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Extrapair paternity in a far northern population of Yellow Warblers Dendroica petechia

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The proportion of extrapair paternity is known to vary greatly among species, but differences between populations of the same species have rarely been considered. We used microsatellite DNA markers to assess parentage of offspring in a subarctic population of the socially monogamous Yellow Warbler Dendroica petechia nesting near Churchill, Manitoba. We found a significantly lower proportion of extrapair young in the Churchill population than in a temperate population nesting approximately 1500 km to the south near the Queen’s University Biological Station (QUBS) in Ontario. We show that the Churchill population also had significantly lower nesting density and significantly higher breeding synchrony; both are factors that have been hypothesized to affect extrapair paternity negatively. We suggest that inter-population comparisons can be used to test proximate mechanisms affecting extrapair paternity and in some cases may be better than interspecific or inter-individual comparisons. Towards this end we list eight other species that have had extrapair paternity measured in different populations.

Studies that use genetic markers to assess the parentage of offspring have shown that extrapair paternity occurs in a wide range of bird species and that there is considerable interspecific variation in the proportion of offspring fathered by extrapair males (see Westneat and Sherman 1997). Understanding the variation in extrapair paternity has become a focus of mating system research. Nearly all species studied to date, however, have had extrapair paternity measured in only one population. Thus, it is not known much of the apparent interspecific variation in extrapair paternity might be due to variation between populations within a species. For example, in the Willow Warbler Phylloscopus trochilus, the proportion of extrapair paternity differs considerably between a population in Sweden (0%; Gyllensten et al. 1990) and one in Norway (33%; Bjornstad and Lifjeld 1997). In this study we use microsatellite DNA markers to assess the parentage of offspring in a far northern population of the socially monogamous Yellow Warbler Dendroica petechia. Our first aim was to test whether the proportion of extrapair paternity in this population at the northern edge of the species' range differs from the 33% extrapair paternity in a population 1500 km to the south (Yezerinac et al. 1995).

Nesting density and breeding synchrony are the most likely proximate causes of variation in the proportion of extrapair paternity (Westneat and Sherman 1997). However, evidence is mixed regarding the effect of either factor. Between-species comparisons provide no evidence that density affects extrapair paternity, whereas comparison of individuals nesting at different densities in the same population does suggest that density sometimes positively affects extrapair paternity (see Westneat and Sherman 1997). The apparent effect of synchrony on extrapair paternity is also debatable based upon results of interspecific and intraspecific studies (see Westneat and Sherman 1997, Stutchbury 1998, Weatherhead and Yezerinac 1998). In this study we measured nesting density and breeding synchrony within each of the two populations for which extrapair paternity was measured. Our second aim was to determine if there were synchrony and density differences between the populations that might explain any differences in extrapair paternity.

Methods

We studied the nesting biology of Yellow Warblers near Churchill, Manitoba (58°40'N, 94°25'W) and near the Queen’s University Biological Station (QUBS), Chaffey’s Locks, Ontario (44°34'N, 76°20'W). Field work at Churchill began in late May or early June and at QUBS in early May, and continued at both sites until mid- to late-July, thus spanning the period from
arrival on the breeding grounds through to the fledging of young (see Briskie 1995, Yezerinac et al. 1995).

For parentage analysis we collected blood samples from adults and nestlings at 12 nests at Churchill in 1994, and at 130 nests at QUBS from 1992 to 1994. We collected blood from all broods within our study areas that reached the age for sampling. The collection of blood, extraction of DNA, execution of multi-locus DNA fingerprinting, and results of parentage analysis for the QUBS population have been described in detail (see Yezerinac et al. 1995, 1996). The same methods were used for Churchill, except that all nestlings were bled at between 4 and 6 days of age, and we used microsatellite loci for parentage analysis. Specifically, we genotyped parents and young using three Yellow Warbler-specific loci (Dpy 01, 15 and 16; see Dawson et al. 1997) and one Brown-headed Cowbird Molothrus ater locus (Ma5 28; see Gibbs et al. 1997) following the protocols described in Dawson et al. (1997). These loci are all highly variable in Yellow Warblers and provide an accurate system for determination of parentage; the probability of detecting extrapair fertilization given known maternity in the Churchill population was 0.991 (see Dawson et al. 1997). We examined each Churchill nestling’s genotype at each of the four loci for novel alleles not found in the putative parents; if any novel alleles were found we then determined whether the pattern across all loci was consistent with inheritance by extrapair paternity and true maternity (see Dawson et al. 1997 for methods).

To estimate breeding synchrony we found nests by regularly searching areas where males were singing and by following females to nests. We determined clutch initiation dates by direct observation or by backdating using clutch size, date of hatching, and the average incubation period (Briskie 1995, Yezerinac et al. 1995). From these data we calculated an index of breeding synchrony (see Yezerinac and Weatherhead 1997a for details) for each population for each year. The synchrony index accounts for differences in sample size and the duration of the female’s fertile period and provides a standardized measure of the average percentage of females that were fertile per day during the breeding season. The index ranges from 0% when females are fertile at different times to 100% when all females are fertile at the same time. We defined the female fertile period as beginning either 5 days before the first egg was laid or the day a previous nesting attempt failed (whichever was later), and lasting until the day the penultimate egg was laid.

Nesting density was measured as the distance between the approximate centerpoint of neighboring territories. We measured the distance between the centers of adjacent territories only in study areas where we collected blood for parentage analysis and in which all adults were banded. At Churchill this area included 10 territories in 1994; at QUBS it included 20 territories in each year from 1992 to 1994.

Results

Genetic results showed no maternal mismatches with any nestlings in either population. At Churchill we found extrapair paternity in 25% of 12 nests (95% CL = 5–57%). At QUBS extrapair paternity occurred in 53.8% of 130 nests (95% CL = 45–63%; yearly range 40–59%; Yezerinac et al. 1996). This difference in the proportion of broods with any extrapair paternity is almost statistically significant (G = 3.797, P = 0.051, d.f. = 1).

Among the 53 nestlings from Churchill, 13% (95% CL = 5–25%) were sired by an extrapair male. The distribution of extrapair young among the 12 broods was not significantly different from random (χ² = 7.75, P = 0.10; analytical methods in Yezerinac et al. 1995, p. 184). At QUBS 33.1% of 484 nestlings (95% CL = 30–37%; yearly range 22–43%) were sired by an extrapair male and extrapair young were non-randomly distributed among nests (χ² = 49.89, P < 0.001, d.f. = 4; Yezerinac et al. 1995). We compared the proportion of offspring that were extrapair sired between the two populations using broods as the unit of replication. We employed regression with binomial errors and a logit link function (Crawley 1993, p. 265). The average frequency of extrapair paternity in a brood was significantly lower in the Churchill population (χ² = 9.749, P = 0.002, d.f. = 1).

The average distance between territory centers was significantly larger at Churchill (149.5 m, 95% CL = 93.2–205.8 m, n = 9) than at QUBS (54.8 m, 95% CL = 51.1–58.5 m, n = 57; t = 12.23, P < 0.001). As a result, the density of breeding pairs at QUBS (3.9 pairs/ha) was almost ten times that at Churchill (0.42 pairs/ha).

In the years in which parentage was measured, the average proportion of females that were fertile per day (synchrony index) was significantly higher at Churchill (72%, 95% CL = 63.2–81.2%, n = 22) than at QUBS (40.4%, 95% CL = 38–42.8%, n = 130; Mann-Whitney U = 347, z = 5.67, P < 0.001).

Discussion

The Yellow Warbler has one of the most widespread, continuous breeding ranges of any North American passerine. It breeds in habitats as diverse as mangrove swamps, hardwood forest wetlands and the subarctic treeline. In this study of the Churchill, Manitoba population at the northern edge of the breeding range we found less extrapair paternity, greater nesting synchrony and lower nesting density than at QUBS in
Ontario, a population in the center of the species’ range. These results add to a small but growing dataset containing measures of extrapair paternity in geographically separate populations of the same species. These data show that genetic mating systems vary within species, sometimes as much as they do among species (see Phylloscopus trochilus, Gyllensten et al. 1990, Bjørnstad and Lifjeld 1997; Ficedula hypoleuca, Gelter and Tegelström 1992, Lifjeld et al. 1991, Ellegren et al. 1995; Parus major, Lubjuhn et al. 1993, Blakey 1994, Verboven and Mateman 1997; Agelaius phoeniceus, Gibbs et al. 1990, Westneat 1993, Gray 1996; Stilts sialis, Gowaty and Bridges 1991, Meek et al. 1994; Tachycineta bicolor, Dunn et al. 1994; Sturnus vulgaris, Pinxten et al. 1993, Smith and von Schantz 1993; Delichon urbica, Riley et al. 1995, Whittingham and Lifjeld 1995). Thus, inter-population comparisons can be used in the same manner that inter-specific comparisons have been used to study proximate effects on extrapair paternity. Such an inter-population approach has two advantages over comparisons between species or between individuals within a population. The closer phylogenetic relationships between populations than between species should reduce the likelihood that evolutionary changes rather than proximate effects of density and synchrony account for differences in extrapair paternity. Second, when comparing populations, differences in synchrony and density are independent of differences in individual quality that may confound non-experimental comparisons of extrapair paternity between individuals within populations.

Nesting density at Churchill was almost an order of magnitude lower than at QUBS, probably due to habitat and climatic differences. Decreased breeding density presumably reduces the frequency of direct interactions between residents of adjacent territories, and is thereby expected to reduce opportunities for extrapair mating. Thus, the higher extrapair paternity and density at QUBS versus Churchill, is consistent with the hypothesis that density positively affects extrapair paternity.

Nesting synchrony in Yellow Warblers at Churchill averaged about 50% higher than at QUBS, probably because the time available for breeding in the subarctic is approximately 3 to 4 weeks shorter than that for warblers in temperate populations and because spring weather synchronizes the start of nesting (Briskie 1995). The higher synchrony, along with lower extrapair paternity at Churchill, is consistent with the hypothesis that synchrony negatively affects extrapair paternity.

As synchrony and density both differ substantially between our two populations, distinguishing their separate effects is not possible. Moreover, as only two populations were compared it is possible that chance or correlated factors other than synchrony and density influenced extrapair paternity. However, this result indicates that comparisons using a number of different populations in which density and synchrony do not differ in the same ways could distinguish the effects of synchrony and density. Indeed, such an inter-population approach is possible with Yellow Warblers as they nest at a wide variety of densities over their breeding range, including a reported high of 19.1 pairs/ha at Delta Marsh, in southern Manitoba (Goossen and Sealy 1982), which is almost five times greater than the density of warblers at QUBS (3.9 pairs/ha).

Finally, the fact that males and females can alter their reproductive success through extrapair mating has focused attention on extrapair paternity as a cause of sexual selection, particularly in socially monogamous species. At Churchill, a lower proportion of females had extrapair paternity in their broods and extrapair paternity was lower overall. Thus, the potential for sexual selection through extrapair mating was lower. At QUBS, extrapair paternity produced sexual selection on male plumage and body size (Yezerinac and Weatherhead 1997b). Comparison of these and other populations for differences in extrapair mating behavior, and sexually selected characters such as song, plumage and size could be useful for understanding the relationship between sexual selection and extrapair mating.

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