Genetic mating system and population history of the endangered Western Yellow-breasted Chat (*Icteria virens auricollis*) in British Columbia, Canada

Carolina I. Miño, Ingrid L. Pollet, Christine A. Bishop, and Michael A. Russello

Abstract: The Western Yellow-breasted Chat (*Icteria virens auricollis* (Deppe, 1830)) is a Neotropical migrant, with a Canadian distribution restricted to breeding populations in southern British Columbia. Given its small population size and diminishing breeding habitat, Yellow-breasted Chats are federally endangered in Canada. We used genotypic data at eight microsatellite loci to assess genetic diversity, reconstruct population structure and demographic history, and characterize genetic mating system of Yellow-breasted Chats sampled across 60 nesting sites at five locations in the Okanagan Valley ($n = 148$). Microsatellite-based analyses indicated lack of significant genetic differentiation among breeding sites and no genetic evidence of population decline. Parentage assignments indicated moderate levels of extra-pair paternity, with 30.7% offspring not sired by attending males. Patterns of sibship among nestlings revealed 49.1% of the clutches were composed entirely of full-siblings, with half-siblings and unrelated nestlings present in some broods. These findings suggest that extra-pair paternity is common in Yellow-breasted Chats, similar to other avian species, and present the first evidence of conspecific brood parasitism in warblers. Our findings add to a growing body of research informing the need to establish a national park in the south Okanagan to preserve critical habitat and connect populations of species at risk.

Résumé : La paruline polyglotte de l'Ouest (*Icteria virens auricollis* (Deppe, 1830)) est un migrateur néotropical dont la répartition au Canada se limite à des populations reproductrices dans le sud de la Colombie-Britannique. À cause de la petite taille de la population et de la réduction de son habitat de reproduction, la paruline polyglotte est considérée une espèce à risque au Canada au sens de la loi fédérale. Des données génotypiques à huit locus microsatellites nous ont permis d'évaluer la diversité génétique, de reconstituer la structure de la population et son histoire démographique et de caractériser le système génétique d'accouplement de parulines polyglottes échantillonnées dans 60 sites de nidification à cinq localités dans la vallée de l'Okanagan ($n = 148$). Les analyses basées sur les microsatellites indiquent une absence de différenciation génétique significative entre les sites de reproduction et aucune indication génétique de déclin de la population. Les déterminations de filiation révèlent un niveau modéré de paternité à l'extérieur des couples, puisque 30,7 % des rejetons n'ont pas comme père le mâle qui veille au nid. Les patrons de fratrie chez les petits au nid révèlent que 49,1 % des couvées sont composées entièrement de rejetons de même fratrie et qu'il y a des individus de demi-fratrie et des individus non apparentés dans certaines couvées. Ces observations indiquent que la paternité hors du couple est courante chez les parulines polyglottes, comme chez d'autres espèces d'oiseaux; elles présentent aussi les premières preuves de parasitisme de reproduction conspécifique chez les parulines. Nos résultats s'ajoutent à un ensemble croissant de recherches qui établissent la nécessité de créer un parc national dans le sud de l'Okanagan afin de préserver des habitats critiques et relier entre elles les populations d'espèces à risque.

[Traduit par la Rédaction]

Introduction

Yellow-breasted Chats (*Icteria virens* (L., 1758)) are large, Neotropical migratory warblers with a transcontinental breeding distribution that extends from southwestern Canada south into northern and central Mexico. Two subspecies have been described, differing subtly in size, plumage coloration, and song structure (Eckerle and Thompson 2001), as well as genetically (Lovette et al. 2004). The eastern subspecies (*Icteria virens virens* (L., 1758); Lowery and Monroe 1968; American Ornithologists' Union 1998) breeds in eastern North America and is distributed continuously from the Atlantic

C.I. Miño* and M.A. Russello. Department of Biology, The University of British Columbia, Okanagan Campus, 3333 University Way, Kelowna, BC V1V 1V7, Canada.
**I.L. Pollet.** Department of Biology, Acadia University, 33 Westwood Avenue, Wolfville, NS B4P 2R6, Canada.
C.A. Bishop. Environment Canada, Science and Technology Branch, 5421 Robertson Road, Delta, BC V4K 3N2, Canada.

Corresponding author: M.A. Russello (e-mail: michael.russello@ubc.ca).

*Present address: Departamento de Genética e Evolução, Universidade Federal de São Carlos–UFSCar, Rodovia Washington Luis km 235 SP-310, 13.565-905, São Carlos, SP, Brazil.

doi:10.1139/Z11-061
Published by NRC Research Press

Fig. 1. Locations of Western Yellow-breasted Chats (*Icteria virens auricollis*) sampled in the Okanagan and Similkameen Valleys, British Columbia, Canada: Penticton (PEN); Inkameep (INK); Oliver (OLI); Fairview (FAI); south Okanagan (SOW); and Trail (TRA). Number of territories, nesting sites, and samples collected per location are summarized in Table 1. Detailed information for each sample is presented in supplementary Table S1.
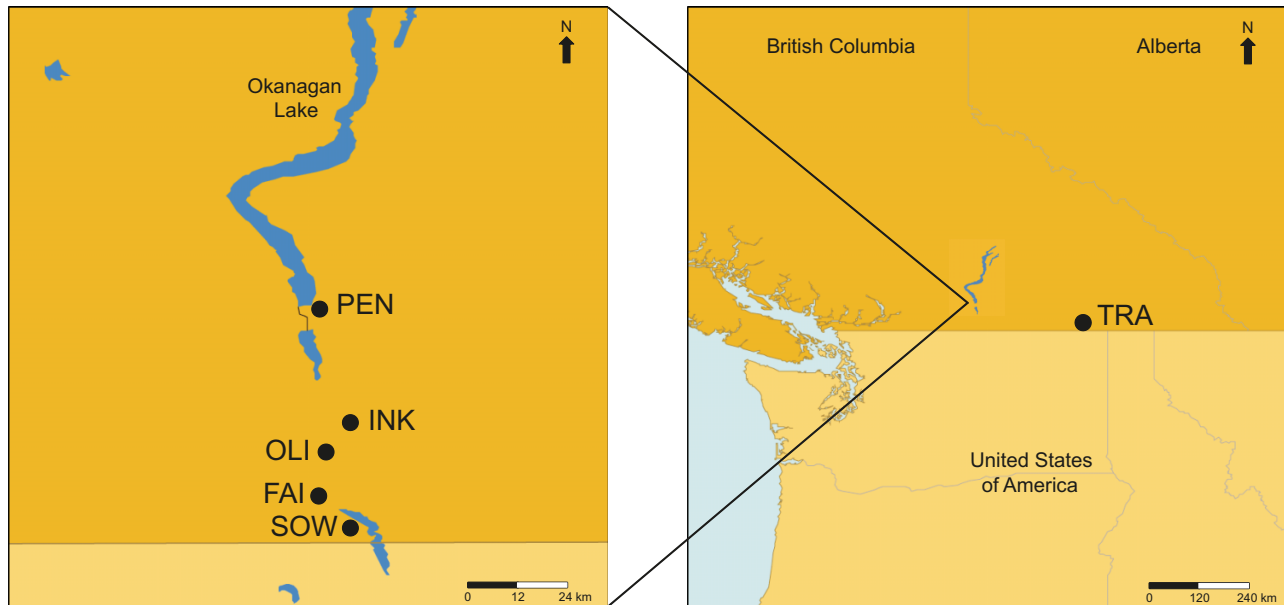
coast to the Great Plains. The western subspecies (*Icteria virens auricollis* (Deppe, 1830)) breeds discontinuously throughout western North America, with its northernmost breeding distribution stretching 150 km into southern British Columbia (BC). Specifically, Canadian Western Yellow-breasted Chats are restricted to densely vegetated riparian breeding sites in interior BC, primarily in the south Okanagan and Similkameen Valleys. Although chats were common in riparian areas as recently as 1920s (Cannings et al. 1987), dense thickets of wild rose (genus *Rosa* L.) and early successional riparian habitat that existed in 1938 has been reduced by more than 80% since the 1990s (Lea 2008) because of widespread habitat conversion. Currently, there are only an estimated 152 breeding pairs of Western Yellow-breasted Chats in BC (Environment Canada 2010). The BC population of this subspecies is federally listed as endangered under the *Species At Risk Act* (COSEWIC 2009). Despite their tenuous status, little is known about the breeding behavior and population history of Western Yellow-breasted Chats from BC.

Western Yellow-breasted Chats typically lay 3–6 eggs (mean of 3.5 eggs in the Okanagan; Morgan et al. 2007) incubated only by the females. Young are fed by both sexes after hatching and the longevity of this species has been estimated at 5–6 years in the Okanagan Valley (McKibbin and Bishop 2008a). This species is particularly vulnerable to brood parasitism from Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783)) (Friedmann 1963), Bronzed Cowbirds (*Molothrus aeneus* (Wagler, 1829)) (Friedmann et al. 1977), and Black-billed Cuckoos (*Coccyzus erythropthalmus* (A. Wilson, 1811)) (Thomas 1995).

In BC, breeding sites of Western Yellow-breasted Chat are

exclusively found in low-lying (<500 m) riparian areas in the south Okanagan and south Similkameen Valleys, from Kelowna to Osoyoos, and a small disjunct breeding population (≤8 breeding pairs) as far east as Waneta near the town of Trail in the Kootenay Valley, BC (Dulisse et al. 2005; Environment Canada 2010; Fig. 1). Within this restricted area, male and female Western Yellow-breasted Chats are thought to exhibit relatively high breeding-site fidelity (McKibbin and Bishop 2010, 2011[1]) in contrast to the low breeding-site fidelity exhibited by the Eastern Yellow-breasted Chats (Thompson and Nolan 1973; Eckerle and Thompson 2001). Within years, observations of color-banded individuals in the south Okanagan Valley population revealed dispersal as far as 15 km from natal territories and adult dispersal up to 43 km from breeding territories (McKibbin and Bishop 2010, 2011[1]). Yet, it remains unknown whether these activities contribute to the local gene pools. The implications of these behavioral patterns for population genetic structure and the degree of connectivity among habitat patches have not been investigated to date.

Available data from behavioral observations indicate that Yellow-breasted Chats are socially monogamous (Eckerle and Thompson 2001; Mays 2001), although social polygyny has been observed (rate 1%–5%; Thompson and Nolan 1973; Dussourd 1998). Telemetry data have shown that both female and male Yellow-breasted Chats engage in extra-territorial forays, and intruder females have been reported to sexually interact with extra-pair males during extra-territorial forays (Mays and Hopper 2004; Mays and Ritchison 2004). Yellow-breasted Chats also move and sing at night, activities that are associated with extra-pair copulation behavior and indicative of breeding territories' quality (Alessi 2010). How-

[1]R. McKibbin and C.A. Bishop. 2011. Return rates, territory and site fidelity, dispersal and annual survival of the western yellow-breasted chat (*Icteria virens auricollis*) at the northern periphery of its range. Submitted for publication.

ever, as sexual contacts are hard to observe, the direct link between extra-territorial forays and extra-pair copulations remains unclear (Mays 2001). Preliminary data on multilocus DNA fingerprinting suggests that up to 24% of nestlings can be extra pair (*n* = 9 pairs; Mays and Ritchison 2004). Although Yellow-breasted Chats are known to engage in extra-pair copulations, no detailed genetic study has been carried out to investigate the existence and frequency of extra-pair offspring for this species.

The objectives of the current work were to investigate the genetic mating system of Western Yellow-breasted Chats and to reconstruct demographic history and population structure for the south Okanagan Valley breeders. Specifically, we collected nuclear (microsatellite) DNA genetic data from 148 georeferenced samples of Western Yellow-breasted Chats from the south Okanagan Valley to address the following research questions: (*i*) do breeding Western Yellow-breasted Chats from the south Okanagan constitute a single panmictic population in BC or do they exhibit evidence of population subdivision corresponding to distinct breeding sites; (*ii*) is there a detectable genetic signature of the documented 20th century population reduction; and (*iii*) does the social mating system correspond to the genetic mating system in Western Yellow-breasted Chats from BC?

Materials and methods

Sampling and DNA extraction

Blood (*n* = 85) and feathers (*n* = 56) were collected from Western Yellow-breasted Chats during breeding seasons between 2002 and 2009 at 60 nesting sites within 57 territories at five locations in the Okanagan Valley (Fig. 1, Table 1, supplementary Table S1[2]), including Fairview (FAI), Oliver (OLI), Penticton (PEN), south Okanagan (SOW), and Inkameep (INK). Territories are defined as the space used by a single male, whereas locations are different conglomerates of territories. An additional seven individuals (blood, *n* = 6; feathers, *n* = 1) were sampled in 2007 or 2009 within three territories in Trail (TRA) in the West Kootenay region (Fig. 1, Table 1, supplementary Table S1). Feathers were plucked from adult Western Yellow-breasted Chats and stored dry in separate envelopes. Blood samples of approximately 0.2 mL were taken by brachial venipuncture of birds and placed in microtubes containing 1 mL Longmire's lysis buffer (Longmire et al. 1997) (0.1 mol/L Tris-HCl, 0.1 mol/L EDTA, 0.01 mol/L NaCl, 0.5% SDS). Feather samples were stored at room temperature while in the field and at –20 °C long term. DNA was extracted from 10 μL of blood or 2–10 feathers using the column-based NucleoSpin® Tissue kit (Macherey-Nagel, Düren, Germany), following the manufacturer's protocols.

Data collection

Thirty-two microsatellite loci developed for other warblers (Yellow Warbler, *Dendroica petechia* (L., 1766): Dawson et al. 1997; Golden-winged Warbler, *Vermivora chrysoptera* (L., 1766): Stenzler et al. 2004; Swainson's Warbler, *Limnothlypis swainsonii* (Audubon, 1834): Winker et al. 1999) were initially tested for their ability to amplify within Yel-

low-breasted Chats. Following optimization and preliminary screening, eight loci were polymorphic in Western Yellow-breasted Chats, providing consistent and scorable genotypes for a large proportion of our samples (*Dp01*: Dawson et al. 1997; *VeCR02*, *VeCR05*, *VeCR08*, *VeCR10*, *VeCR11*: Stenzler et al. 2004; *Lsw09*, *Lsw12*: Winker et al. 1999). Polymerase chain reactions (PCRs) were carried out using an M13-fluorescent labeling technique (Schuelke 2000) on an ABI Veriti® thermal cycler in 12.5 μL mixes containing the following: ~20 to 50 ng of DNA, PCR buffer A (Kapa Biosystems, Woburn, Massachusetts, USA), 1.5 mmol/L MgCl$_2$, 200 μmol/L dNTPs, 7.5 μg of bovine serum albumin (BSA), 0.08 μmol/L of the M13-tailed forward primer, 0.8 μmol/L of each of the reverse primer, and the M13 fluorescent dye labeled primer and 0.5 U (1 U ≈ 16.67 nkat) of *Taq* DNA polymerase (Kapa Biosystems). Cycling conditions for all primers were optimized using a "touchdown" cycling program that consisted of the following: 95 °C for 10 min; 35 cycles of 95 °C for 30 s, annealing for 30 s, and 72 °C for 45 s; and a final step of 72 °C for 7 min (Russello et al. 2001). The annealing step in the "touchdown" program decreased 2 °C every other cycle from 59 °C until it reached 51 °C (the 9th cycle), at which point the remaining cycles continued with a 51 °C annealing temperature. Genotypic data were collected for all samples on an ABI 3130XL DNA sequencer (Applied Biosystems, Foster City, California, USA) and microsatellite alleles were scored using Gene-Mapper® version 4.0 software (Applied Biosystems).

Microsatellite genotypic variation, population differentiation, and demographic history

Population genetic analyses were based only on the four locations with 11 or more putatively unrelated individuals (*n* = 92): OLI (*n* = 14), PEN (*n* = 11), SOW (*n* = 41), and INK (*n* = 26) (Table 1). Genotypic quality, specifically the presence of null alleles, was assessed using MICRO-CHECKER version 2.2.3 (Van Oosterhout et al. 2004). Allelic diversity, as well as observed (*H*$_o$) and expected (*H*$_e$) heterozygosities, were computed using GENALEX version 6.3 (Peakall and Smouse 2006). Allelic richness, an estimate of allelic diversity corrected using rarefaction, was calculated using FSTAT (Goudet 1995). Exclusion probabilities were calculated according to the equations in Dodds et al. (1996) using GERUD version 2.0 software (Jones 2005). Deviation from Hardy–Weinberg (H–W) equilibrium was assessed using exact tests based on the Markov chain method of Guo and Thompson (1992) as implemented in GENEPOP version 3.3 (1 000 dememorization, 1 000 batches, and 10 000 iterations; Raymond and Rousset 1995). Linkage disequilibrium was investigated for all pairs of loci using GENEPOP version 3.3 (Raymond and Rousset 1995). Type I error rates for tests of linkage disequilibrium and departure from H–W expectations were corrected for multiple comparisons using the sequential Bonferroni procedure (Rice 1989).

Levels of differentiation among populations were estimated by pairwise population comparisons of θ, an analogue of F_{ST} (Weir and Cockerham 1984), calculated in GENETIX (Belkhir et al. 2002). In addition, an analysis of molecular variance (AMOVA) (Excoffier et al. 1992) was performed in

---

[2]Supplementary Table S1 is available with the article through the journal Web site (http://nrcresearchpress.com/doi/suppl/10.1139/z11-061).

Table 1. Summarized sampling information associated with blood and feather samples from Western Yellow-breasted Chat (*Icteria virens auricollis*) collected in the Okanagan and Similkameen Valleys, British Columbia, Canada.

Location	Sample size	No. of territories	Territory name
Fairview (FAI)	8	2	Gate Keeper,[a] Lower Fairview
Inkameep (INK)	26	18	Beaver Dam, Casper, Cliffhanger, Curlew Field, Falls, Ghostrider, Haunted House, High North, Highlander, House Sitter, Lukus, Pumpkin, Quicksand, Throne N, Tickleberry, Twin Pines, Wizard, Yogi
Oliver (OLI)	33	12	Athlete, Biker Blue, Heeler, Ink PP,[a] Maple Syrup, Pasty, Ranger, Runner,[a] Stinger, Superchunk, Warden, Wildebeest
Penticton (PEN)	14	7	Center Stage, Eastside Bird, nMamachin, Penticton, Richard, Trampled, Westside Bird
South Okanagan (SOW)	60	18	Arctic, Drifter, Dunes, Historian, Late Bloomer, Mac, Nettles, North Pole, Powerline North, Prince Charming, Roady, Rosy, Ryan, Ryka, Siberia, Superpower, Trampled, Westside Story
Trail (TRA)	7	3	Aspen Groove, Elk Path, Highliner
Total	148	60	

Note: Number and names of territories surveyed and number of samples collected per location are shown. Unless noted otherwise, all territories contained one nesting site. Detailed information for each individual sampled is shown in supplementary Table S1.

[a]Two nesting sites sampled.

ARLEQUIN version 3.0 (Excoffier et al. 2005) to quantify the hierarchical distribution of genetic variance within and among sites. Correspondence of geographically separated sites as discrete genetic units was further tested using the Bayesian method of Pritchard et al. (2000) as implemented in STRUCTURE. Run length was set to 1 000 000 MCMC replicates after a burn-in period of 500 000 using correlated allele frequencies under a straight admixture model. The most likely number of clusters in our sample was determined using the ΔK approach (Evanno et al. 2005) by varying the number of clusters K from 1 to 10 with 20 iterations per value of K.

Genetic signatures of demographic contraction based on microsatellite genotypic data were assessed using two different approaches: (1) the heterozygote excess test and (2) the mode shift test, both implemented in the software package BOTTLENECK version 1.2.02. For the heterozygote excess test, significance was assessed using 10 000 iterations with the Wilcoxon's sign-rank test and two different allele mutation models: stepwise mutation model (SMM) and two phase model (TPM) consisting of 10% multistate change and a variance among multiple steps of 12 as recommended by Piry et al. (1999).

Parentage and relatedness

Parentage analyses were based on blood samples from 73 offspring and 18 adults collected during the 2009 breeding season (supplementary Table S1). Samples included five mother–offspring–male trios (three sites), eight mother–offspring pairs (three sites), and eight attending male–offspring pairs (three sites), as well as 52 offspring without social parents. In total, 37 nesting sites were surveyed in 34 territories at five locations in the Okanagan Valley and West Kootenay regions (BC): Fairview (3 sites), Oliver (13 sites), Penticton (4 sites), south Okanagan (15 sites), and Trail (2 sites) (Fig. 1, supplementary Table S1).

We conducted a series of analyses to determine whether attending males and (or) females were genetic parents of the offspring sampled with them. The same criteria were applied both to offspring with both social parents sampled and to offspring with only one social parent sampled at the nest. First, we visually compared the genotypes of mother–offspring pairs to identify any mismatching loci. To account for genotypic errors and (or) null alleles, we considered mismatches at >1 locus as excluding a social parent as being a genetic parent. Secondly, we investigated parentage assignments using a likelihood-based approach in CERVUS version 3.0 (Marshall et al. 1998) with corrected equations (Kalinowski et al. 2007). We calculated LOD scores (the sum of log-likelihood ratios at each locus) for potential parent–offspring pairs and identified the potential parent–offspring pair with the highest LOD score that included the most likely parent. LOD scores were calculated separately for father–offspring pairs and mother–offspring pairs. We computed critical delta scores (the difference in log-likelihood ratio scores between the two most likely candidate parents) at 95% level of confidence by simulating 100 000 parent–offspring pairs based on allele frequencies derived from the study population using CERVUS (Marshall et al. 1998). Simulation parameters were as follows: 100% of loci typed, 0.01 genotyping error rate, and 10% of adults were sampled in the population (based on field data). Additional analyses in which these parameters were changed did not alter our results.

As the accuracy of parentage analysis can be influenced by the level of relatedness (r) among adult candidate parents (both females and males) (Marshall et al. 1998), we first computed pairwise values of relatedness among all breeding females and among all breeding males using Queller and Goodnight's (1989) index. Information on relatedness was incorporated into simulations of paternity in CERVUS. The Queller and Goodnight's (1989) r values were also used to apply the "cut-off" values method of Blouin et al. (1996) to classify pairs in relationship categories. Using this method, there is a higher than zero probability of falsely excluding true relationships because observed values can fall outside the theoretical expected ranges (Blouin et al. 1996). To minimize this error, we first identified the relatedness values to be used as cut-off specific for our study sample (Russello and Amato 2004). For this, the program IREL version 1.0 (Gonçalves da Silva and Russello 2011) computed, as cut-off values, the midpoints between the means of the distributions of pairwise r

values for 1000 simulated pairs of each relationship category (FS, full-siblings; HS, half-siblings; PO, parent–offspring; UR, unrelated) using as input data genotypes and population allele frequencies specific to our study population of Western Yellow-breasted Chats. To avoid false rejection of a true parent–offspring pair, LOD scores, the method of *r*-based cut-off values and the number of mismatches among mother–offspring–father trios were considered together in the final decision of parentage assignment.

For each of the 38 pairs composed of offspring lacking both social parents, we applied a multistep approach based on maximum-likelihood (ML) estimates of relatedness, computation of pairwise relatedness values, and hypothesis testing. ML-RELATE (Kalinowski et al. 2006) was used to compute ML estimates of relatedness for each pair of juveniles sampled within a brood. Then, for the same pairs, we estimated pairwise values of genetic relatedness using Queller and Goodnight's (1989) index, as this estimator performed best with our data set according to Monte Carlo simulations implemented in IREL version 1.0 (Gonçalves da Silva and Russello 2011) (data not shown). We applied the cut-off values method of Blouin et al. (1996) to classify pairs in relationship categories as described above. In addition, we performed hypothesis testing to assess the significance of the relationship suggested by both ML-RELATE and cut-off values method, versus the alternative hypothesis derived from behavioral information (FS, assuming genetic monogamy between the adult pair that produced the analyzed progeny). All hypothesis tests were conducted randomly simulating 10 000 genotype pairs in ML-RELATE (Kalinowski et al. 2006) and KINGROUP version 2 (Konovalov et al. 2004), and results of these two programs were compared.

Results

Data quality

The quality of the PCR amplification varied across the blood and feather samples. All eight loci successfully amplified in the blood samples, whereas only six loci (*Dp01*, *VeCr02*, *VeCr05*, *VeCr08*, *VeCr10*, *VeCr11*) provided consistent and scorable products from the feather samples.

As population genetic analyses relied on a combination of blood and feather samples, patterns of genetic diversity, population differentiation, and demographic history were inferred based on genotypic data at six loci (*Dp01*, *VeCr02*, *VeCr05*, *VeCr08*, *VeCr10*, *VeCr11*). In addition, evidence for null alleles was detected at one locus (*VeCr10*) for one sampling site (OLI), thus data for this locus and site were removed for all subsequent population genetic analyses. *Dp01* exhibited significant deviation from H–W expectations for the SOW and INK sites following Bonferroni correction (Table 2). Furthermore, there was no evidence of nonrandom association of genotypes (*p* > 0.05) in any of the pairwise tests for linkage disequilibrium performed for all possible pairwise comparisons of the sampled loci.

Parentage and relatedness analyses were based on eight microsatellites that amplified successfully in all blood samples (*Dp01*, *VeCr02*, *VeCr05*, *VeCr08*, *VeCr10*, *VeCr11*, *Lsw09*, and *Lsw12*; supplementary Table S1). Similar to the population genetic analyses, data at locus (*VeCr10*) for one

Table 2. Patterns of population genetic variation at six microsatellite DNA loci for Western Yellow-breasted Chats (*Icteria virens auricollis*) captured at four sites in the south Okanagan Valley, British Columbia, Canada.

Location	n_L	A	A_R	H_o	H_e
Inkameep (INK)	26	3.19	2.70	0.40	0.43
Oliver (OLI)[a]	15	3.00	2.79	0.48	0.51
Penticton (PEN)	11	3.14	3.08	0.46	0.44
South Okanagan (SOW)	40	4.18	3.07	0.41	0.46

Note: n_L, sample size per locus; A, number of alleles; A_R, number of alleles corrected for $n = 10$; H_o, observed heterozygosity; H_e, unbiased expected heterozygosity.

[a]Estimates based on five loci owing to presence of null alleles at locus *VeCr10*.

sampling site (OLI) were removed owing to evidence of null alleles.

Nuclear genetic diversity, population differentiation, and demographic history

Levels of genetic variation within each location were low across the sampled loci, averaging 3.2 alleles/locus (range 2–6 alleles/locus) with mean $H_o = 0.44$ and mean $H_e = 0.46$ across all sites (Table 2). There was no evidence of genetic structure among sites, with the AMOVA analysis revealing that 99.9% of genetic diversity was distributed at the within-site level. Similarly, θ values were low for all possible pairwise comparisons, none of which were significant. Bayesian analyses indicated that only 34% of individuals were correctly self-assigned to their populations of origin. Likewise, STRUCTURE analyses revealed a high degree of admixture among sites and $K = 1$ ($K = 1$, lnP(D) = –893.3; $K = 2$, lnP(D) = –935.1; $K = 3$, lnP(D) = –1072.1; $K = 4$–10, lnP(D) ≤ –1167.6). Although a very small sample size, inclusion of individuals sampled in the disjunct Trail location to the east (Fig. 1) did not change these inferences ($K = 1$, lnP(D) = –941.8; $K = 2$, lnP(D) = –998.8; $K = 3$, lnP(D) = –1141.0; $K = 4$–10, lnP(D) ≤ –1189.9).

There was no genetic evidence for demographic contraction at any site based on the tests implemented in BOTTLENECK (Piry et al. 1999). Specifically, there were no significant deviations from mutation–drift equilibrium conditions under a TPM model for microsatellite evolution according to the heterozygote excess test (Wilcoxon test, *p* values for all tests >0.05). Similarly, allele frequency distributions did not depart significantly from a L-shaped distribution expected under mutation–drift equilibrium based on the mode shift test.

Relatedness and parentage assignment

The combined exclusion probability for all eight loci used for parentage and relatedness analyses was 0.99 for chicks with both parents genotyped, 0.93 when only one parent genotype was known, and 0.73 when neither parent was known; the latter being the case for most sampled chicks. Mean pairwise relatedness among adults was low (females: mean = –0.100, range = –0.999 to 0.837; males: mean = –0.143, range = –0.713 to 0.871); however, first-order relatives were detected both among and within locations: 7 female–female pairs (out of 45 pairwise comparisons) had a *r* value ≥0.348

Table 3. Parentage assignment for nestling Western Yellow-breasted Chats (*Icteria virens auricollis*) with social parents sampled at nest.

Nesting site No.	Offspring ID	Social mother	Genotype	CERVUS	Pairwise *r*	ML-RELATE *p*	Attending male	Genotype	CERVUS	Pairwise *r*	ML-RELATE *p*
19	2241–36858	2241–36794	Yes	Yes*	0.4870	0.0783	2241–36859	No	Yes	0.3531	0.0526
21	2241–36831	2241–36834	Yes	Yes*	0.7877	0.0056	2241–36873	Yes	Yes*	0.9063	0.0020
21	2241–36832	2241–36834	Yes	Yes*	0.8831	0.0052	2241–36873	Yes	Yes*	0.7982	0.0070
21	2241–36833	2241–36834	Yes	Yes*	0.7217	0.0054	2241–36873	Yes	Yes*	0.6678	0.0070
31	2241–36815	2241–36816	Yes	No	0.2101	0.1814	*2241–38423*	No	No	–0.0212	0.2829
10	2241–36824	2241–36847	Yes	Yes*	0.2318	0.0240	—			—	—
10	2241–36825	*2241–36847*	No	No	–0.0584	0.7655	—			—	—
23	2241–36807	2241–36817	Yes	Yes*	0.2839	0.3425	—			—	—
23	2241–36808	*2241–36817*	No	Yes	0.1527	0.4425	—			—	—
23	2241–36809	2241–36817	Yes	Yes	0.4861	0.3218	—			—	—
26	2241–36854	*2241–38004*	No	No	0.2682	0.4922	—			—	—
26	2241–36855	2241–38004	Yes	Yes	0.4109	0.1007	—			—	—
26	2241–36856	2241–38004	Yes	No	0.6630	0.0876	—			—	—
14	2241–36844	—			—	—	*1931–29264*	No	No	–0.3588	0.4567
14	2241–36845	—			—	—	*1931–29264*	No	No	–0.0511	0.2436
14	2241–36846	—			—	—	*1931–29264*	No	No	–0.2911	0.2264
22	2241–36826	—			—	—	2241–36769	Yes	Yes*	0.5224	0.0387
22	2241–36827	—			—	—	2241–36769	Yes	Yes	0.3105	0.1132
22	2241–36828	—			—	—	2241–36769	Yes	Yes	0.0456	0.8760
37	2241–36836	—			—	—	2241–36841	Yes	No	0.3820	0.3162
37	2241–36837	—			—	—	2241–36841	Yes	Yes	0.3599	0.1256

Note: Social mothers and attending males with genotypic transmission (Genotype column) consistent with maternity and paternity, respectively, for a given nestling are indicated by "Yes" and deviation at more than one locus are indicated by "No". Social mothers and attending males assigned maternity and paternity, respectively, according to the algorithm implemented in CERVUS are indicated by "Yes" with results significant at 95% confidence level marked with an asterisk. Queller and Goodnight (1989) pairwise relatedness value (*r*) of the social parent with the sampled nestling are displayed, with the empirically determined parent–offspring versus unrelated cut-off value equal to 0.2101. The *p* value corresponds to testing of a putative hypothesis of parent–offspring versus an alternative hypothesis of unrelated (a small *p* value indicates that the putative relationship fits the data better than the alternative) as implemented in ML-RELATE. Social mothers and attending males deviating from expected genetic ancestry over two or more of these approaches were considered not to be genetic parents of the sampled nestling, and are indicated in boldface italic type.

Table 4. Maximum-likelihood estimates of relationship (*R*), Queller and Goodnight (1989) pairwise values of relatedness (*r*), and hypothesis testing computed for nestling Western Yellow-breasted Chats (*Icteria virens auricollis*) based on data on eight microsatellite loci.

Territory	Nesting site No.	Individual 1	Individual 2	*R*	*r*	$H_p/H_a = p$
Gate Keeper	1	2241–36805	2241–36806	HS	0.3450	FS/FS = 0.126
	2	2241–36862	2241–36863	FS	0.5608	HS/FS = 0.076
Lower Fairview	3	2241–36820	2241–36822	FS	0.5680	HS/FS = 0.413
	3	2241–36820	2241–36821	HS	0.2568	FS/HS = 0.392
	3	2241–36821	2241–36822	HS	0.2480	FS/HS = 0.075
	3	2241–36821	2241–36823	HS	0.3229	FS/HS = 0.125
	3	2241–36820	2241–36823	UR	−0.0976	HS/UR = 0.429
	3	2241–36822	2241–36823	UR	0.1031	HS/UR = 0.076
Athlete	4	2241–36872	2241–36873	FS	0.5899	HS/FS = 0.492
Blue Heeler	6	2241–38498	2241–38499	UR	0.1256	HS/UR = 0.361
Ink PP	7	2241–36810	2241–36811	FS	0.4316	HS/FS = 0.078
	7	2241–36810	2241–36812	FS	0.7671	HS/FS = 0.936
	7	2241–36811	2241–36812	FS	0.4297	HS/FS = 0.138
	7	2241–36811	2241–36813	HS	0.1917	UR/HS = 0.011
	7	2241–36810	2241–36813	UR	0.0676	HS/UR = 0.145
	7	2241–36812	2241–36813	UR	0.0439	HS/UR = 0.019
	8	2241–36869	2241–36870	FS	0.5859	HS/FS = 0.384
	8	2241–36869	2241–36871	FS	0.4241	HS/FS = 0.118
	8	2241–36870	2241–36871	FS	0.9091	HS/FS = 0.788
Maple Syrup	9	2241–36877	2241–36878	UR	0.0219	HS/UR = 0.625
Pasty	10	2241–36824	2241–36825	FS	0.7010	HS/FS = 0.858
Runner	12	2241–36829	2241–36830	FS	0.8177	HS/FS = 0.764
	13	2241–36874	2241–36875	FS	0.5565	HS/FS = 0.892
	13	2241–36874	2241–36876	FS	0.7510	HS/FS = 0.791
	13	2241–36875	2241–36876	FS	0.6446	HS/FS = 0.605
Stinger	14	2241–36844	2241–36845	HS	−0.1692	FS/HS = 0.799
	14	2241–36844	2241–36846	HS	−0.1553	FS/HS = 0.866
	14	2241–36845	2241–36846	HS	−0.2103	FS/HS = 0.745
Superchunk	15	2241–36803	2241–36804	FS	0.7787	HS/FS = 0.868
Warden	16	2241–36866	2241–36867	UR	0.2412	HS/UR = 0.322
Eastside bird	18	2241–36850	2241–36851	FS	0.5436	HS/FS = 0.933
Westside bird	20	2241–36842	2241–36843	FS	0.4766	HS/FS = 0.264
Arctic	21	2241–36831	2241–36832	FS	0.9004	HS/FS = 0.941
	21	2241–36831	2241–36833	FS	0.7554	HS/FS = 0.490
	21	2241–36832	2241–36833	FS	0.8246	HS/FS = 0.639
Drifter	22	2241–36827	2241–36828	HS	0.2316	FS/HS = 0.350
	22	2241–36826	2241–36827	UR	0.0393	HS/UR = 0.706
	22	2241–36826	2241–36828	UR	0.1377	HS/UR = 0.383
Dunes	23	2241–36807	2241–36809	HS	0.3014	FS/HS = 0.330
	23	2241–36807	2241–36808	UR	−0.0895	FS/UR = 0.615
	23	2241–36808	2241–36809	UR	0.1847	FS/UR = 0.010
Historian	24	2241–36864	2241–36865	UR	0.2527	FS/UR = 0.191
Nettles	26	2241–36854	2241–36855	FS	0.4938	HS/FS = 0.203
	26	2241–36855	2241–36856	FS	0.4633	HS/FS = 0.267
	26	2241–36854	2241–36856	UR	0.1217	FS/UR = 0.550
North Pole	27	2241–36852	2241–36853	FS	0.5686	HS/FS = 0.332
Powerline North	28	2241–36818	2241–36819	FS	0.4220	HS/FS = 0.312
Superpower	34	2241–36880	2241–36881	UR	0.2755	FS/UR = 0.202
Trampled	35	2241–36801	2241–36802	HS	0.3325	FS/HS = 0.587
	35	2241–36801	2241–38500	UR	−0.1596	FS/UR = 0.875
	35	2241–36802	2241–38500	UR	−0.1314	FS/UR = 0.740
Elk Path	36	2241–36838	2241–36839	FS	0.5489	HS/FS = 0.187
	36	2241–36838	2241–36840	FS	0.7495	HS/FS = 0.578
	36	2241–36839	2241–36840	FS	0.4879	HS/FS = 0.179
Highliner	37	2241–36836	2241–36837	HS	0.3358	FS/HS = 0.628

Note: UR, unrelated; HS, half-siblings; FS, full-siblings; H_p, putative hypothesis; H_a, alternative hypothesis (a small *p* value indicates that the putative hypothesis fits the data better than the alternative hypothesis).

Fig. 2. Proportion of nestling pairs of Yellow-breasted Chats (*Icteria virens auricollis*) classified as unrelated (UR), half-siblings (HS), and full-siblings (FS). Sample sizes (*n*) indicate the actual number of dyads corresponding to that category.
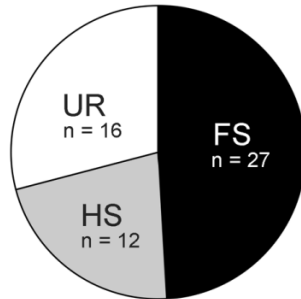
(the FS–HS cut-off value according to simulations), with a mean *r* value of 0.605. Likewise, 3 male–male pairs (out of 28 pairwise comparisons) were first-order relatives and had a mean *r* value of 0.400. Pairwise relatedness among breeding adults differed among locations, but not significantly: –0.5075 for OLI, –0.0376 for PEN, and –0.0353 for SOW. The three known male–female mating pairs had pairwise relatedness values similar to those expected for first- and second-order relatives (0.2168, 0.6737, and 0.2156).

Using our criteria, both social parents were confirmed as genetic parents of all offspring in two clutches (Table 3). In one clutch, only the social female was identified as the genetic mother of the sampled offspring, whereas the attending male was excluded as the genetic father (territory: Ryan; Table 3).

As for the offspring for which only the female was available for comparison, none of the females were confirmed as genetic mothers of all the nestlings in their sampled clutches (Table 3), although maternity was confirmed for one (territories: Pasty and Dunes) or two nestlings within each clutch (territory: Nettles). For the three nests where only the attending males and nestlings were sampled, two were assigned paternity of the entire clutch (Table 3). In one territory (Stinger), the attending male was not the genetic father of any of the nestlings (Table 3).

As for the 20 nests for which ≥2 offspring and no social parents sampled, 11 nests were entirely composed of full-sibling offspring (Table 4), one brood was composed of half-siblings only, 5 nests were composed of likely unrelateds with the remaining three clutches composed of full-siblings together with half-siblings and unrelateds (Table 4). Considering all nests with ≥2 nestlings, our criteria identified 27 full-siblings, 12 half-siblings, and 16 unrelated pairs (Fig. 2).

Discussion

Genetic diversity, population structure, and demographic history

We found no significant genetic structure among Western Yellow-breasted Chats sampled in the south Okanagan Valley, suggesting that there is extensive gene flow among breeding populations within BC. Although the population of Western Yellow-breasted Chats shows high fidelity for the restricted riparian habitats of the south Okanagan Valley, Western Yellow-breasted Chats also breed in the Similkameen Valley (50 km east of the Okanagan Valley) in alternating

years (C.A. Bishop, unpublished data). Likewise, observations of color-banded birds from the Okanagan and in Washington state near the Canadian border suggest that some Western Yellow-breasted Chats may also choose to nest farther south in some years (C.A. Bishop, unpublished data). The difficulty in correctly assigning individuals to their sampling sites suggests substantial mixing of breeding populations. The assumption of one single population cluster in BC is also supported by the lack of substructure in the genotypes from the studied sites (*q* values from Bayesian analyses). Identifying distinct breeding populations using microsatellite markers has proven to be difficult in other highly vagile warblers (Gibbs et al. 2000; Clegg et al. 2003), likely reflecting the intrinsically high potential for gene flow in these organisms. The lack of genetic signal of the reduction in population size during the 20th century might also reflect high ongoing gene flow in our studied populations despite the extreme loss of nesting habitat since 1938 (Lea 2008). The importance of individual immigration for restoring genetic diversity in bottlenecked warbler populations has already been demonstrated (Procházka et al. 2008). Additional population genetic studies employing a larger set of markers and expanded sampling including US breeding populations are required, however, before the role of gene flow for Western Yellow-breasted Chats in BC can be fully assessed. Our preliminary findings suggest that Western Yellow-breasted Chats from the south Okanagan should be considered a single genetic unit for conservation management. In spite of the capability of migratory birds to move across large distances, habitat fragmentation in their breeding grounds can pose barriers to gene flow (Lindsay et al. 2008). Consequently, ensuring connectivity among habitat patches may still be important for maintaining high levels of genetic exchange among breeding Western Yellow-breasted Chats in the south Okanagan.

Genetic mating system

Our study found genetic evidence for a moderate rate of extra-pair paternity in Western Yellow-breasted Chats, where 4 of 13 nestlings (30.7%) were not sired by the attending male (Table 3). In addition, the social mother was excluded from maternity in 3 of 13 sampled nestlings (Table 3). Power of parentage assignment tests was limited by the low percentage of candidate parents sampled in the population (Jones et al. 2010). The majority of sampled broods (75.7%; *n* = 28) did not have social parents available for direct comparison of genotypes between adults and offspring. Regardless, the application of multiple methodologies of analyses for classification of offspring pairs revealed that 49.1% of the clutches were composed entirely of full-siblings (Table 4, Fig. 2), supporting genetic monogamy between the adult pairs that sired those progeny. Extra-pair paternity and (or) conspecific brood parasitism were suggested in the remaining broods with more than one offspring, as evidenced by the presence of half-sibling and unrelated offspring pairs within them (Table 4, Fig. 2). It is important to note that the level of extra-pair paternity and (or) conspecific brood parasitism identified in clutches with social parents (7 of 21 nestlings; 33.3%) was substantially lower than those estimated from nestling-only comparisons (28 of 55 nestling pairs; 50.9%; Table 4), suggesting the latter approach may underestimate relatedness, and consequently, overestimate the degree of extra-pair off-

spring. However, the overall level of extra-pair paternity found in this study when attending males were sampled (30.7%) was consistent with unpublished estimates (24%) based on multilocus DNA fingerprinting in a central Kentucky population of Yellow-breasted Chats (Mays and Ritchison 2004). Studies in other warblers have reported similar extra-pair paternity rates. For example, in a Scottish population of the Willow Warbler (*Phylloscopus trochilus* (L., 1758)), 23.5% of young were not related to the social father and 47% of nests had at least one extra-pair young (Gil et al. 2007). In addition, more than 30% of nestlings in 55% of sampled nests were the result of extra-pair copulations in a population of Golden-winged Warblers (*Vermivora chrysoptera* (L., 1766)) in the initial stages of hybridization with Blue-winged Warblers (*Vermivora pinus* (L., 1766)) (Vallender et al. 2007).

Generally, extra-pair paternity appears to be more the norm rather than the exception in socially monogamous birds (Griffith et al. 2002), including warblers (Morton and Stutchbury 2005), suggesting that this is an important aspect of the reproductive ecology of these species. Both males and females can increase their reproductive success by engaging in extra-pair copulation with neighboring mates, with males, in particular, enjoying a substantial increase in their fitness (Stutchbury 1997; Stutchbury et al. 1998; Neudorf et al. 1997). The moderate level of extra-pair paternity observed in this study might result from a balance between monogamy, promoted by strategies such as female–female aggression (Kinsey 1934; Mays and Ritchison 2004) and mate guarding (Mays 2001), and successful extra-pair copulations during extra-territorial forays (Alessi 2010).

A rather interesting finding of this study was that genetic data suggested the occurrence of conspecific brood parasitism, as evidenced by the attending female being excluded from maternity of sampled nestlings and by the presence of unrelated offspring in clutches for which no social parents were available. Although conspecific brood parasitism has been demonstrated in over 234 avian species (Yom-Tov 2001), to our knowledge, the results presented here represent the first reported incidence of conspecific brood parasitism in warblers. It has been proposed that conspecific brood parasitism would be a beneficial strategy in species parasitized by other birds, because it could increase the survival rate of a female's offspring (Power et al. 1989; Sandell and Diemer 1999). The Yellow-breasted Chat is parasitized by Brown-headed Cowbirds (Friedmann 1963), Bronzed Cowbirds (Friedmann et al. 1977), and Black-billed Cuckoos (Thomas 1995), with frequency of brood parasitism ranging from 5% to 91% across its breeding range. In the south Okanagan, Western Yellow-breasted Chats are parasitized at a rate of up to 44%, but the species is also capable of fledging cowbirds together with their own offspring (Morgan et al. 2007). However, conspecific brood parasitism may also be the strategy of females that are unable to locate a nest site of their own (Eadie et al. 1998), which may be the case in the Okanagan Valley where suitable nesting habitat is extremely limited.

Our study revealed that overall pairwise relatedness among breeding adults within locations was low, in spite of the relatively high return rates observed for adult chats (38% of banded males) and fledged birds returning to the natal breeding area (10%) in the south Okanagan Valley (McKibbin and Bishop 2010, 2011[1]). We found three highly related known male–female mating pairs (mean $r = 0.3687$) that might reflect some degree of territory and site fidelity detected in the Okanagan population by color-banding of breeding birds (McKibbin and Bishop 2008*b*). The mating of related individuals has important implications for species at risk, such as Yellow-breasted Chats, since it can promote loss of genetic diversity and associated fitness consequences.

Inferring population history and mating system of the Yellow-breasted Chat is imperative because characterization of the genetic mating system of endangered avian species inhabiting threatened ecosystems is of fundamental importance for informing management strategies (Morton and Stutchbury 2005), as these life-history characteristics can have profound influences on the establishment of individuals in breeding sites. Birds with extra-pair breeding systems, such as Yellow-breasted Chats, may preferentially choose areas with a profusion of neighbors (Morton 1992). Yet, ongoing loss of riparian areas and native shrub thickets in the south Okanagan Valley, mainly owing to urbanization, agriculture, and water management, has led to the extensive fragmentation of once suitable nesting habitat for Western Yellow-breasted Chats. Although we found no genetic evidence of population contraction, increasingly smaller forest fragments will likely contribute to the reported population decline of this already endangered species by limiting establishment of nesting sites and access to neighboring mates. Immigration from southern populations in the US may help maintain population sizes in BC; however, the US Fish and Wildlife Service lists the Yellow-breasted Chat as a "species of concern" in some regions (US Fish and Wildlife Service 2010), including Oregon and California. The deteriorating status of Yellow-breasted Chats in the US coupled with our findings here add to a growing body of research informing the need to establish a national park in the south Okanagan, one of the six most endangered ecoregions in Canada, to preserve critical habitat and connect populations of species at risk.

Acknowledgements

References

Alessi, M. 2010. Nocturnal behavior of chats in Illinois. M.Sc. thesis, University of Illinois at Urbana–Champaign, Urbana–Champaign.

American Ornithologists' Union. 1998. Checklist of North American birds. 7th ed. American Ornithologists' Union, Washington, D.C.

Belkhir, K., Castric, V., and Bonhomme, F. 2002. IDENTIX, a software to test for relatedness in a population using permutation

methods. Mol. Ecol. Notes, **2**(4): 611–614. doi:10.1046/j.1471-8286.2002.00273.x.

Blouin, M.S., Parsons, M., Lacaille, V., and Lotz, S. 1996. Use of microsatellite loci to classify individuals by relatedness. Mol. Ecol. **5**(3): 393–401. doi:10.1046/j.1365-294X.1996.00094.x. PMID: 8688959.

Cannings, R.A., Cannings, R.J., and Cannings, S.G. 1987. Birds of the Okanagan Valley, British Columbia. Royal British Columbia Museum, Victoria.

Clegg, S.M., Kelly, J.F., Kimura, M., and Smith, T.B. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). Mol. Ecol. **12**(4): 819–830. doi:10.1046/j.1365-294X.2003.01757.x. PMID:12753204.

COSEWIC. 2009. Canadian wildlife species at risk. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ont. Available from http://www.cosewic.gc.ca/eng/sct0/index_e.cfm#sar [accessed 19 October 2010].

Dawson, R.J.G., Gibbs, H.L., Hobson, K.A., and Yezerinac, S.M. 1997. Isolation of microsatellite DNA markers from a passerine bird, *Dendroica petechia* (the yellow warbler), and their use in population studies. Heredity, **79**(5): 506–514. doi:10.1038/hdy.1997.190. PMID:9369012.

Dodds, K.G., Tate, M.L., McEwan, J.C., and Crawford, A.M. 1996. Exclusion probabilities for pedigree testing farm animals. Theor. Appl. Genet. **92**(8): 966–975. doi:10.1007/BF00224036.

Dulisse, J.A., Ogle, S.K., and Machmer, M.M. 2005. First nest record for yellow-breasted chat (*Icteria virens auricollis*) in southeastern British Columbia. Northwest. Nat. **86**(3): 160–162. doi:10.1898/1051-1733(2005)086[0160:FNRFYC]2.0.CO;2.

Dussourd, N. 1998. Morphology, singing behavior, and reproductive success: possible relationships among and between male and female yellow-breasted chats (*Icteria virens*). Master's thesis, Eastern Kentucky University, Richmond.

Eadie, J., Sherman, P., and Semel, B. 1998. Conspecific brood parasitism, population dynamics, and the conservation of cavity nesting birds. *In* Behavioral ecology and conservation biology. *Edited by* T. Caro. Oxford University Press, New York. pp. 306–340.

Eckerle, K.P., and Thompson, C.F. 2001. Yellow-breasted chat (*Icteria virens*). *In* The birds of North America online. *Edited by* A. Poole. Cornell Laboratory of Ornithology, Ithaca, N.Y. Available from http://bna.birds.cornell.edu/bna/species/575/articles/introduction [accessed 19 October 2010].

Environment Canada. 2010. Recovery strategy for the yellow-breasted chat *auricollis* subspecies (*Icteria virens auricollis*) (British Columbia population) in Canada [draft]. Species at Risk Act Recovery Strategy Series, Environment Canada, Ottawa, Ont.

Evanno, G., Regnaut, S., and Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol. Ecol. **14**(8): 2611–2620. doi:10.1111/j.1365-294X.2005.02553.x. PMID:15969739.

Excoffier, L., Smouse, P.E., and Quattro, J.M. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics, **131**(2): 479–491. PMID:1644282.

Excoffier, L., Laval, G., and Schneider, S. 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evol. Bioinform. Online, **1**: 47–50. PMID:19325852.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. No. 233.

Friedmann, H., Kiff, L.F., and Rothstein, S.I. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithson. Contrib. Zool. No. 235. doi:10.5479/si.00810282.235.

Gibbs, H.L., Dawson, R.J.G., and Hobson, K.A. 2000. Limited differentiation in microsatellite DNA variation among northern populations of the yellow warbler: evidence for male-biased gene flow. Mol. Ecol. **9**(12): 2137–2147. doi:10.1046/j.1365-294X.2000.01136.x. PMID:11123625.

Gil, D., Slater, P.J.B., and Graves, J.A. 2007. Extra-pair paternity and song characteristics in the willow warbler *Phylloscopus trochilus*. J. Avian Biol. **38**(3): 291–297.

Gonçalves da Silva, A., and Russello, M.A. 2011. *iREL*: software for implementing pairwise relatedness estimators and evaluating their performance. Conserv. Genet. Res. **3**(1): 69–71. doi:10.1007/s12686-010-9292-4.

Goudet, J. 1995. FSTAT (version 1.2): a computer program to calculate *F* statistics. J. Hered. **86**(6): 485–486.

Griffith, S.C., Owens, I.P.F., and Thuman, K.A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol. Ecol. **11**(11): 2195–2212. doi:10.1046/j.1365-294X.2002.01613.x. PMID:12406233.

Guo, S.W., and Thompson, E.A. 1992. Performing the exact test of Hardy–Weinberg proportion for multiple alleles. Biometrics, **48**(2): 361–372. doi:10.2307/2532296. PMID:1637966.

Jones, A.G. 2005. GERUD 2.0: a computer program for the reconstruction of parental genotypes from half-sib progeny arrays with known or unknown parents. Mol. Ecol. Notes, **5**(3): 708–711. doi:10.1111/j.1471-8286.2005.01029.x.

Jones, A.G., Small, C.M., Paczolt, K.A., and Ratterman, N.L. 2010. A practical guide to methods of parentage analysis. Mol. Ecol. Res. **10**(1): 6–30. doi:10.1111/j.1755-0998.2009.02778.x. PMID:21564987.

Kalinowski, S.T., Wagner, A.P., and Taper, M.L. 2006. ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. Mol. Ecol. Notes, **6**(2): 576–579. doi:10.1111/j.1471-8286.2006.01256.x.

Kalinowski, S.T., Taper, M.L., and Marshall, T.C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol. Ecol. **16**(5): 1099–1106. doi:10.1111/j.1365-294X.2007.03089.x. PMID:17305863.

Kinsey, E.C. 1934. Notes on the sociology of the long-tailed yellow-breasted chat. Condor, **36**(6): 235–237. doi:10.2307/1363816.

Konovalov, D.A., Manning, C., and Henshaw, M.T. 2004. KINGROUP: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. Mol. Ecol. Notes, **4**(4): 779–782. doi:10.1111/j.1471-8286.2004.00796.x.

Lea, T. 2008. Historical (pre-settlement) ecosystems of the Okanagan Valley and Lower Similkameen Valley of British Columbia — pre-European contact to the present. Davidsonia, **19**(1): 3–38. Available from http://www.davidsonia.org/files/davidsonia_19_1.pdf [accessed 19 October 2010].

Lindsay, D.L., Barr, K.R., Lance, R.F., Tweddale, S.A., Hayden, T.J., and Leberg, P.L. 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (*Dendroica chrysoparia*). Mol. Ecol. **17**(9): 2122–2133. doi:10.1111/j.1365-294X.2008.03673.x. PMID:18397218.

Longmire, J.L., Maltbie, M., and Baker, R.J. 1997. Use of "lysis buffer" in DNA isolation and its implications for museum collections. Occas. Pap. Mus. Texas Tech. Univ. **163**: 1–3.

Lovette, I.J., Clegg, S.M., and Smith, T.B. 2004. Limited utility of mtDNA markers for determining connectivity among breeding and overwintering locations in three Neotropical migrant birds. Conserv. Biol. **18**(1): 156–166. doi:10.1111/j.1523-1739.2004.00239.x.

Lowery, G.H., Jr., and Monroe, B.L., Jr. 1968. Family Parulidae. *In* Checklist of birds of the world. Vol. 14. *Edited by* R.A. Paynter. Museum of Comparative Zoology, Cambridge, Mass. pp. 3–93.

Marshall, T.C., Slate, J., Kruuk, L.E.B., and Pemberton, J.M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol. Ecol. **7**(5): 639–655. doi:10.1046/j.1365-294x.1998.00374.x. PMID:9633105.

Mays, H.L. 2001. Extra-pair copulations, sexual conflict and constraints on female breeding tactics in a monogamous passerine, *Icteria virens*. Ph.D. thesis, University of Kentucky, Lexington.

Mays, H.L., and Hopper, K.R. 2004. Differential responses of yellow-breasted chats, *Icteria virens*, to male and female conspecific model presentations. Anim. Behav. **67**(1): 21–26. doi:10.1016/j.anbehav.2003.01.003.

Mays, H.L., and Ritchison, G. 2004. The effect of vegetation density on male mate guarding and extra-territorial forays in the yellow-breasted chat (*Icteria virens*). Naturwissenschaften, **91**(4): 195–198. doi:10.1007/s00114-004-0510-3. PMID:15085279.

McKibbin, R., and Bishop, C.A. 2008a. Observations on the longevity and fecundity of the western yellow-breasted chat in the south Okanagan Valley, British Columbia, Canada. British Columbia Birds, **18**: 26–27.

McKibbin, R., and Bishop, C.A. 2008b. Capture success rates of the western yellow-breasted chat in the south Okanagan Valley, British Columbia, Canada during 2005 to 2007. North American Bird Bander, **33**(4): 179–184.

McKibbin, R., and Bishop, C.A. 2010. Habitat characterization of breeding territories of the western yellow-breasted chat in the south Okanagan, British Columbia, Canada. Northwest. Nat. **91**(2): 145–156. doi:10.1898/NWN-09-07.1.

Morgan, T.C., Bishop, C.A., and Williams, T.D. 2007. Yellow-breasted Chat and Gray Catbird productivity in a fragmented western riparian system. Wilson J. Ornith. **119**(3): 494–498. doi:10.1676/05-071.1.

Morton, E.S. 1992. What do we know about the future of migrant landbirds? *In* Ecology and conservation of Neotropical migrant landbirds. *Edited by* J.M. Hagen III, and D.W. Johnston. Smithsonian Institution Press, Washington, D.C. pp. 579–589.

Morton, E.S., and Stutchbury, B.J.M. 2005. The significance of mating system and non-breeding behavior to population and forest patch use by migrant birds. USDA For. Serv. Gen. Tech. Rep. No. PSW-GTR-191.

Neudorf, D.L., Stutchbury, B.J.M., and Piper, W.H. 1997. Covert extraterritorial behavior of female hooded warblers. Behav. Ecol. **8**(6): 595–600. doi:10.1093/beheco/8.6.595.

Peakall, R., and Smouse, P.E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol. Ecol. Notes, **6**(1): 288–295. doi:10.1111/j.1471-8286.2005.01155.x.

Piry, S., Luikart, G., and Cornuet, J.-M. 1999. BOTTLENECK: a computer program for detecting recent reductions in the effective population size using allele frequency data. J. Hered. **90**(4): 502–503. doi:10.1093/jhered/90.4.502.

Power, H.W., Kennedy, E.D., Romagnano, L.C., Lombardo, M.P., Hoffenberg, A.S., Stouffer, P.C., and McGuire, T.R. 1989. The parasitism insurance hypothesis: why starlings leave space for parasitic eggs. Condor, **91**(4): 753–765. doi:10.2307/1368058.

Pritchard, J.K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics, **155**(2): 945–959. PMID:10835412.

Procházka, P., Bellinvia, E., Fainova, D., Hajkova, P., Elhalah, A., and Alomari, K. 2008. Immigration as a possible rescue of a reduced population of a long-distant migratory bird: Reed warblers in the Azraq Oasis, Jordan. J. Arid Environ. **72**(7): 1184–1192. doi:10.1016/j.jaridenv.2008.02.005.

Queller, D.C., and Goodnight, K.F. 1989. Estimating relatedness using genetic markers. Evolution, **43**(2): 258–275. doi:10.2307/2409206.

Raymond, M., and Rousset, F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Hered. **86**(3): 248–249.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**(1): 223–225. doi:10.2307/2409177.

Russello, M.A., and Amato, G. 2004. Ex situ population management in the absence of pedigree information. Mol. Ecol. **13**(9): 2829–2840. doi:10.1111/j.1365-294X.2004.02266.x. PMID:15315693.

Russello, M., Calcagnotto, D., DeSalle, R., and Amato, G. 2001. Characterization of microsatellite loci in the endangered St. Vincent Parrot, *Amazona guildingii*. Mol. Ecol. Notes, **1**(3): 162–164. doi:10.1046/j.1471-8278.2001.00061.x.

Sandell, M.I., and Diemer, M. 1999. Intraspecific brood parasitism: a strategy for floating females in the European starling. Anim. Behav. **57**(1): 197–202. doi:10.1006/anbe.1998.0936. PMID:10053087.

Schuelke, M. 2000. An economic method for the fluorescent labeling of PCR fragments. Nat. Biotechnol. **18**(2): 233–234. doi:10.1038/72708. PMID:10657137.

Stenzler, L.M., Fraser, R., and Lovette, I.J. 2004. Isolation and characterization of 12 microsatellite loci from Golden-winged Warblers (*Vermivora chrysoptera*) with broad cross-taxon utility in emberizine songbirds. Mol. Ecol. Notes, **4**(4): 602–604. doi:10.1111/j.1471-8286.2004.00750.x.

Stutchbury, B.J.M. 1997. Effects of female cowbird removal on reproductive success of Hooded Warblers. Wilson Bull. **109**(1): 74–81.

Stutchbury, B.J.M., Morton, E.S., and Piper, W.H. 1998. Extra-pair mating system of a synchronously breeding tropical songbird. J. Avian Biol. **29**(1): 72–78. doi:10.2307/3677343.

Thomas, B.T. 1995. Black-billed cuckoo parasitizes the nest of a yellow-breasted chat. Raven, **66**: 3–5.

Thompson, C.F., and Nolan, V. 1973. Population biology of yellow-breasted chat (*Icteria virens* L.) in southern Indiana. Ecol. Monogr. **43**(2): 145–171. doi:10.2307/1942192.

US Fish and Wildlife Service. 2010. Federally listed, proposed, candidate species, and species of concern under the jurisdiction of the Fish and Wildlife Service which may occur within Coos County, Oregon. US Fish and Wildlife Service, Eugene, Oreg. Available from http://www.fws.gov/oregonfwo/Species/Lists/Documents/County/COOS%20COUNTY.pdf [accessed 27 September 2010].

Vallender, R., Friesen, V.L., and Robertson, R.J. 2007. Paternity and performance of golden-winged warblers (*Vermivora chrysoptera*) and golden-winged × blue-winged warbler (*V. pinus*) hybrids at the leading edge of a hybrid zone. Behav. Ecol. Sociobiol. **61**(12): 1797–1807. doi:10.1007/s00265-007-0413-3.

Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M., and Shipley, P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol. Ecol. Notes, **4**(3): 535–538. doi:10.1111/j.1471-8286.2004.00684.x.

Weir, B.S., and Cockerham, C.C. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution, **38**(6): 1358–1370. doi:10.2307/2408641.

Winker, K., Glenn, T.C., and Graves, G.R. 1999. Dinucleotide microsatellite loci in a migratory wood warbler (Parulidae: *Limnothlypis swainsonii*) and amplification among other songbirds. Mol. Ecol. **8**(9): 1553–1556. doi:10.1046/j.1365-294X.1999.07113.x.

Yom-Tov, Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis, **143**(1): 133–143. doi:10.1111/j.1474-919X.2001.tb04177.x.