527–856 m; 51°7'24"N, 83°2'14"E).

### Study Species and Natural History

*Phylloscopus trochiloides* is a small (~8 g) insectivorous bird that overwinters in southern India and Southeast Asia and breeds from the Himalayas north through Siberia (Katti & Price, 2003; Price, Helbig, & Richman, 1997). Male *P. trochiloides* arrive on the breeding grounds in late May (dates of first arrival: 19 May in India; 21 May in Kyrgyzstan; 25 May in Siberia) and establish territories. Females arrive 1–3 weeks later and build a ground nest in a male's territory. At all sites, birds are socially monogamous and produce a single brood per breeding season. Extrapair paternity rates range between 30% and 35% (Scordato, 2012). Both parents provision offspring.

Using a combination of passive mist netting and targeted playbacks, my field assistants and I attempted to capture every territorial male on predefined study areas (8 ha in India, 34 ha in Kyrgyzstan and 53 ha in Siberia) as they arrived on the breeding grounds. Each study plot captured the full elevational range occupied by *P. trochiloides* in that population. Study areas were defined to ensure we monitored approximately 25 pairs at each site, and differences in size of study areas thus reflect variation in population density among sites. Each bird was given an individually numbered aluminium leg band (size 0A), as well as a unique combination of colour bands (2.3 mm, Darvic leg bands), in accordance with guidelines set by the University of Chicago Institutional Animal Care and Use Committee. We monitored all colour-banded males for territory formation, pairing and nest building throughout the breeding season. We did not observe any obviously adverse effects of banding, handling or playbacks on behaviour.

### Ecological Data

I quantified habitat structure, food abundance, population density and breeding synchrony in each population. To measure forest structure, we set 50 m transects at 100–200 m intervals across each study plot (India,  $N = 17$  transects; Kyrgyzstan,  $N = 9$ ; Siberia,  $N = 11$ ). At the end of the season we used a pole to circumscribe a 5 m radius around each 50 m transect point. Within this circle, we estimated the following variables: percentage of area shaded between 120 cm and 2 m; percentage of canopy cover at the transect point; and the species, height and diameter at breast height (DBH) of all trees with DBH > 1.5 cm. Lastly, we estimated foliage density by sighting along a pole held vertically over the transect point and counting the number and estimated height of all leaves that touched the pole, should it extend all the way through the canopy (MacArthur & MacArthur, 1961).

We measured changes in food abundance throughout the season by sampling the 0 m, 25 m and 50 m points of each transect every 5–9 days. At each point we estimated insect abundance by banging on a low-hanging branch with a 90 cm pole and capturing falling insects in a 38 cm diameter pan (Irwin, 2000; Price, 1991). We beat two branches at each transect point, from two different tree species when possible, resulting in six arthropod samples per transect per visit. We counted all insects that fell into the pan, categorizing them as follows: 0–2 mm, 2–4 mm, >4 mm, and caterpillars.

I defined the population density of a site as the number of breeding pairs per hectare. I calculated a breeding synchrony index (SI) as the total length of the fertile period in each population (Kempnaers, 1993), assuming each female for which we had data was fertile for 5 days prior to laying the first egg and for 3 days following the onset of egg laying (clutch size = 3–5 eggs).

### Parental Care

To confirm that our measures of insect abundance translated to differences in food available for provisioning offspring, we monitored parental feeding rates at nests in India and Kyrgyzstan. We conducted 15 min observations at each nest, during which we scored how many times each parent fed the chicks. We aimed to observe nests once when chicks were small (3–5 days old) and again when they were larger (7–10 days), although predation resulted in some nests only having one observation. We also scored the size of the food parents carried (small: insects just visible in the bill; medium: insect ball clearly visible in bill; large: caterpillar or large insects sticking out sides of bill; NA: food size not visible). Feeding observations in Siberia were not possible due to the difficulty of finding nests.



### Construction of Playback Stimuli

Only songs recorded prior to the onset of breeding were used as playback stimuli to control for variation in song length over the breeding season (Scordato, 2012). I recorded natural male song bouts on a Marantz PMD-660 solid-state recorder attached to a Sennheiser ME67 shotgun microphone. Songs were recorded 5–10 m from singing birds, digitized at 44.1 kHz and downloaded into Raven v.1.3 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). High-quality recordings from local individuals were used to construct digital (.wav) playback files. Each file consisted of 10 songs sung in a single bout by one bird. I attempted to use 10 consecutive songs; however, if songs were of poor quality, they were deleted and the next high-quality song was used. Intersong intervals were standardized to 10 s, and background noise below 3000 Hz was filtered out. Final playback files were standardized to the same amplitude with a hand-held sound meter. Each file began with 10 songs, repeated at 10 s intervals, followed by 2 min of quiet. Then the first five songs were played again, followed by 1 min of quiet, and the second five songs were played again, followed by 3 min of quiet. For each population, I created 10–15 natural playback stimulus files, each recorded from a different bird. In Kyrgyzstan and Siberia, I also created manipulated stimulus files, which comprised natural songs that were either longer or shorter than the population average. These were only played during the incubation period. Because the effects of manipulation were small (Scordato, 2012), these experiments were averaged and included in analyses of seasonal change.

### Playback Experiments

We observed pairing and nesting behaviour on each territory, so the breeding status of each focal male was known. I conducted playback experiments at three stages during the breeding season: (1) the 'building stage', beginning when males were establishing territories and ending when females completed egg laying, (2) the 'incubation stage', when females were incubating, and (3) the 'chick stage', when both males and females were feeding chicks in the nest. I attempted to do one playback experiment in each breeding stage for each colour-banded male. Start dates of playback experiments were on average later in India due to a wide range of arrival times and greater breeding asynchrony at this site. Sites did not differ in the time lag between the date of the first playback experiment and the nest fledging date (ANOVA followed by Tukey HSD:  $F_{2,77} = 1.96$ , all  $P > 0.1$ ).

An individual male heard the same song stimulus file in the building, incubation and chick stages. No file was played to more than two different birds to minimize concerns about simple pseudoreplication (Kroodsmma, 1990). The repeated measures design controls for sources of extraneous variation, and also means that the number of playback files required was manageable. Playbacks were done at least 4 days apart for each male to avoid habituation. I discarded experiments where the territory owner did not respond to the playback ( $N = 30$ ). Of these nonresponsive experiments, 6 were from India, 8 were from Kyrgyzstan and 16 were from Siberia. Of the unsuccessful experiments from Siberia, 12 out of 16 were from late in the breeding season; inclusion of these experiments as zeroes would have magnified the pattern of temporal decline in territoriality reported in the Results. By contrast, three of the six nonresponsive trials from India occurred early in the breeding season, consistent with the comparatively lower response levels observed earlier in the season in this population.

I conducted 217 successful playback experiments across the three sites (53 in India, 81 in Kyrgyzstan, 83 in Siberia), between 0600 and 1200 hours. For each trial, I set the playback speaker

(Mineroff AFS) 1–1.5 m off the ground at a central site in a territory and conducted a 5 min pretrial observation period during which I scored all behaviours of the focal male. The playback file was then started, and trials were videotaped and narrated on a hand-held camcorder approximately 10 m from the speaker. Birds did not appear to respond to the presence of the observer during playback experiments.

For each phase of the experiment (pretrial, playback phase, quiet phase), I scored the following behaviours from videotapes: number of songs, number of calls, number of flyovers (flights > 1 m), number of wing flicks and number of soft songs. I also recorded whether the focal male approached within 5, 10 or 20 m of the speaker in that phase of the trial. Behaviours not observed were scored as zeros. The various behaviours are graded signals of aggressive response: singing at a distance in response to a playback stimulus reflects a low aggressive response from the territory owner. Closely approaching the speaker, flying back and forth, wing flicking and producing soft songs all occur during natural aggressive interactions with other males (personal observation), and are thus interpreted as stronger aggressive responses. With the exception of approach distance, birds cannot produce more than one behaviour simultaneously.

For each of the eight behaviours, I calculated the difference between the pretrial rates and the average rate across the three playback phases. I then conducted a principal components analysis on the correlation matrix of the eight rate differences. The first principal component (PC1) explained 34% of the total variance (Table 1) and is interpretable as an aggressiveness score (high loadings for the most aggressive behaviours on PC1). Consequently, I used PC1 as the response variable in the following analyses except where noted. The second principal component explained 19% of the variance and can be interpreted as singing at a distance (high loading of song and approach within 20 m; Table 1).

To further dissect how aggressive response to playback varies among populations, I also divided the rates of each of the eight response behaviours into two biologically relevant categories: 'singing' (i.e. rate of singing in response to the playback, loading primarily on PC2) and 'display' (i.e. rates of wing flicks, flyovers, soft song, approach within 5 m, loading primarily on PC1). I used an ANOVA to determine how rates of singing versus displaying varied among the three populations.

### Statistical Analysis

#### Geographical variation in habitat and caterpillar abundance

I analysed variation in habitat characteristics among sites using ANOVAs followed by Tukey's post hoc tests. Caterpillars comprise

**Table 1**  
Factor loadings for the principal components analysis

	PC1	PC2
Eigenvalue	2.685	1.517
Variance explained	0.336	0.190
Factor loadings		
Song	−0.135	<b>0.584</b>
Call	0.264	0.342
Flyover	<b>0.543</b>	−0.028
Wing flick	0.370	−0.113
Soft song	0.324	−0.358
Approach 5 m	<b>0.480</b>	−0.040
Approach 10 m	0.372	0.371
Approach 20 m	0.083	<b>0.511</b>

The first two principal components together explained 53% of the total variance in eight different aggressive behaviours. The most aggressive behaviours (flyover and approach within 5 m, boldfaced type) loaded strongly onto PC1. Less overtly aggressive behaviours (song and approach to 20 m, boldfaced type) loaded onto PC2.

the main component of *P. trochiloides* diet (Price, 1991), and I therefore considered variation in caterpillar abundance within and among sites to reflect variation in the abundance of the primary food source. I assessed variation in total caterpillar abundance across the season using GLMs with Poisson errors. Temporal variation in caterpillar abundance was nonlinear within populations, so I used generalized additive models (GAMs) to test for seasonal variation in mean daily caterpillar abundance between sites. I ran two different models with nonparametric cubic regression splines as smoothers and site included as a parametric factor to control for differences in means among sites. The first model included a single smoother for all three sites, which varied only by a constant. The second model included a different smoother for each site; this allows the overall shape of temporal variation to differ between sites. Models were checked for normality and homogeneity of residuals. The model with the lowest Akaike's information criterion (AIC) was considered the best fit. Differences between the best and second-best models were >2 AIC units in all cases. Analyses were done using the 'mgcv' package (Wood, 2012) in R. Models using total insect abundance rather than caterpillars alone revealed very similar patterns of variation both within and between sites (data not shown).

#### Geographical and seasonal variation in aggressive behaviour

To analyse differences in the temporal pattern of aggressive behaviour between sites, I first calculated the mean PC1 (aggressiveness) score for each day of the breeding season (averaged from 2–6 playback experiments per day). I then fitted a GAM to the entire data set of mean PC1 scores against day. As in the analysis of caterpillar abundance, I fitted a model with a single nonparametric smoother for all three sites, and a model that fitted separate smoothers for each site, with study site always included as a parametric factor to account for differences in means between sites. I chose the model with the lowest AIC.

#### Consistency of aggressive behaviour

Although it is labile and context dependent, aggressive behaviour may also be heritable and evolve in response to selection (Dingemanse, Kazem, Réale, & Wright, 2010; Duckworth, 2006). An assessment of heritability is beyond the scope of this study, but one requirement of heritability is that the trait be repeatable (i.e. an individual be consistently more or less aggressive). I analysed individual consistency of aggressive behaviour across trials by calculating the intraclass correlation coefficient for individuals that were the subjects of at least two playback experiments. I calculated the intraclass correlation coefficients from linear mixed models using PC1 of aggressive behaviour as the response variable,

including breeding stage (nest building, incubation or feeding chicks) as a fixed effect, and individual as a random effect using the 'lme4' package (Bates et al., 2015). I tested the significance of the random effect using the 'lmerTest' package (Kuznetsova, Brockhoff, & Christensen, 2013).

## RESULTS

### Ecological Variation Across Populations

Consistent with Irwin's (2000) surveys, there were marked differences in ecology between populations. Population density was highest in India (furthest south) and lowest in Siberia (furthest north; Table 2). Birds bred least synchronously in India and most synchronously in Siberia (Table 2). Understorey density was similar across sites, but the forest canopy was broadest and highest in Siberia, intermediate in India, and relatively low and sparse in Kyrgyzstan (Table 2). Total food abundance integrated over the season varied significantly among sites (Table 2), with overall caterpillar abundance significantly lower in India than in both Kyrgyzstan (GLM with Poisson errors:  $\beta = 1.69$ ,  $z = 7.24$ ,  $P < 0.001$ ) and Siberia ( $\beta = 1.18$ ,  $z = 4.30$ ,  $P < 0.001$ ), using sampling beat as the replicate. Kyrgyzstan had a higher density of caterpillars than Siberia ( $\beta = 0.51$ ,  $z = 2.46$ ,  $P = 0.01$ ).

The best-fit model of temporal variation in caterpillar abundance over the season included site as a parametric factor to control for differences in means among sites, as well as a separate smoother for each site ( $\Delta\text{AIC} = 13$ , deviance explained = 43%,  $R^2 = 0.35$ ; Fig. 2). The smoother for mean daily caterpillar abundance over the season was significant in Kyrgyzstan ( $F = 5.77$ , effective degrees of freedom ( $edf$ ) = 5.12,  $P < 0.001$ ), but smoothers were not significant in Siberia ( $F = 0.98$ ,  $edf = 4.56$ ,  $P = 0.37$ ) or India ( $F = 0.019$ ,  $edf = 1.67$ ,  $P = 0.97$ ). The significance of the smooth term in GAMS indicates whether the smoother decreases the deviance of the model, and the effective degrees of freedom ( $edf$ ) indicate departures from linearity (larger  $edf$  = greater departure from linearity; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The results thus show that food abundance varied seasonally and nonlinearly in Kyrgyzstan (Fig. 2), but did not depart from a linear pattern in India or Siberia (Fig. 2). Inspection of autocorrelation plots showed no temporal autocorrelation in the model residuals. However, whereas number of caterpillars per beat was highest in Kyrgyzstan, total canopy volume was greatest, and the canopy was tallest, in Siberia and intermediate in India (Table 2). When daily caterpillar counts in all populations were adjusted for mean foliage height and density (i.e. differences in forest structure), there were significantly more caterpillars in Siberia and Kyrgyzstan compared

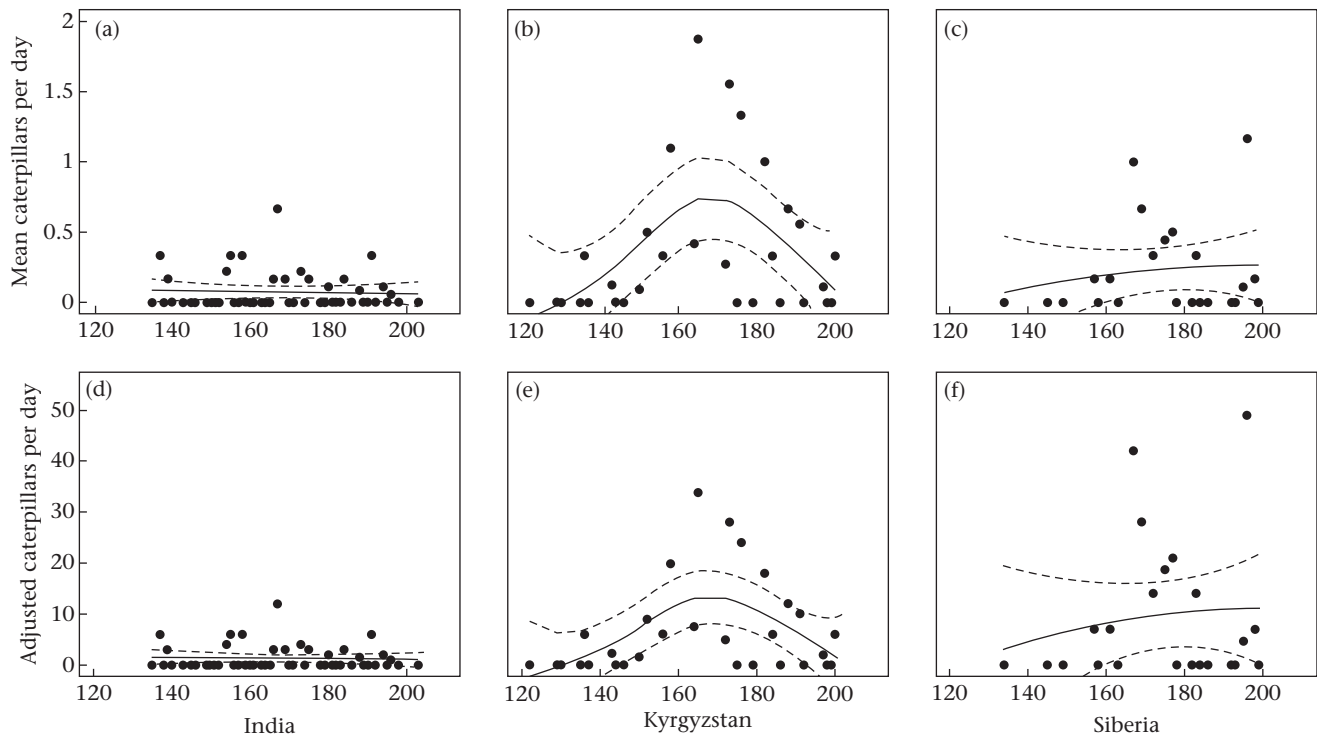
**Table 2**  
Summary of environmental characteristics at each site

Habitat variable	India	Kyrgyzstan	Siberia	<i>F</i>	<i>df</i>	<i>P</i>
Population density (pairs/km <sup>2</sup> )	2.8	1.2	0.8			
Breeding synchrony index	24	22	17			
Food abundance (caterpillars/beat)	0.18	1.6	1.2			
Paternal feeding rate (feeds per chick per 15 min)	0.99	0.51	NA	9.05	15.30	<b>0.009</b>
Forest structure						
Tree height (m)	6.8	4.8	<b>11.1<sup>a</sup></b>	4.54	2, 31	<b>0.01</b>
Tree diameter (cm)	72.7	<b>18.4<sup>b</sup></b>	55.5	3.21	2, 31	<b>0.04</b>
Canopy cover	49.6	16.3	<b>61.7<sup>a</sup></b>	4.04	2, 30	<b>0.03</b>
Percent shade	18.5	37.3	41.8	0.30	2, 31	NS
Foliage density	2.64	3.75	3.78	0.49	2, 21	NS
Foliage height (m)	5.23	2.66	<b>11.0<sup>a</sup></b>	4.83	2, 21	<b>0.03</b>

Columns show means for each site. Statistics for caterpillar abundance are given in the main text.

<sup>a</sup> Significant difference between Kyrgyzstan and Siberia (bold values); other comparisons were nonsignificant.

<sup>b</sup> Significant differences between India and Kyrgyzstan (bold values); other comparisons were nonsignificant.



**Figure 2.** Mean number of caterpillars collected per day in (a) India, (b) Kyrgyzstan and (c) Siberia. Values on the X axis show days since the first of January. Lower panels (d–f) show caterpillar abundance at each site adjusted for foliage height and volume. Lines show cubic splines  $\pm$  SE for separate models fitted to caterpillar abundance at each site.

to India (ANOVA followed by Tukey HSD: Siberia–India:  $P = 0.001$ ; Kyrgyzstan–India:  $P = 0.02$ ) and no difference between Siberia and Kyrgyzstan ( $P = 0.26$ ). There were also significant late-season peaks in caterpillar abundance (i.e. significant smooth terms) in Siberia ( $F = 3.50$ ,  $edf = 6.05$ ,  $P = 0.002$ ) and Kyrgyzstan ( $F = 3.20$ ,  $edf = 3.67$ ,  $P = 0.012$ ), but not India ( $F = 0.03$ ,  $edf = 1.67$ ,  $P = 0.96$ ; Fig. 2). These patterns are consistent with a large flush of insects observed when chicks were hatching in Kyrgyzstan and Siberia (personal observation) as well as previous accounts of higher seasonal insect abundance in more temperate regions (Hails, 1982; Rabenold, 1978).

#### Parental Care

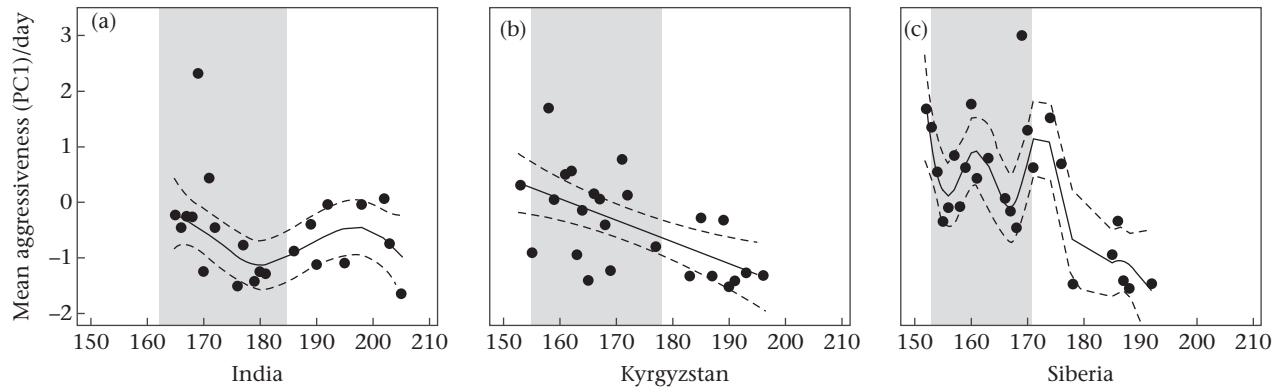
The per-chick feeding rate (number of feeds per 15 min divided by the number of chicks in the nest) was higher in India than in Kyrgyzstan ( $N = 25$  observations of 13 nests in India,  $N = 30$  observations of 18 nests in Kyrgyzstan; Table 2). Indian birds also brought significantly smaller food items (proportion of total feeds composed of small food: India, 37%; Kyrgyzstan, 8%;  $\chi^2_1 = 22.48$ ,  $P < 0.001$ ). Despite greater paternal feeding effort and a 40% smaller brood size ( $t_{45} = 6.56$ ,  $P < 0.001$ ), Indian chicks were slightly smaller on day 10 posthatching than chicks in Kyrgyzstan ( $t_{21.2} = 1.90$ ,  $P = 0.07$ ). Parents in India thus worked harder to feed fewer chicks, consistent with lower food abundance in this population. These results imply a greater premium on paternal investment in contributing to both male and female fitness in India compared to Kyrgyzstan.

#### Geographical Variation in Seasonal Patterns of Aggressive Behaviour

Mean aggressive responses were much stronger in Siberia than in Kyrgyzstan and India (ANOVA:  $F_{2,214} = 15.71$ ,  $P < 0.001$ ), indicating geographical variation in population-level aggressiveness.

The strongest aggressive responses were observed in the population with the lowest population density and greatest food abundance. However, seasonal patterns of mean aggressive behaviour per day differed among the three populations when controlling for differences in population means between sites (Fig. 3, Table 3). The GAM that fitted a separate cubic spline smoother for each site had a lower AIC than the single-smoother model ( $\Delta AIC = 5.2$ ). In India, aggressive responses remained mostly constant throughout the season with no departures from linearity (Fig. 3a), whereas in Kyrgyzstan, aggression was highest early in the season and then declined linearly (Fig. 3b). In Siberia, aggression showed a large spike early in the season and then declined throughout the incubation and chick phases (Fig. 3c). The peaks of aggressive behaviour in Kyrgyzstan and Siberia corresponded to the comparatively short periods of female fertility ( $t$  test comparing fertile and nonfertile periods: Kyrgyzstan:  $t_{20.2} = 2.64$ ,  $P = 0.016$ ; Siberia:  $t_{12.2} = 2.02$ ,  $P = 0.066$ ; Fig. 3), whereas there was no increase in aggressive behaviour during the longer fertile period in India ( $t_{19.5} = 0.47$ ,  $P = 0.64$ ; Fig. 3).

To further confirm the patterns of seasonal variation revealed by the GAMs, I used linear models to regress mean daily aggressiveness score (PC1) on Julian date for each site. Aggressiveness declined over the season in Kyrgyzstan ( $F_{1,11} = 12.07$ ,  $P = 0.002$ ) and Siberia ( $F_{1,22} = 17.15$ ,  $P = 0.0004$ ), but remained constant in India ( $F_{1,19} = 0.38$ ,  $P = 0.54$ ). A model that included all sites together and an interaction term between site and date ( $F_{5,63} = 10.27$ ) showed a significant interaction for both Kyrgyzstan–India ( $P = 0.05$ ) and Siberia–India ( $P = 0.006$ ), but no significant interaction between Kyrgyzstan and Siberia ( $P = 0.34$ ). Inspection of residuals versus fitted values and normal Q–Q plots showed no departures from linearity for either set of models. Linear models thus confirmed that aggressive responses remained constant over the season in India but declined significantly in Kyrgyzstan and Siberia. Together, these results show that males engage in season-long territorial defence in India, whereas males in Kyrgyzstan and Siberia exhibit a burst of



**Figure 3.** Seasonal variation in mean aggressive response to playback stimuli shown as daily mean PC1 scores in (a) India, (b) Kyrgyzstan and (c) Siberia. Values on the X axis show days since the first of January. Lines are cubic splines  $\pm$  95% confidence intervals, fitted to the data at each site individually. Note that the two outliers (one in India and one in Siberia) are  $>2$  standard deviations from the mean and are thus included in the plot but not in the fitted models. Shaded areas show periods of female fertility.

**Table 3**

Generalized additive model (GAM) of mean aggressiveness per day over the course of the season

Parametric coefficients	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	-0.17	0.42	-0.41	0.69
Site				
India	0.00			
Kyrgyzstan	-0.16	0.22	-0.74	0.46
Siberia	0.17	0.39	0.44	0.66
Smooth terms	<i>edf</i>	<i>Ref.df</i>	<i>F</i>	<i>P</i>
Day: India	3.20	3.78	1.26	0.29
Day: Kyrgyzstan	1.42	1.42	3.31	0.06
Day: Siberia	2.30	2.75	7.53	<b>0.0004</b>
Deviance explained=50.5%		$R^2=0.44$		

Site was fitted as a parametric factor, and a separate cubic spline smoother was fitted for each site (*edf* = effective degrees of freedom; *Ref.df* = reference degrees of freedom). There was significant departure from linearity over the season in Siberia (bold values).

early aggressive territorial behaviour generally coincident with female fertility, which declines later in the season.

#### Differences in Traits Used in Aggressive Interactions

Patterns of variation in aggressive behaviour within populations, and differences in overall intensity of aggressive behaviour among populations, were derived from analysing PC1, which was most heavily loaded by display behaviours such as flyovers, wing flicks and close approaches. The orthogonal axis (PC2) was characterized by singing from a distance. I explicitly compared rates of singing versus displaying in response to playbacks to determine whether populations differed in the traits used in aggressive interactions. Birds in all three populations sang at similar rates ( $F_{2,214} = 0.81$ ,  $P = 0.4$ ; Fig. 4), but, consistent with analysis of PC1, display rates differed significantly among populations, with birds in India displaying at the lowest rates, birds in Siberia displaying at the highest rates, and birds in Kyrgyzstan displaying at intermediate rates ( $F_{2,214} = 11.17$ ,  $P < 0.001$ ; Fig. 4). In India, singing was thus the primary response to simulated intruders, with displays occurring comparatively infrequently. Farther north, males additionally displayed in response to playbacks, significantly so in Siberia, and produced these displays at higher rates than songs.

#### Geographical Variation in Individual Consistency

The overall intraclass correlation coefficient, which reflects within-individual repeatability of aggressive response, was fairly

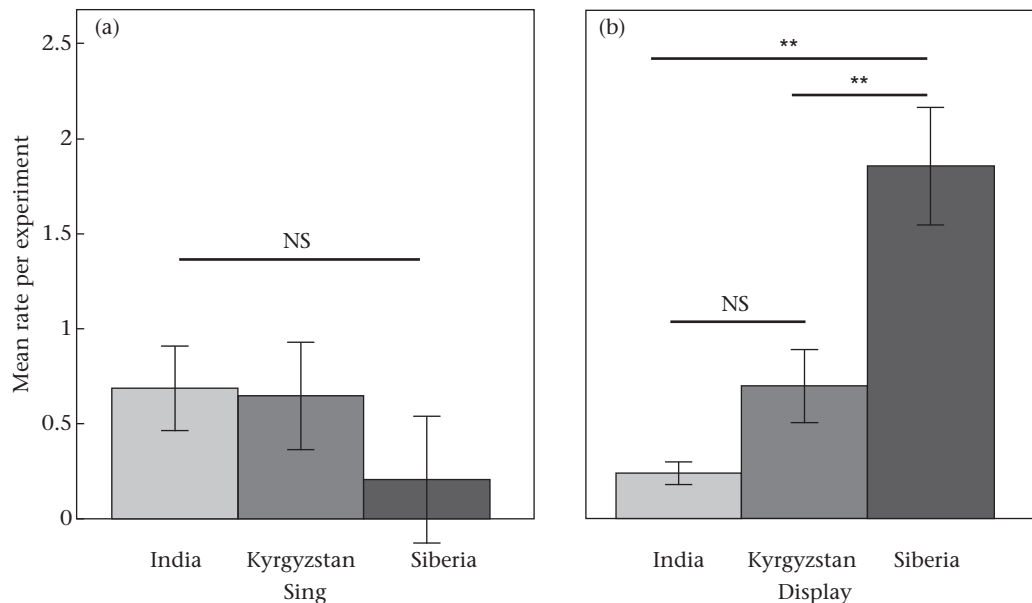
low and nonsignificant ( $r = 0.10$ ,  $P = 0.2$ ) when controlling for population. Intraclass correlation coefficients varied across sites when controlling for breeding stage. Repeatability of aggressive behaviour was very low in India ( $r = 0.008$ ,  $P = 1$ ) and in Siberia ( $r = 0.07$ ,  $P = 0.7$ ), and comparatively highest and significant (but still low overall) in Kyrgyzstan ( $r = 0.29$ ,  $P = 0.02$ ).

## DISCUSSION

Covariation between male competitive strategies and ecology has rarely been studied among natural populations (Qvarnström et al., 2012). I found that the intensity and seasonal pattern of territorial behaviour differed among three populations of greenish warblers living in habitats that varied in food abundance and population density. The population in India had consistently low food abundance over the course of the breeding season, whereas Kyrgyzstan and Siberia experienced a flush of insect food later in the season. Males were also three times denser in India compared to Siberia (Table 2), which should further exacerbate competition for scarce food in this population. The timing of male territory defence behaviour varied among populations and appeared to correspond to limitations in food versus mates. Intensity of aggressive behaviour peaked early and then declined at the two sites where food was abundant but mates were comparatively scarce. By contrast, aggressive behaviour remained constant throughout the season in food-scarce India, with males maintaining territory defence even while feeding chicks. The results imply that there is a shift in the function of male aggressive behaviour between populations, from food resource defence in India to mate guarding in Kyrgyzstan and Siberia.

Numerous ecological factors, including food abundance, population density, habitat and breeding synchrony, have been shown to affect both intensity of male aggressive behaviour and male territorial strategies across diverse taxa (Johnson, Revell, & Losos, 2010; Kneil, 2009; Kokko & Rankin, 2006; Kolluru & Grether, 2005). However, previous studies of interactions between male competition and ecology have produced diverse and often conflicting results (Kelly, 2008; Maher & Lott, 2000; Qvarnström et al., 2012). For example, the effects of resource scarcity on the intensity of aggressive behaviour depend on the limited resource. Food limitation sometimes decreases male aggressive behaviour, perhaps because poor-condition males cannot bear the costs of territory defence (Golabek et al., 2012), whereas nest site limitation typically increases aggressive behaviour and corresponding elaboration of traits used in competitive interactions (Borg, Forsgren, & Magnhagen, 2002; Forsgren et al., 1996; Jacot, Valcu, van Oers, &





**Figure 4.** Mean  $\pm$  SE number of (a) songs and (b) display behaviours per playback experiment produced by greenish warblers in India, Kyrgyzstan and Siberia. \*\* $P < 0.001$ .

Kempnaers, 2009; Wacker & Amundsen, 2014). Moreover, many biotic and abiotic factors covary geographically, with the consequence that multiple alternative hypotheses for how ecology shapes male competition have been difficult to tease apart (Maher & Lott, 2000; Singh & Price, 2015). By conducting a detailed study on a single species inhabiting a range of environments, I was able to control for some ecological differences (e.g. all populations are migratory and have the same mating system) and directly measure variation in others (food abundance, population density, breeding synchrony).

In a ground-nesting species such as *P. trochiloides*, nest sites are unlikely to be limited, but food availability varies among populations. If aggressive behaviour is used primarily to defend food resources necessary for raising offspring, males may be expected to guard their territories throughout the entire breeding season. This appears to be the case in India, where food abundance was low and territories were small. Food limitation translated to differences in paternal care as well, with male birds feeding nestlings at higher rates in India than in Kyrgyzstan, despite having smaller broods and lighter chicks. The food that parents brought to the nest was also smaller in India, suggesting limited access to high-quality resources. Finally, males in India primarily used long-range signals (singing) to communicate territory occupancy and respond to simulated intruders, rather than close-range aggressive displays. High encounter rates in the high-density, low-quality habitat of India may discourage repeated, costly physical interactions with neighbours. These patterns of aggressive behaviour are consistent with a study of juncos (*Junco hyemalis*), in which a migratory, high-altitude population has a shorter and more pronounced spike in aggression than a neighbouring lowland population that occupies a less seasonal environment (Newman, Yeh, & Price, 2006; Yeh, 2004), and males in the less seasonal environment contribute more parental care (Atwell, Cardoso, Whittaker, Price, & Ketterson, 2014).

In both Kyrgyzstan and Siberia, caterpillars are abundant, particularly later in the season, territories are large and population density is low. Since food is less limited at these sites, males are unlikely to guard resource-based territories. Instead, males direct aggressive displays towards simulated territorial intruders during peak female fertility, and then reduce their territorial behaviour

once females have mated and the chances of obtaining extrapair copulations are low. Although it was not possible to observe males following or directly guarding females, this pattern of aggressive behaviour is consistent with a mate/paternity defence strategy. Besides differing in food abundance, breeding was more synchronous in these populations (Table 2), a likely consequence of the longer migratory distance from the wintering grounds that should also affect male competitive strategies (Spottiswoode & Møller, 2004). Males in synchronously breeding populations have access to a pool of simultaneously fertile females, which has been found to decrease aggressive behaviour if males mate promiscuously and/or pursue extrapair copulations during periods of female fertility (Chuang-Dobbs et al., 2001; Grant et al., 1995), but increase aggressive behaviour if males mate-guard when females are fertile (Hammers et al., 2009; Michener & McLean, 1996). The effects of breeding synchrony on territorial strategies are thus shaped in part by population density and mate availability (Kneil, 2009; Kokko & Rankin, 2006; Thusius, Dunn, Peterson, & Whittingham, 2001). The early aggressive responses observed in Kyrgyzstan and Siberia imply that females in these populations are both scarce and simultaneously fertile. The combination of low population density and high breeding synchrony may lead males to mate-guard rather than pursue extrapair copulations with scarce females, as predicted by some models when female availability is low (Harts & Kokko, 2013).

My results add to the growing body of work showing that mating strategies are flexible within and among populations and vary according to limited ecological resources (e.g. Cotton, Small, & Pomiankowski, 2006; Jennions & Petrie, 1997; Kvarnemo & Simmons, 1999) as well as social and competitive contexts (Elias, Sivalinghem, Mason, Andrade, & Kasumovic, 2014; Jordan, Kokko, & Kasumovic, 2014). However, several recent studies have also established a heritable component to aggression, wherein the intensity of agonistic behaviour is consistently correlated with other behavioural or morphological traits, such as dispersal propensity (Duckworth & Kruuk, 2009) and colour morph (Bastiaans, Morinaga, Gaytán, Marshall, & Sinervo, 2013; While et al., 2015). These studies indicate the potential for selection to shape territorial strategies as part of broader phenotypic syndromes (Dingemanse et al., 2010; Luttbeg & Sih, 2010). I found some evidence for



repeatability of aggressive behaviour, particularly in Kyrgyzstan, which is a requirement for heritable variation and genetic evolution, although repeatabilities overall were low. Populations with high within-individual repeatabilities reflect males pursuing different competitive strategies within (as well as between) populations. For example, some individuals may aggressively mate-guard, whereas others might pursue extrapair copulations, depending on the combination of food availability, population density and breeding stage in that population. Nevertheless, the variation between populations was generally greater than variation within populations, supporting consistent among-population differences in competitive behaviour. Future work that measures the repeatability of aggressive behaviour across a larger sample size of birds and assesses the heritability of aggressive behaviour in *P. trochiloides* populations would help to determine the limits of plasticity in male competitive strategies and the extent to which these strategies can respond to selection.

Inconsistent effects reported in previous studies of associations between male aggressive behaviour and ecology may be attributed in part to multiple ecological variables leading to different optimal competitive strategies under different conditions and in different systems (Emlen & Oring, 1977; Härdling et al., 2004; Head, Lindholm, & Brooks, 2007; Thusius et al., 2001; Wacker & Amundsen, 2014). I have shown that in a socially monogamous, migratory bird with biparental care, seasonal patterns of male response to intruder song differ among populations. These changes appear to be concordant with differences in multiple ecological variables, suggesting an among-population shift in the function of territory defence. The results underscore the importance of assaying temporal variation in behaviour within as well as between populations. Intensive monitoring over an entire breeding season meant that it was not possible to study the same population in different years. However, my findings are consistent with Irwin (2000), who visited sites near all of my study populations in the 1990s and found the same variation in caterpillar abundance, population density and forest structure. Ecological variation thus appears to be much greater between sites than within sites across years, which is expected given the large geographical scale of the study.

Sexual selection has been suggested to drive song divergence and associated premating reproductive isolation in *P. trochiloides*, primarily because males do not respond to playbacks of heterotypic songs (Irwin, 2000). The patterns of male response to local conspecific songs observed in this study suggest that changes in intrasexual competition across environments may initiate or maintain population divergence despite ongoing gene flow. Male competition is often overlooked as a diversifying force, but inter-population variation in competitive phenotypes can reduce gene flow if, for example, immigrant males are unable to successfully defend territories and thus cannot attract mates (Dijkstra, Hemelrijk, Seehausen, & Groothuis, 2009; Drury, Okamoto, Anderson, & Grether, 2015; Pearson & Rohwer, 2000; Slabbekoorn & Smith, 2002). In *P. trochiloides*, males that sing rather than display in response to a conspecific challenge, or that fail to maintain territory defence in food-limited habitats, might suffer fitness reductions. Although sexual selection may be a strong force driving divergence in *P. trochiloides*, both mate choice and male competition occur on an ecological stage, and thus the direction and form these selective pressures take will inevitably be shaped by environmental variation. Male aggressive behaviour in this system varies in both strength and function in different environments. The next step in understanding how male competition contributes to population divergence is to determine how variation in aggressive behaviour affects reproductive success and shapes traits involved in premating isolation.

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## References

- Alcaide, M., Scordato, E. S. C., Price, T. D., & Irwin, D. E. (2014). Genomic divergence in a ring species complex. *Nature*, *511*, 83–85.
- Andersson, M. B. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Price, T. D., & Ketterson, E. D. (2014). Hormonal, behavioral, and life-history traits exhibit correlated shifts in relation to population establishment in a novel environment. *American Naturalist*, *184*(6), E147–E160. <http://www.jstor.org/stable/10.1086/678398>.
- Bastiaans, E., Morinaga, G., Gaytán, J. G. C., Marshall, J. C., & Sinervo, B. (2013). Male aggression varies with throat color in 2 distinct populations of the mesquite lizard. *Behavioral Ecology*, *24*(4), 968–981. <http://dx.doi.org/10.1093/beheco/art010>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., et al. (2015). *lme4: Linear mixed-effects models using 'Eigen' and S4 (R Package)*. Vienna, Austria: R Foundation for Statistical Computing. <https://cran.r-project.org/web/packages/lme4/index.html>.
- Borg, Å. A., Forsgren, E., & Magnhagen, C. (2002). Plastic sex-roles in the common goby: The effect of nest availability. *Oikos*, *98*(1), 105–115.
- Catchpole, C. K. (1982). The evolution of bird sounds in relation to mating and spacing behavior. *Acoustic Communication in Birds*, *1*, 297–319.
- Catchpole, C. K., & Slater, P. J. (2008). *Bird song: Biological themes and variations* (2nd ed.). Cambridge, U.K.: Cambridge University Press.
- Chuang-Dobbs, H. C., Webster, M. S., & Holmes, R. T. (2001). The effectiveness of mate guarding by male black-throated blue warblers. *Behavioral Ecology*, *12*(5), 541–546.
- Cotton, S., Small, J., & Pomiankowski, A. (2006). Sexual selection and condition-dependent mate preferences. *Current Biology*, *16*(17), R755–R765.
- Dijkstra, P. D., Hemelrijk, C., Seehausen, O., & Groothuis, T. G. G. (2009). Color polymorphism and intrasexual competition in assemblages of cichlid fish. *Behavioral Ecology*, *20*(1), 138–144.
- Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*(2), 81–89.
- Drury, J. P., Okamoto, K. W., Anderson, C. N., & Grether, G. F. (2015). Reproductive interference explains persistence of aggression between species. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1804), 20142256.
- Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, *17*(6), 1011–1019.
- Duckworth, R. A., & Kruuk, L. E. B. (2009). Evolution of genetic integration between dispersal and colonization ability in a bird. *Evolution*, *63*(4), 968–977.
- Elias, D. O., Sivalinghem, S., Mason, A. C., Andrade, M. C. B., & Kasumovic, M. M. (2014). Mate-guarding courtship behaviour: Tactics in a changing world. *Animal Behaviour*, *97*, 25–33.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223.
- Forsgren, E., Kvarnemo, C., & Lindstrom, K. (1996). Mode of sexual selection determined by resource abundance in two sand goby populations. *Evolution*, *50*(2), 646–654.
- Golabek, K. A., Ridley, A. R., & Radford, A. N. (2012). Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. *Animal Behaviour*, *83*, 613–619.
- Grant, J. W., Bryant, M. J., & Soos, C. E. (1995). Operational sex ratio, mediated by synchrony of female arrival, alters the variance of male mating success in Japanese medaka. *Animal Behaviour*, *49*, 367–375.
- Grether, G. F. (2011). The neuroecology of competitor recognition. *Integrative and Comparative Biology*, *51*(5), 807–818.
- Hails, C. J. (1982). A comparison of tropical and temperate aerial insect abundance. *Biotropica*, *14*(4), 310–313.
- Hammers, M., von Engelhardt, N., Langmore, N. E., Komdeur, J., Griffith, S. C., & Magrath, M. J. L. (2009). Mate-guarding intensity increases with breeding

- synchrony in the colonial fairy martin, *Petrochelidon ariel*. *Animal Behaviour*, 78, 661–669.
- Hårdling, R., Kokko, H., & Elwood, R. W. (2004). Priority versus brute force: When should males begin guarding resources? *American Naturalist*, 163(2), 240–252.
- Harts, A. M. F., & Kokko, H. (2013). Understanding promiscuity: When is seeking additional mates better than guarding an already found one? Mate-guarding, monogamy, and promiscuity. *Evolution*, 67, 2838–2848.
- Head, M. L., Lindholm, A. K., & Brooks, R. (2007). Operational sex ratio and density do not affect directional selection on male sexual ornaments and behavior: Demographic effects on sexual selection. *Evolution*, 62(1), 135–144.
- Irwin, D. E. (2000). Song variation in an avian ring species. *Evolution*, 54(3), 998–1010.
- Irwin, D. E. (2005). Speciation by distance in a ring species. *Science*, 307(5708), 414–416.
- Irwin, D. E., Bensch, S., & Price, T. D. (2001). Speciation in a ring. *Nature*, 409(6818), 333–337.
- Jacot, A., Valcu, M., van Oers, K., & Kempenaers, B. (2009). Experimental nest site limitation affects reproductive strategies and parental investment in a hole-nesting passerine. *Animal Behaviour*, 77, 1075–1083.
- Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews*, 72(2), 283–327.
- Jirotkul, M. (1999). Population density influences male–male competition in guppies. *Animal Behaviour*, 58, 1169–1175.
- Johnson, M. A., Revell, L. J., & Losos, J. B. (2010). Behavioral convergence and adaptive radiation: Effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution*, 64(4), 1151–1159.
- Jordan, L. A., Kokko, H., & Kasumovic, M. (2014). Reproductive foragers: Male spiders choose mates by selecting among competitive environments. *American Naturalist*, 183(5), 638–649.
- Katti, M., & Price, T. D. (2003). Latitudinal trends in body size among over-wintering leaf warblers (genus *Phylloscopus*). *Ecography*, 26(1), 69–79.
- Kelly, C. D. (2008). The interrelationships between resource-holding potential, resource-value and reproductive success in territorial males: How much variation can we explain? *Behavioral Ecology and Sociobiology*, 62(6), 855–871.
- Kempenaers, B. (1993). The use of a breeding synchrony index. *Ornis Scandinavica*, 24(1), 84.
- Knell, R. J. (2009). Population density and the evolution of male aggression. *Journal of Zoology*, 278(2), 83–90.
- Kokko, H., & Rankin, D. J. (2006). Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1466), 319–334.
- Kolluru, G. R., & Grether, G. F. (2005). The effects of resource availability on alternative mating tactics in guppies (*Poecilia reticulata*). *Behavioral Ecology*, 16(1), 294–300.
- Kolluru, G. R., Grether, G. F., & Contreras, H. (2007). Environmental and genetic influences on mating strategies along a replicated food availability gradient in guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, 61(5), 689–701.
- Kroodsmá, D. E. (1990). Using appropriate experimental designs for intended hypotheses in 'song' playbacks, with examples for testing effects of song repertoire sizes. *Animal Behaviour*, 40, 1138–1150.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2013). *lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package) (R Package)*. Vienna, Austria: R Foundation for Statistical Computing. <https://CRAN.R-project.org/package=lmerTest>.
- Kvarnemo, C., & Simmons, L. W. (1999). Variance in female quality, operational sex ratio and male mate choice in a bushcricket. *Behavioral Ecology and Sociobiology*, 45(3–4), 245–252.
- Kwiatkowski, M. A., & Sullivan, B. K. (2002). Geographic variation in sexual selection among populations of an iguanid lizard, *Sauromalus obesus* (= *ater*). *Evolution*, 56(10), 2039–2051.
- Lackey, A. C. R., & Boughman, J. W. (2013). Divergent sexual selection via male competition: Ecology is key. *Journal of Evolutionary Biology*, 26(8), 1611–1624.
- Luttbegg, B., & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3977–3990.
- Maan, M. E., & Seehausen, O. (2011). Ecology, sexual selection and speciation. *Ecology Letters*, 14(6), 591–602.
- MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42(3), 594–598.
- Maher, C. R., & Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist*, 143(1), 1–29.
- Martin, T. E. (1987). Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics*, 18, 453–487.
- Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, 65(1), 101–127.
- Martin, M. D., & Mendelson, T. C. (2016). Male behaviour predicts trait divergence and the evolution of reproductive isolation in darters (Percidae: *Etheostoma*). *Animal Behaviour*, 112, 179–186.
- Michener, G. R., & McLean, I. A. N. (1996). Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. *Animal Behaviour*, 52, 743–758.
- Newman, M. M., Yeh, P. J., & Price, T. D. (2006). Reduced territorial responses in dark-eyed juncos following population establishment in a climatically mild environment. *Animal Behaviour*, 71, 893–899.
- Panhuis, T. M., Butlin, R., Zuk, M., & Tregenza, T. (2001). Sexual selection and speciation. *Trends in Ecology & Evolution*, 16(7), 364–371.
- Pearson, S. F., & Rohwer, S. (2000). Asymmetries in male aggression across an avian hybrid zone. *Behavioral Ecology*, 11(1), 93–101.
- Price, T. (1991). Morphology and ecology of breeding warblers along an altitudinal gradient in Kashmir, India. *Journal of Animal Ecology*, 60, 643–664.
- Price, T. D., Helbig, A. J., & Richman, A. D. (1997). Evolution of breeding distributions in the old world leaf warblers (genus *Phylloscopus*). *Evolution*, 51(2), 552–561.
- Qvarnström, A., Vallin, N., & Rudh, A. (2012). The role of male contest competition over mates in speciation. *Current Zoology*, 58(3), 493–509.
- Rabenold, K. N. (1978). Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. *Ecological Monographs*, 48(4), 397–424.
- Reichard, M., Ondračková, M., Bryjová, A., Smith, C., & Bryja, J. (2009). Breeding resource distribution affects selection gradients on male phenotypic traits: An experimental study on lifetime reproductive success in the bitterling fish (*Rhodeus amarus*). *Evolution*, 63(2), 377–390.
- Safran, R. J., Scordato, E. S. C., Symes, L. B., Rodriguez, R. L., & Mendelson, T. C. (2013). Contributions of natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. *Trends in Ecology & Evolution*, 28(11), 643–650.
- Scordato, E. S. C. (2012). *Geographical and temporal variation in sexually selected traits: Environmental variation, multiple signals, and consequences for population divergence* (Ph.D. thesis). Chicago, IL: The University of Chicago.
- Scordato, E. S. C., Symes, L. B., Mendelson, T. C., & Safran, R. J. (2014). The role of ecology in speciation by sexual selection: A systematic empirical review. *Journal of Heredity*, 105(Suppl. 1), 782–794.
- Seddon, N., & Tobias, J. A. (2007). Song divergence at the edge of Amazonia: An empirical test of the peripatric speciation model. *Biological Journal of the Linnean Society*, 90(1), 173–188.
- Singh, P., & Price, T. D. (2015). Causes of the latitudinal gradient in birdsong complexity assessed from geographical variation within two Himalayan warbler species. *Ibis*, 157(3), 511–527.
- Slabbekoorn, H., & Smith, T. B. (2002). Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1420), 493–503.
- Spottiswoode, C., & Møller, A. P. (2004). Extrapair paternity, migration, and breeding synchrony in birds. *Behavioral Ecology*, 15(1), 41–57.
- Thusius, K. J., Dunn, P. O., Peterson, K. A., & Whittingham, L. A. (2001). Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. *Behavioral Ecology*, 12(5), 633–639.
- Tobias, J. A., Gamarra-Toledo, V., Garcia-Olaechea, D., Pulgarin, P. C., & Seddon, N. (2011). Year-round resource defence and the evolution of male and female song in subsocial birds: Social armaments are mutual ornaments. *Journal of Evolutionary Biology*, 24(10), 2118–2138.
- Uy, J. A. C., Moyle, R. G., & Filardi, C. E. (2009). Plumage and song differences mediate species recognition between incipient flycatcher species of the Solomon Islands. *Evolution*, 63(1), 153–164.
- Wacker, S., & Amundsen, T. (2014). Mate competition and resource competition are inter-related in sexual selection. *Journal of Evolutionary Biology*, 27(3), 466–477.
- Wacker, S., Mobley, K., Forsgren, E., Myhre, L. C., de Jong, K., & Amundsen, T. (2013). Operational sex ratio but not density affects sexual selection in a fish: Effects of OSR and density on sexual selection. *Evolution*, 67(7), 1937–1949.
- Wauters, L. A., Bertolino, S., Adamo, M., Dongen, S. V., & Tosi, G. (2005). Food shortage disrupts social organization: The case of red squirrels in conifer forests. *Evolutionary Ecology*, 19(4), 375–404.
- Weir, L. K., Grant, J. W. A., & Hutchings, J. A. (2011). The influence of operational sex ratio on the intensity of competition for mates. *American Naturalist*, 177(2), 167–176.
- West-Eberhard, M. J. (1983). Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, 48, 155–183.
- While, G. M., Michaelides, S., Heathcote, R. J., MacGregor, H. E., Zajac, N., Beninde, J., et al. (2015). Sexual selection drives asymmetric introgression in wall lizards. *Ecology Letters*, 18(12), 1366–1375.
- Wong, B. B. M., & Candolin, U. (2005). How is female mate choice affected by male competition? *Biological Reviews*, 80(4), 559–571.
- Wood, S. (2012). *mgcv: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation (R Package)*. Vienna, Austria: R Foundation for Statistical Computing. <https://stat.ethz.ch/R-manual/R-devel/library/mgcv/html/mgcv-package.html>.
- Yeh, P. J. (2004). Rapid evolution of a sexually selected trait following population establishment in a novel habitat. *Evolution*, 58(1), 166–174.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. In M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, & W. Wong (Eds.). New York, NY: Springer Science and Business Media.