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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.

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 (Härdling, 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.

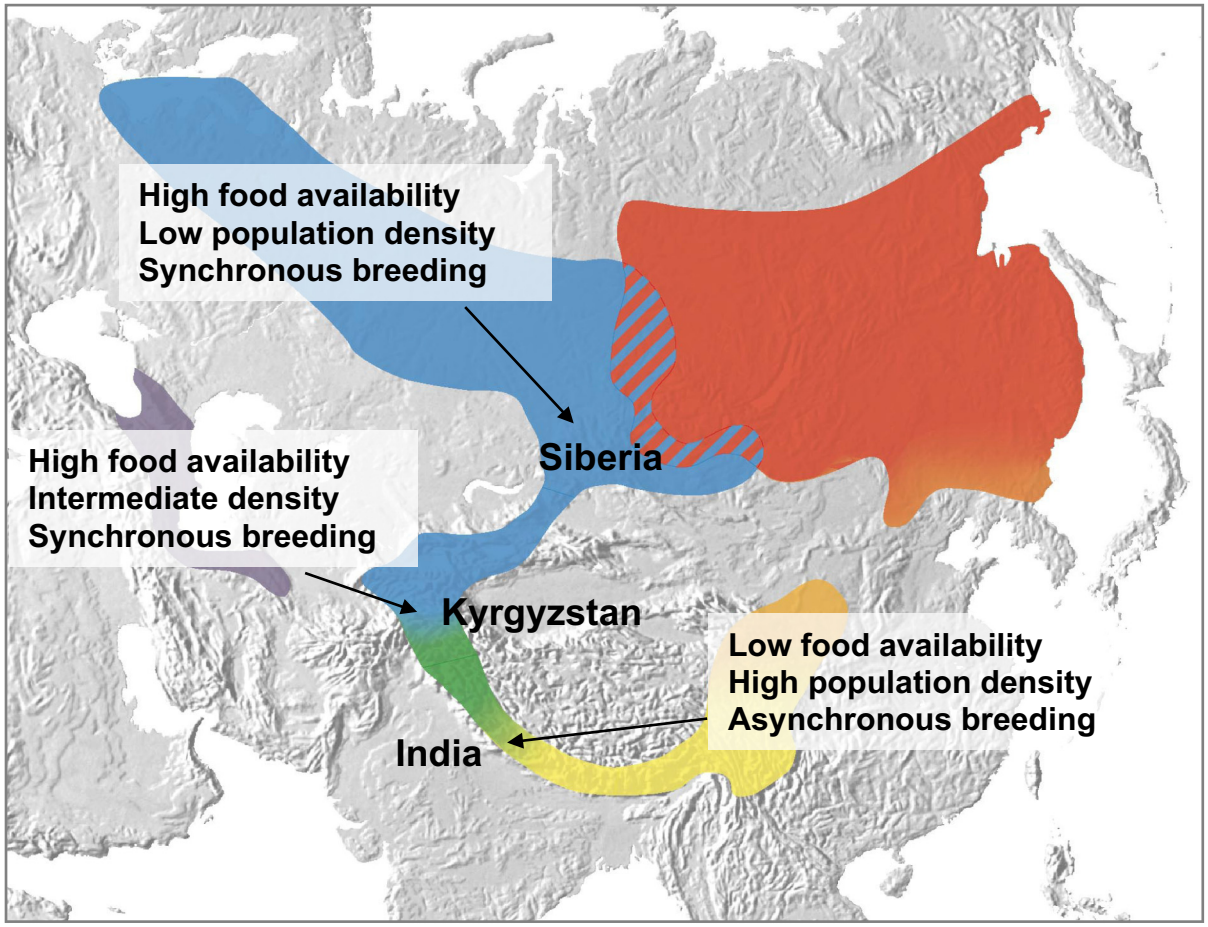

Figure 1. Map of the greenish warbler breeding range. Study sites in India, Kyrgyzstan and Siberia are marked with arrows. Ecological characteristics for each site are summarized. Adapted from Irwin et al. (2001).