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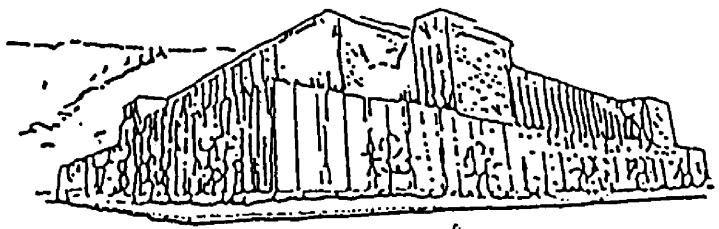
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# SURVIVAL AND DISPERSAL OF YELLOW WARBLERS IN MONTANA

by

Amy B. Cilimburg

B. A. The College of Wooster, 1987

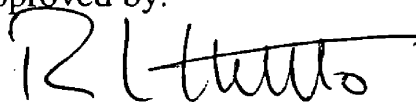
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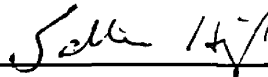
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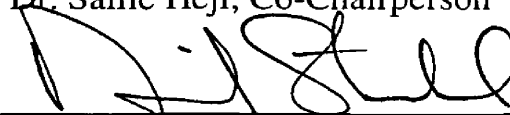
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
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## SURVIVAL AND DISPERSAL OF YELLOW WARBLERS IN MONTANA

Advisors: Dr. R. L Hutto   
Dr. S. J. Hejl 

Survival probability estimates for songbirds are generally conservative because dispersal between breeding seasons is not differentiated from mortality. Presently, knowledge of between-year breeding dispersal is lacking for most songbirds. To assess adult survival probabilities and dispersal, 436 Yellow Warblers (*Dendroica petechia*) were color-banded and resighted over five breeding seasons at 11 study sites in the Bitterroot Valley, Montana as part of the Bitterroot Riparian Bird Project (BRBP). During the last two seasons, field assistants and I searched extensively for marked warblers between and surrounding these study sites.

In the first chapter, I compare Yellow Warbler survival probabilities with and without data on dispersal and assess the effectiveness of estimating survival probabilities with transient models. Survival probabilities were calculated using open population models, and model selection was based on Akaike's Information Criterion. The best model indicated that survival probabilities differed between males and females and varied among years. I found that dispersal was common (30% of resighted birds dispersed off their original study site in 1999), and survival probabilities increased by 6.5-22.9% with the inclusion of dispersed birds. Overall, transient models appeared ineffective at distinguishing permanent emigrants from mortalities. I suggest emigration can have substantial effects on survival probabilities and advise against the use of return rates from small study areas. My results also suggest that transient models may not reliably increase the accuracy of survival probability estimates.

In the second chapter, I use these dispersal data together with BRBP nest success data to determine whether movements were related to reproductive success in the previous year. I compare dispersal distance, dispersal rates and return rates of successful and unsuccessful males and females. Results indicate that median dispersal distance was greater for females than males, and breeding dispersal was related to nest success for females. Unsuccessful females dispersed farther and returned at significantly lower rates than successful females. There were no differences in dispersal distance, dispersal rates, or return rates between successful and unsuccessful males. I suggest other unsuccessful females likely dispersed, and this may explain why survival probabilities for females of this population are lower than those of males.

## ACKNOWLEDGMENTS

I am especially grateful for the support given to me by my committee members; each provided their own unique contributions to this thesis and my graduate education. My co-advisor Dick Hutto was willing to take me as a graduate student even with my rather non-traditional experience and vague plans, and he stuck with me and provided support even as my thesis changed dramatically. Co-advisor Sallie Hejl went to bat for me from the very beginning and was instrumental in both helping me settle on this topic and secure the necessary funds. Kevin McKelvey helped with critical advice, commentary, and funding when I needed it most. Finally, Mark Lindberg came to the University of Montana in just the nick of time to help me define my study and understand just what I trying to do. I am indebted to him for many hours of conversation as I learned about mark-recapture, program MARK and the infamous transient model. Additionally, I thank Erick Greene, who stepped in to provide support when D. Hutto was on sabbatical.

Funding for this study was provided by US Fish and Wildlife Service Nongame Migratory Bird Program, with thanks to Stephanie Jones; US Forest Service Region 1, with thanks to Skip Kowalski; the US Forest Service Rocky Mountain Research Station, with thanks to Kevin McKelvey; and Montana Audubon. The Rocky Mountain Research Station (specifically the Forestry Sciences Lab) and the Montana Cooperative Wildlife Research Unit (especially Vanetta Burton) also provided in-kind support. The USFS Fire Sciences Laboratory provided both the GPS units and the necessary instruction. Greg McDaniels helped greatly with both GPS and GIS. Bausch and Lomb and Eagle Optics also assisted with binoculars. This study could not have been done without the generosity of the Bitterroot National Forest, the Teller Wildlife Refuge and the many

private landowners within the Bitterroot Valley, especially Mr. Evans. Many of these private landowners were very accommodating, and some, honestly, have no idea how much they helped.

I am grateful to Josh Tewksbury who began the larger study, the Bitterroot Riparian Bird Project (BRBP), and with Sallie Hejl's encouragement, realized that he just couldn't do "dispersal" justice as part of his dissertation. Josh generously shared his data and knowledge over the years. I thank the many hard-working, early-rising field assistants for my study and the BRBP, especially Masa Abe, Mike Kuehn, Todd Musci, Natasha Osborne, Pete Ryerson and Carol Snetsinger – their contribution to this study was not trivial and remains much appreciated. Carol in particular helped sort out the methods in my first season. Mary McFadzen assisted greatly in the office, in the kayak and on the slopes.

The graduate students at the University of Montana, particularly in the Wildlife Biology Program and Department of Biological Sciences, helped to make my time both educational and enjoyable. I particularly thank the Hutto/Greene W-T lab, especially Hugh Powell, Karen Short, Brett Walker, Jock Young, Jen Jolivette, Dalit Ucitel, Charles Eldermire, Chris Templeton and Crow White.

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## PREFACE

“Lack of data on dispersal is the major gap in understanding the population dynamics of Neotropical migrants and prescribing effective conservation measures.”

Brawn and Robinson (1996)

Songbird dispersal remains one of the demographic parameters of which we understand the least (Rockwell and Barrowclough 1987). Often, logistical constraints are cited as one of the main reasons for our lack of knowledge of movement patterns (Haas 1998, Lindberg et al. 1998). However, as I discovered, these constraints are surmountable, at least for some species. In the following thesis, I present results from two years of field studies in which my assistants and I searched for marked adult Yellow Warblers (*Dendroica petechia*) to study dispersal patterns.

This study benefited from collaboration with another graduate research study. In 1995 Josh Tewksbury initiated the Bitterroot Riparian Bird Project (BRBP) to study riparian songbirds in the Bitterroot Valley, Montana for his PhD dissertation. One component of the BRBP involved color banding Yellow Warblers on a number of different study sites. During the second and third BRBP seasons, Tewksbury noted that a few individuals banded at one study site had dispersed between years and were breeding at different study sites. With the encouragement of my advisors, I decided to explore these movement patterns for my Master's thesis work, and while Tewksbury and the BRBP continued their research, I spent two field seasons searching for dispersed individuals. Without the collaboration and subsequent sharing of data, this study would

not have been feasible. I have benefited immensely from five years of data and eleven study sites, a treasure for a Master of Science study.

The following thesis is divided into two chapters. The first chapter, *Survival Probability of Adult Yellow Warblers in Montana: Effects of Dispersal and Model Types* compares adult apparent survival probabilities for this population with and without the additional dispersal information. I also explore the applicability of transient models to help quantify dispersal. In the second chapter, *Are patterns of Yellow Warbler breeding dispersal related to nest success?*, I compare differences in dispersal related to seasonal nest success in the previous breeding season. Because these chapters are each written for eventual separate publication, there is considerable overlap in some of the sections, especially the Study Area and Methods.

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## CHAPTER 1:

# SURVIVAL PROBABILITY OF ADULT YELLOW WARBLERS IN MONTANA: EFFECTS OF DISPERSAL AND MODEL TYPES

### ABSTRACT

Annual survival probability estimates for songbirds are generally conservative because dispersal between breeding seasons is not differentiated from mortality. Presently, knowledge of between-year breeding dispersal is lacking for most songbirds. To assess adult survival probabilities and dispersal, 436 Yellow Warblers (*Dendroica petechia*) were color-banded and resighted over five breeding seasons at 11 study sites in the Bitterroot Valley, Montana. During the last two of these seasons, field assistants and I searched extensively for marked warblers between and surrounding these sites. I compared survival probabilities estimated with and without this added dispersal information and assessed the effectiveness of adjusting survival probabilities with transient models. Survival probabilities were calculated using open population models, and model selection was based on Akaike's Information Criterion (AIC) within program MARK. The best model indicated that survival probabilities differed between males and females and varied among years. I found that dispersal off the study site was common (in 1999, 30% of resighted birds were found off their original study site), and survival probabilities increased by 6.5-22.9% ( $0.02 \pm 0.07 - 0.106 \pm 0.06$ ) with the inclusion of dispersed birds. Overall, transient models appeared ineffective at distinguishing permanent emigrants from mortalities. I suggest that emigration can have substantial

effects on survival probabilities and advise against the use of return rates from small study areas. In addition, my results suggest that transient models may not reliably increase the accuracy of survival probability estimates.

Keywords: apparent survival probability, breeding dispersal, *Dendroica petechia*, mortality, transient models, Yellow Warbler

## INTRODUCTION

Loss, alteration, and fragmentation of songbird habitat may cause changes in population status (Terborgh 1989, Hagen and Johnston 1992, Donovan et al. 1995a, 1995b, Faaborg et al. 1995, Freemark et al. 1995). Population status is commonly assessed by monitoring trends in abundance over time through programs such as the North American Breeding Bird Survey (Sauer et al. 1999). Presently, analyses of trend data are disputable, at times contradictory (e.g., Bohning-Gaese et al. 1993, James et al. 1996, Sauer et al. 1996), and cannot inform us of the reasons for population changes (Van Horn 1983, James and McCulloch 1995, Thompson et al. 1998, Nichols 1999). Accurate estimates of demographic parameters are necessary to understand songbird population dynamics and the underlying mechanisms causing population changes (Temple and Wiens 1989, Brawn and Robinson 1996, Loery et al. 1997). Knowledge of demographic parameters may also clarify discrepancies in population trend analyses (Brawn and Robinson 1996).

The demographic parameters responsible for changes in population size are fecundity, survival probability, and dispersal probability (emigration and immigration)



(Temple and Wiens 1989, Hestbeck et al. 1991, Brownie et al. 1993, Loery et al. 1997, Koenig et al. 2000). Fecundity in birds is estimated by combining data from nest monitoring studies with seasonal productivity models (Donovan et al. 1995b, Pease and Gryzbowski 1995). Adult survival probability is commonly estimated from recapturing or resighting marked individuals over multiple years at one or more study sites (Clobert and Lebreton 1991, Lebreton et al. 1992). Estimates of juvenile survival probability are not generally available because juveniles commonly disperse from natal areas (Greenwood and Harvey 1982). These estimates have often been obtained by dividing adult mortality by mean number of young fledged (Ricklefs 1973, Anders et al. 1997), resulting in rates  $\frac{1}{2}$  to  $\frac{3}{4}$  of adult survival (Greenberg 1980, Temple and Carey 1988, Thompson 1993, Donovan et al. 1995b, Brawn and Robinson 1996). Arguably, the least known and most often ignored parameter is dispersal (Rockwell and Barrowclough 1987, Brawn and Robinson 1996; Koenig et al. 2000; Walters 2000). Because natal and breeding dispersal are difficult to observe, permanent emigration and mortality are not distinguished in estimates of passerine survival (Zeng and Brown 1987, Payne and Payne 1990, Peach 1993, Johnston et al. 1997).

Although avian adult survival probability is a commonly reported and critical demographic parameter, its use and definition are inconsistent. *True survival probability* ( $s$ ), often the parameter of interest, is defined as the probability that an individual alive at time  $t$  survives to time  $t + 1$ . This parameter is generally estimated with band recovery models (Brownie et al. 1985) and, in some cases, with multistate models (Brownie et al. 1993, Nichols and Kaiser 1999). *Apparent survival probability* ( $\phi$ ) is defined as the probability that an individual alive at time  $t$  survives to time  $t + 1$  and does not

permanently emigrate from the study area between time  $t$  and  $t + 1$ . Apparent survival probability is usually estimated with open population models (Lebreton et al. 1992), and in these models, true survival and permanent emigration probabilities are confounded, but the detection probability ( $p$ ; the probability of detection, given a bird is alive and in the population associated with the study area) is estimated separately. *Return rates* are the product of apparent survival probability and detection probability (Martin et al. 1995, Lindberg et al. 1998, Anderson et al. *in press*). True survival, permanent emigration, and capture probabilities are all confounded in this metric, yet many bird studies erroneously report the *return rate*, as an estimate of *apparent or true survival probability* (Lebreton et al. 1993; Martin et al. 1995).

Estimates of true survival probability are unlikely to be obtained for small passerines without additional advances in radio marking technology (or the initiation of a hunting season on songbirds). Therefore, we need assessments of the extent that permanent emigration affects estimates of apparent survival probability. These assessments require data on the movements of birds between breeding seasons. In breeding bird studies from relatively small, single study areas, dispersal is generally not considered in demographic analysis, although some have proposed mathematical adjustments to correct for bias in dispersal distance due to finite study areas (Cunningham 1986, Barrowclough 1987, Zeng and Brown 1987, Baker et al. 1995). However, to my knowledge, few songbird mark-resight studies were designed with the objective of resighting individuals outside the boundaries of the original study area (but see Tiainan 1983, Beletsky and Orians 1987, Jakobsson 1988, Wheelwright and Mauck

1998, Woodworth et al. 1998), and none with the goal of using this information to refine estimates of adult survival probability.

An alternative approach for adjusting estimates of apparent survival probability for permanent emigration is transient modeling (DeSante et al. 1995, Pradel et al. 1997, Loery et al. 1997). These models attempt to identify and exclude transients (individuals that are thought to be permanent emigrants) from estimates of survival probability. However, heterogeneity in survival probability and capture probability may bias estimates of survival probability in these models (Carothers 1973). Individuals that are excluded because they are believed to be transients may be mortalities or individuals with low capture probabilities. Therefore, we might expect these transient models to produce over-estimates of survival probabilities.

This study was inspired by the combination of a paucity of accurate avian survival and dispersal information and evidence of year-to-year movements of a population of Yellow Warblers (*Dendroica petechia*) that breed primarily within riparian corridors. My primary objectives were to 1) refine apparent survival estimates using knowledge of between-year breeding dispersal; 2) determine the value of altering the sampling design to include extended searches for marked individuals surrounding the study sites; and 3) assess the effectiveness of transient models to reduce the effects of permanent emigration on estimates of songbird survival probability.

## **STUDY AREA AND METHODS**

I conducted my research on seven study sites on a combination of public and private lands along the Bitterroot River in western Montana and four smaller sites along

riparian drainages within the western foothills, primarily in the Bitterroot National Forest (Fig. 1) (a subset of the sites described in Tewksbury et al. 1998). These core sites averaged 15 ha in size (range 5-20 ha) with elevations of 1050-1350 m. All sites were primarily deciduous riparian habitats. The Bitterroot River sites were dominated by deciduous trees and shrubs, especially black cottonwood (*Populus trichocarpa*) and were surrounded by residential areas, agricultural lands (cultivated and/or grazed by cattle or horses), and deciduous and coniferous forest communities. The foothill sites were dominated by shrubs and deciduous trees, especially quaking aspen (*Populus tremuloides*), and were surrounded by coniferous forests and some grazed lands. Study sites were initially chosen to minimize differences in habitat character among sites, although there was a range in landscape variation surrounding the sites (see Tewksbury et al. 1998).

During the breeding season, Yellow Warblers are the most common species of deciduous riparian areas within the Rocky Mountain West (Tewksbury et al. *in press*). In western Montana, they arrive on the breeding grounds and begin to establish territories during the last two weeks of May, with males generally arriving two to seven days before females (Tewksbury and Cilimburg unpubl. data). They are found in association with streamside shrubs or large deciduous trees, especially black cottonwood, and may also be found within the deciduous vegetation of residential areas (Hutto and Young 1999; Cilimburg unpubl. data).

During the 1995-1998 breeding seasons (approximately 23 May – 1 August), field assistants and I created territory maps of breeding Yellow Warblers on the 11 core sites and target mist-netted adults, often using playbacks of songs and calls. Both females and

males respond to playbacks, though females less so, especially during incubation. We aged and sexed all birds captured and marked individuals with one US Fish and Wildlife Service aluminum band and a unique combination of three color bands. As this was part of a larger study (Tewksbury et al. 1998, Tewksbury 1999), field assistants searched for and monitored nests, mist-netted, or resighted marked individuals at each core site every one to three days throughout the season. The perimeters of each site (approximately 100-200 m depending on available habitat) were searched for banded birds in 1996 and 1997.

During the 1998 and 1999 seasons, I expanded the resighting area and, together with an assistant, searched for banded individuals within suitable habitat along the Bitterroot River between and surrounding the core sites (Fig. 1). We concentrated our efforts around the sites where the most birds were banded (sites #1, 2, 3, 4, 6). We surveyed about 85-90% of available Yellow Warbler habitat between sites #1-3 during each of these two seasons; surveys around the other sites were less complete (see Fig. 1). For these searches, we systematically traveled sections of the river corridor, sighted individuals and determined the presence or absence of bands and, when present, the color combination. We again used song playbacks to attract pairs and played songs in appropriate warbler habitat when there was no visible or audible activity. As males are commonly located first, we placed extra effort in sighting the female associated with each male. We approached sites by foot whenever possible and used kayaks to access small islands. Resighting time for the expanded dispersal searches totaled approximately 220 hours in 1998 and 380 hours in 1999 and generally occurred between 0600 and 1300 hours. In 1998, sampling occurred from 26 May – 8 July. In 1999, I divided the season in half, resighting from 27 May – 12 June and repeating the surveys from 20 June – 12

July. I split the season to avoid confounding survival probabilities and detection probabilities in the fully time-dependent Cormack-Jolly-Seber models (Lebreton et al. 1992). This allowed time-specific parameter estimations to be assessed in 1999.

Territory centers were used to determine the distance moved between years. I used a *Trimble Geoexplorer* GPS unit to mark exact locations of banded individuals found off the core sites in 1998 and 1999. In 1999, the territory centers for all banded individuals and the boundaries of all core sites were mapped via GPS. From the territory site maps, I digitized the approximate territory center for each bird in 1995-1998, and from these, computed straight-line dispersal distances using UTM coordinates.

*Data analysis – parameter estimation.* – I used Cormack-Jolly-Seber (CJS) models to estimate annual apparent survival probabilities ( $\phi$ ) and detection probabilities ( $p$ ) (Lebreton et al. 1992, Nichols 1996). The model set was determined *a priori* and was based on Yellow Warbler biology and the question of interest (Burnham and Anderson 1998, Anderson and Burnham 1999). For both  $\phi$  and  $p$ , I assessed gender- and year-specificity and the interaction between these variables (Table 1).

To assess how resighting in the expanded search areas affected estimates of apparent survival and detection probabilities, I conducted two analyses. The data for the first analysis included all individuals banded and those resighted in subsequent years on the study site on which they were originally banded (hereafter termed “core analysis”). For the second analysis, I included core analysis data, banded birds sighted off the study sites (via the extended searches in 1998 and 1999), and sightings of individuals on sites other than their site of origin (hereafter termed “dispersal analysis”).

I used program MARK (White and Burnham 1999) to generate maximum likelihood estimates of  $\phi$  and  $p$  and relied on Akaike Information Criteria (AICc, adjusted for sample size) to determine the best approximating model among the suite of candidate models. This approach determines the model that best explains the data while incorporating the fewest parameters, thus balancing tradeoffs between sampling variance and bias (Burnham and Anderson 1998, Anderson and Burnham 1999). To test my assumptions of model fit (lack of independence among individuals, heterogeneity in  $\phi$  and/or  $p$ ), I ran bootstrap Goodness of Fit (GOF) tests (1,000 replications) on the global model for both sets of analyses (Lebreton et al. 1992, Burnham and Anderson 1998). From this analysis, I calculated  $\hat{c}$ , the variance inflation factor, defined as the global model deviance divided by the mean bootstrap deviance (White and Burnham 1999).

*Data analysis – transient models.* – Pradel et al. (1997) developed mark-recapture models that eliminate transients (permanent emigrants) from a sample to provide estimates of true survival for residents. These models assume individuals resighted at least once are residents, and a high but unknown proportion of those initially marked and never resighted are transients. Transients are operationally defined as having an apparent survival probability of 0.00 (Loery et al. 1997, Pradel et al. 1997). According to Pradel et al. (1997), two modeling approaches can be used to detect transients, the ad hoc model and the Robson model. For the ad hoc model, parameters are estimated only for residents, those individuals recaptured or resighted at least once. With the Robson model, apparent survival probabilities are estimated separately for those individuals newly captured and those individuals resighted at least once. The proportion of residents in the population is then estimated by dividing the survival probability of the newly

marked individuals by the survival probability of the residents. Pradel et al. (1997) showed that the ad hoc model was a reasonable approximation of the Robson model when detection probabilities were high, and my data permitted a comparison of both approaches.

To assess the appropriateness of using transient models to clarify the proportion of residents and transients, I ran the ad hoc and Robson models using the core analysis data set and compared these results to estimates obtained from the dispersal analysis. I used program MARK (White and Burnham 1999), altering the input file for the ad hoc model (suppressing the first capture within the capture history for each individual), and altering the parameter index matrix within MARK for the Robson model (Pradel et al. 1997). I report the survival probabilities and detection probabilities using the model structure from the previously determined best approximating model for the core analysis.



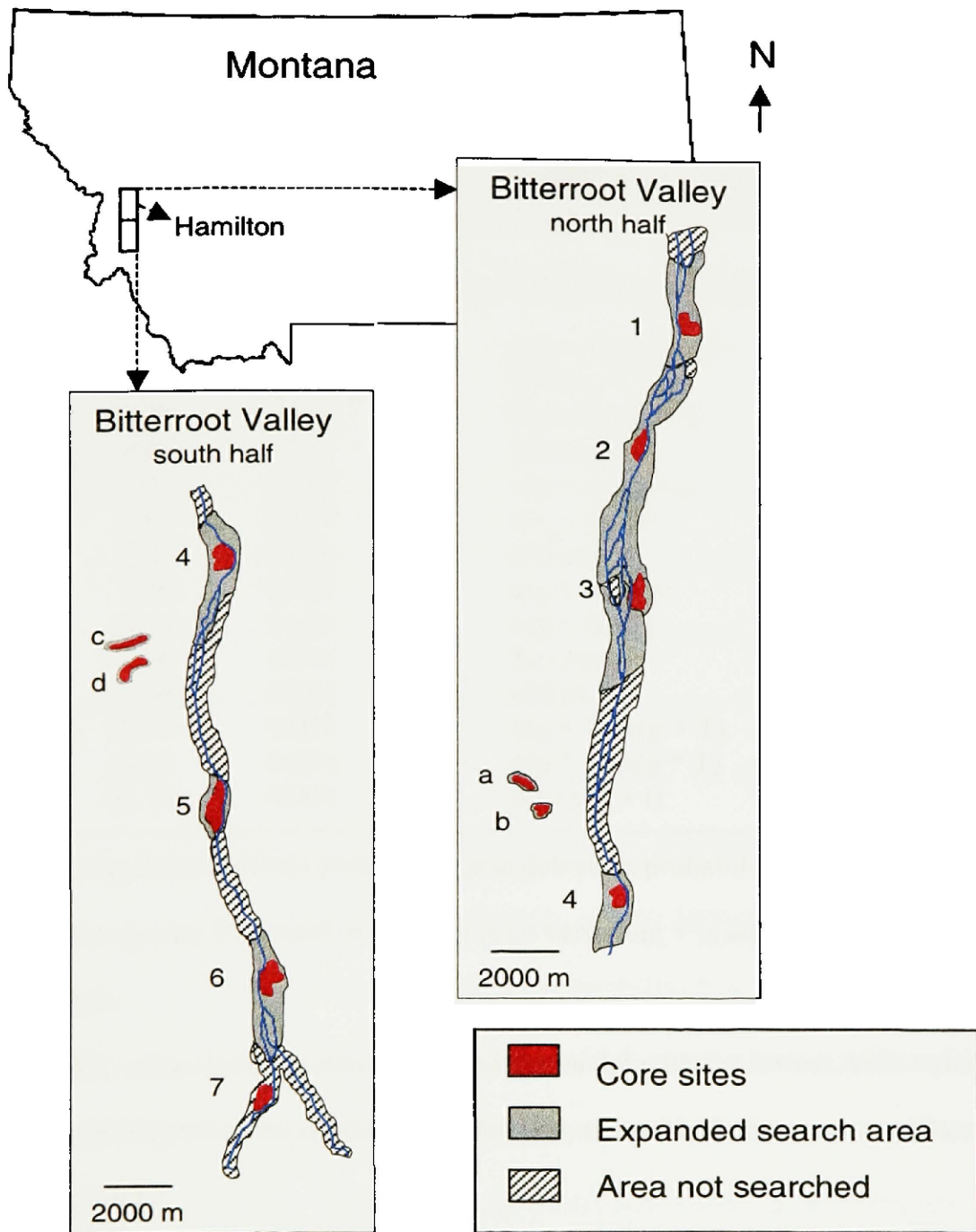


Fig 1. The core sites and expanded search areas within the riparian corridor surrounding the Bitterroot River, Ravalli County, MT. Sites #1 – 7 are the core Bitterroot River sites; sites a – d are the core foothill sites. The core sites were studied 1995-1999; resighting in the expanded search area occurred in 1998-1999.

TABLE 1. Candidate sets of Cormack-Jolly-Seber models used in program MARK ranked by Akaike's Information Criterion (AICc; adjusted for small sample size) for the core and dispersal analyses.

CORE ANALYSIS				DISPERSAL ANALYSIS			
Model <sup>a</sup>	$\Delta$ AICc <sup>b</sup>	AICc weight <sup>c</sup>	np <sup>d</sup>	Model <sup>a</sup>	$\Delta$ AICc <sup>b</sup>	AICc weight <sup>c</sup>	np <sup>d</sup>
$\phi(g + t) p(g + T)$	0.00	0.213	9	$\phi(g + t) p(g + T)$	0.00	0.406	9
$\phi(t) p(g + T)$	0.11	0.202	8	$\phi(t) p(g + T)$	1.08	0.236	8
$\phi(g + t) p(\cdot)$	0.28	0.186	6	$\phi(g + t) p(g + t)$	1.52	0.190	11
$\phi(g + t) p(g)$	0.89	0.137	7	$\phi(t) p(g + t)$	2.31	0.128	10
$\phi(g + t) p(T)$	2.41	0.064	8	$\phi(g * t) p(g * t)$	6.10	0.019	18
$\phi(t) p(g)$	2.57	0.059	6	$\phi(g + t) p(t)$	6.19	0.018	10
$\phi(t) p(g + t)$	2.67	0.056	10	$\phi(t) p(t)$	10.63	0.002	9
$\phi(g + t) p(g + t)$	2.80	0.053	11	$\phi(g + t) p(g)$	14.57	0.000	7
$\phi(t) p(\cdot)$	4.22	0.026	5	$\phi(g + t) p(\cdot)$	15.50	0.000	6
$\phi(t) p(t)$	7.78	0.004	9	$\phi(t) p(g)$	17.17	0.000	6
$\phi(g * t) p(g * t)$	12.50	0.000	18	$\phi(t) p(\cdot)$	21.59	0.000	5
$\phi(g + T) p(g + T)$	32.33	0.000	6	$\phi(g + T) p(g + T)$	43.89	0.000	6
$\phi(g) p(\cdot)$	50.33	0.000	3	$\phi(g * T) p(g * T)$	47.22	0.000	8
$\phi(g + T) p(g)$	60.14	0.000	5	$\phi(g) p(g + t)$	53.72	0.000	7

<sup>a</sup> Model type.  $\phi$  is apparent survival probability;  $p$  is detection probability;  $g$  is group (male, female),  $t$  is time (year);  $T$  is trend in time;  $(\cdot)$  is no variation;  $+$  is additive effect;  $*$  is interaction effect.

<sup>b</sup> Difference in AICc values between this model and the model with the lowest AICc value.

<sup>c</sup> Estimates of the likelihood of the model, given the data; normalized to sum to one (Burnham and Anderson 1998).

<sup>d</sup> Number of estimable parameters.

## RESULTS

*Return and dispersal of marked birds.* – Between 1995-1998, 149 females and 287 males were banded, with 86% of these from the Bitterroot River sites and 14% from the foothill sites. Of these, 44 females and 133 males were resighted at least once in any one or more of the subsequent years. In 1998, the first year of the expanded searches, 17.0% (9 of 47) of the banded birds resighted were found either off the core sites or on a core site other than their site of origin, and in 1999 this increased to 29.6% (21 of 71; five of these 21 were also found dispersed off the sites in 1998). Only four of the birds found via the expanded searches were within 0.5 km of their original banding site. Distance moved between years for all resighted birds ranged from 4 – 24,728 m (for females, median = 153 m; for males, median = 86 m) and the distribution of detected dispersal distance was strongly skewed to the right (Fig. 2). Although the linear area searched surrounding and between the core sites was incomplete (Fig. 1), the farthest distance that an individual could have dispersed and been detected was approximately 45 km.

*CJS model assumptions and model selection.* – The global models fit the data, and no overdispersion adjustments were made (core analysis,  $\hat{c} = 0.952$ ; dispersal analysis,  $\hat{c} = 0.995$ ) (White and Burnham 1999). The best approximating model for both the core and dispersal analyses indicated an additive effect of time on survival probability for males and females (Table 1). Detection probability also differed between sexes with an increasing trend over time (Table 1). Any model with an AIC value within two points of the best model is thought to be a reasonable model given the data (Burnham and Anderson 1998). There were four models for the core analysis and three models for the dispersal analysis with  $\Delta AIC < 2.00$  (Table 1), and estimates of  $\phi$  and  $p$  are slightly

different with each model (Appendix I and II). The second best model for both analyses suggested apparent survival varied over time although not between sexes. For the results described below, I report the estimates from the best model ( $\Delta\text{AICc} = 0.00$ ); however, the inference would not change substantially with any of the other estimates (Appendix I and II).

*Estimates of apparent survival probability and detection probability.* – Apparent survival probabilities from the dispersal analysis were consistently higher than survival probabilities from the core analysis for both males and females (Table 2 and Fig. 3A and 3B). The degree of difference depended on year and gender, with  $\phi$  being 0.024 (SE = 0.066) – 0.106 (SE = 0.064) higher when the dispersed birds were included. For males, the core analysis mean  $\phi$  was 0.418 (SE = 0.034, range 0.346-0.490), and the dispersal analysis mean  $\phi$  was 0.493 (SE = 0.037, range 0.410-0.588). For females, the core analysis mean  $\phi$  was 0.350 (SE = 0.033; range 0.28-0.42), and the dispersal analysis mean  $\phi$  was 0.413 (SE = 0.037; range 0.33-0.588).

For each year, male detection probabilities were consistently higher than those of females (Table 3) in both analyses. Estimates of detection probabilities in the core analysis were consistently higher than in the dispersal analysis (Table 3). The greatest difference between the two analyses occurred in the first two years of resighting for both sexes; the core  $p$ 's were 0.06-0.11 higher. For the last two years,  $p$  estimates differed by only 0.02 – 0.06.

*Estimates using transient models.* – As expected based on Pradel et al's (1997) finding, the ad hoc model and the previously marked birds within the Robson model provided similar estimates of apparent survival probabilities (Table 2). For males, the ad

hoc  $\phi$  were higher than the core analysis  $\phi$  for 1996 only; in the Robson model, previously marked  $\phi$ s were higher than the core  $\phi$  for 1996 and slightly higher for 1998 (Table 2). The ad hoc  $\phi$  estimates were also higher than the dispersal analysis  $\phi$  for 1996, but lower in the following years (Table 2 and Table 4). In 1997,  $\phi$  for the newly marked males was higher (0.02) than the previously marked. Based on the Robson model, an estimated 94% of the sampled population males were residents. For females, survival estimates from the transient models did increase relative to both core and dispersal analysis (Table 2 and Table 4), but the transient model estimates varied considerably year to year and had relatively high levels of variation ( $\pm 0.08$ - $0.17$  SE). The Robson model results suggested 54% of females marked were residents.

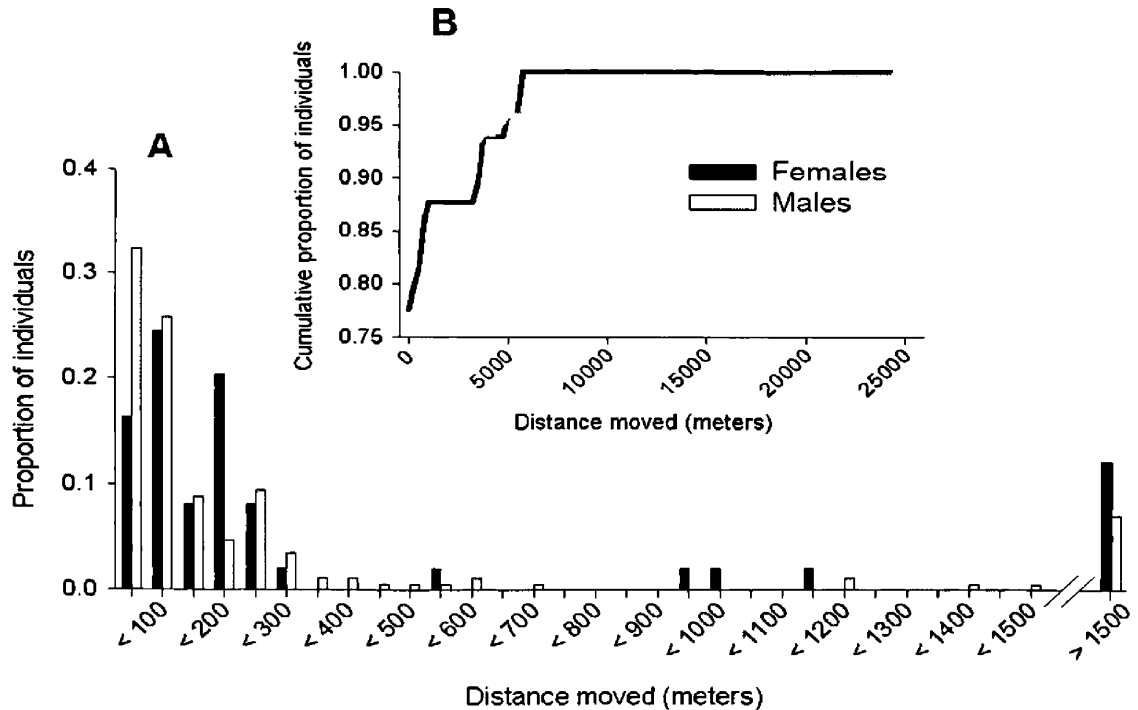


Fig. 2: (A) Distribution of between-year breeding dispersal for adult male ( $n = 169$ ) and female ( $n = 49$ ) Yellow Warblers, 1996 –1999, in 50 m increments to 1500 m (range 4-24,728 m). Twelve percent of females and 7% of males dispersed farther than 1500 m between years. Distance moved is non-cumulative (e.g. "< 200" is between 100 and 200). (B) Cumulative distribution functions of dispersal distance for both sexes, showing the proportion of resighted individuals that were within a given distance of their previous territory center.

TABLE 2. Adult Yellow Warbler estimates of apparent survival probability ( $\pm 1$  SE) from the best approximating model for the four different analyses. Core analysis data include all individuals resighted on their original banding site; dispersal analysis data include all individuals resighted on any of the core sites and within the expanded search areas.

DATA	1995	1996	1997	1998
<b>Core analysis</b>				
males	0.49 (0.06)	0.46 (0.05)	0.35 (0.05)	0.37 (0.05)
females	0.42 (0.07)	0.39 (0.06)	0.28 (0.05)	0.31 (0.05)
<b>Dispersal analysis</b>				
males	0.59 (0.06)	0.49 (0.05)	0.41 (0.05)	0.48 (0.04)
females	0.51 (0.07)	0.41 (0.06)	0.33 (0.05)	0.40 (0.05)
<b>Transient models</b>				
<b>Ad hoc model<sup>a</sup></b>				
males	NA	0.57 (0.11)	0.28 (0.06)	0.38 (0.08)
females	NA	0.64 (0.12)	0.34 (0.09)	0.46 (0.10)
<b>Robson model<sup>b</sup></b>				
Newly marked				
males	0.50 (0.06)	0.43 (0.06)	0.34 (0.08)	0.39 (0.07)
females	0.30 (0.07)	0.26 (0.10)	0.31 (0.10)	0.22 (0.07)
Previously marked (all others)				
males	NA	0.50 (0.08)	0.32 (0.07)	0.39 (0.09)
females	NA	0.62 (0.17)	0.33 (0.13)	0.45 (0.15)

<sup>a</sup> Using core analysis data, capture history was truncated to include only individuals resighted at least once.

<sup>b</sup> Using core analysis data,  $\phi$  for newly marked (one year post banding) were modeled separately from those resighted at least once.

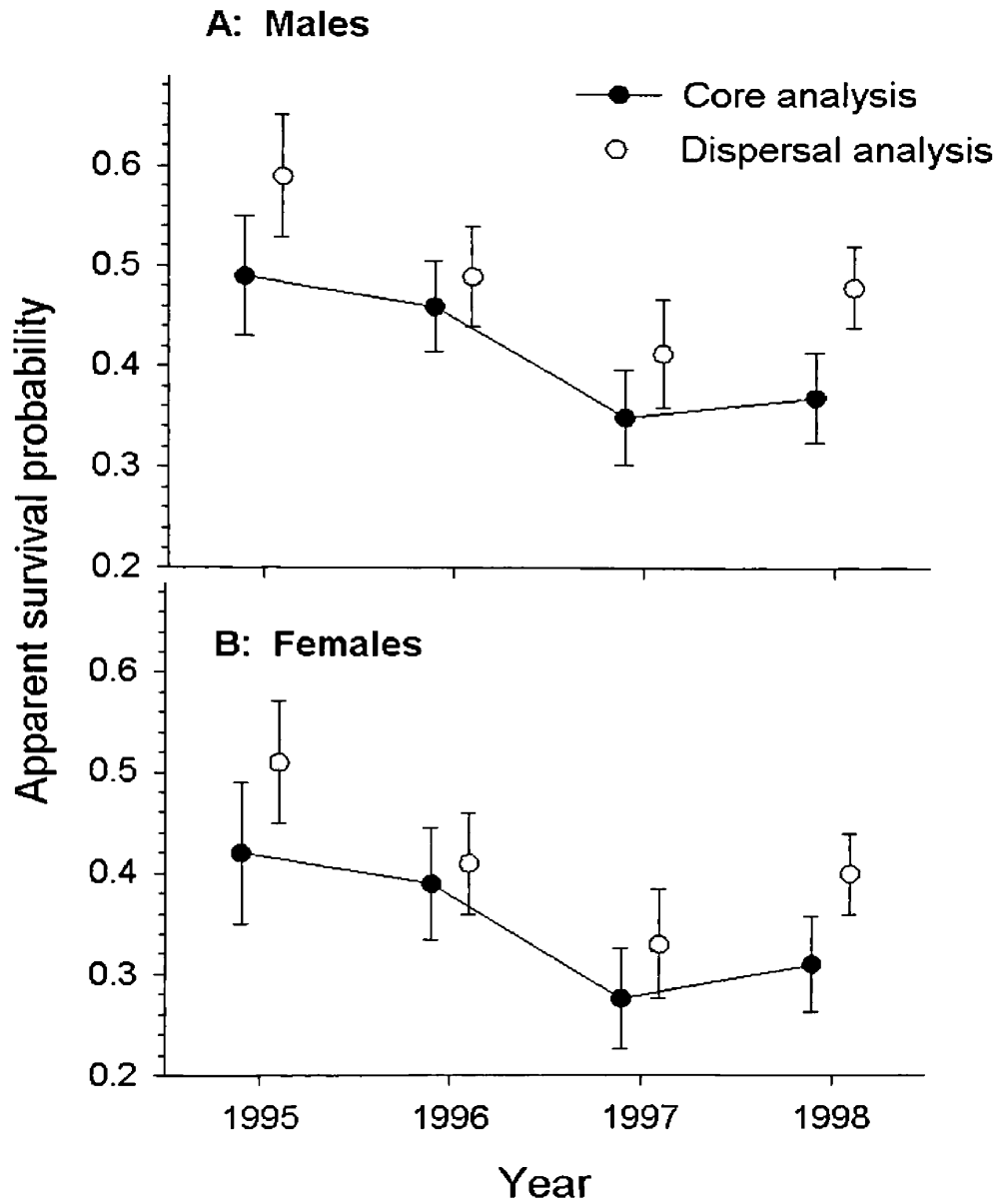


Fig. 3. Apparent survival probabilities ( $\pm 1$  SE) for adult Yellow Warblers in the Bitterroot Valley, MT, 1995-1998 estimated without accounting for dispersal (core analysis) compared to apparent survival probabilities that incorporate dispersal (dispersal analysis). Data for males (A) and females (B) are from the best approximating model (see Table 2).



TABLE 3. Adult Yellow Warbler estimates of detection probability ( $\pm 1$  SE) from the best approximating model for the four different analyses. Core analysis data include all individuals resighted on their original banding site; dispersal analysis data include all individuals resighted on any of the core sites and within the expanded search areas.

DATA	1996	1997	1998	1999
<b>Core analysis</b>				
males	0.78 (0.07)	0.84 (0.06)	0.88 (0.04)	0.92 (0.04)
females	0.56 (0.12)	0.65 (0.09)	0.73 (0.08)	0.80 (0.08)
<b>Dispersal analysis</b>				
males	0.69 (0.07)	0.78 (0.04)	0.85 (0.03)	0.90 (0.03)
females	0.45 (0.09)	0.56 (0.08)	0.67 (0.07)	0.77 (0.07)
<b>Transient models</b>				
<b>Ad hoc model <sup>a</sup></b>				
males	NA	0.79 (0.14)	0.92 (0.06)	0.97 (0.03)
females	NA	0.57 (0.20)	0.81 (0.12)	0.93 (0.08)
<b>Robson model <sup>b</sup></b>				
males	0.80 (0.07)	0.84 (0.04)	0.88 (0.04)	0.90 (0.04)
females	0.67 (0.11)	0.73 (0.08)	0.78 (0.07)	0.83 (0.07)

<sup>a</sup> Using core analysis data, capture history was truncated to include only individuals resighted at least once.

<sup>b</sup> Detection probability modeled as with the core analysis. *A priori* there was no reason to believe detection probability would differ between the newly marked individuals and those resighted at least once.

TABLE 4. Differences in estimates of Yellow Warbler apparent survival

probability ( $\pm 1$  SE of the difference) for the transient models relative to the dispersal analysis (from Table 2). “+” indicates the transient estimate was higher than the dispersal estimate; “-” indicates the transient estimate was lower.

DATA	1995	1996	1997	1998
<b>Dispersal analysis</b>				
males	0.59 (0.06)	0.49 (0.05)	0.41 (0.05)	0.48 (0.04)
females	0.51 (0.07)	0.41 (0.06)	0.33 (0.05)	0.40 (0.05)
<b>Transient models</b>				
<b>Ad hoc model <sup>a</sup></b>				
males	NA	+ 0.08 (0.12)	- 0.13 (0.08)	- 0.10 (0.09)
females	NA	+ 0.23 (0.13)	+ 0.01 (0.10)	+ 0.06 (0.11)
<b>Robson model <sup>b</sup></b>				
Newly marked				
males	- 0.09 (0.08)	- 0.06 (0.08)	- 0.07 (0.09)	- 0.09 (0.08)
females	- 0.21 (0.10)	- 0.15 (0.12)	- 0.02 (0.11)	- 0.18 (0.09)
Previously marked (all others)				
males	NA	+ 0.01 (0.09)	- 0.09 (0.09)	- 0.09 (0.10)
females	NA	+ 0.21 (0.18)	0.00 (0.14)	+ 0.05 (0.16)

<sup>a</sup> Using core analysis data, capture history was truncated to include only individuals resighted at least once.

<sup>b</sup> Using core analysis data,  $\phi$  for newly marked (one year post banding) were modeled separately from those resighted at least once.

## DISCUSSION

*Apparent survival probabilities.* – My analysis indicates that emigration can have substantial effects on estimates of apparent survival probability for Yellow Warblers. Depending on the year, estimates of  $\phi$  increased by 6.5 to 22.9% for males and 5.1 to 29.0% for females when I increased the search area. These results suggest that researchers must carefully consider the factors affecting apparent survival probability (permanent emigration and mortality) when study areas are small relative to the ecology of the species of interest.

Given the potential impacts of permanent emigration on interpretation of apparent survival probability as an estimate of true survival probability, I believe that any attempt to use return rates as an estimate of true survival probability is probably unwise. For example, in 1998 there were 37 female and 52 males banded on the Bitterroot River sites. The return rate in 1999 for these sites combined would have been 0.24 for females, compared to an apparent survival probability of 0.40 for the dispersal analysis; for males the return rate would have been 0.42, compared to an apparent survival probability of 0.48. Additionally, differences in return rates for males and females in this study were caused by varying effects of permanent emigration and detection probability on these estimates. These results contradict the suggestion by some investigators that movements of migratory songbirds are well understood and that return rates are reasonable substitutes for survival rates (e.g. Mewaldt and King 1985, Villard et al. 1995). Furthermore, return rates are difficult to compare because of spatial and temporal variation in both survival and movement probabilities. For example, at least three passerine studies incorporating multiple study areas have shown that the character of the site affected site fidelity and

therefore rates of return. Lawn (1994) color banded Willow Warblers (*Phylloscopus trochilus*) at four adjacent sites of varying habitat quality and found rates of return to the site of banding varied from 14 – 41%. However, he documented breeding dispersal between sites, demonstrating that these return rates differed because of inconsistencies in site fidelity, not survival. Two other studies found differential returns depending on breeding success and quality of site (Black-throated Blue Warbler, *Dendroica caerulescens*, Holmes et al. 1996; Bobolink, *Dolichonyx oryzivorus*, Bollinger and Gavin 1989). However, if individuals are highly site faithful, they may return to unsuitable habitat, resulting in a time lag of responses to habitat modifications (Wiens and Rotenberry 1985, Temple and Wiens 1989).

Studies that find differential returns of one or both sexes based on breeding success in the year prior (e.g., Beletsky and Orians 1987, Bollinger and Gavin 1989, Roth and Johnson 1993, Lemon et al. 1996, Haas 1998, Forero et al. 1999; reviewed in Greenwood and Harvey 1982) are widespread in the avian literature, yet most cannot differentiate dispersal from mortality because those birds that were assumed to have dispersed were never located. In this study, four of the six female Yellow Warblers that experienced seasonal nest failure and were located again had dispersed over 2000 m (see Chapter 2). Haas (1998) experimentally showed that differences in returns for American Robins (*Turdus migratorius*) and Brown Thrashers (*Toxostoma rufum*) were related to breeding success in the previous season and not because of reneating stress (i.e. increased reproductive effort) or the quality of the individual.

To my knowledge, this is the first songbird study explicitly designed to use observations of banded songbirds to compare apparent survival probabilities and

detection probabilities in an expanded search area to those from a core search area. Others have used mark-recapture with the Constant Effort Mist Netting scheme (CEMN) and assessed changes in the apparent survival probabilities of songbirds when one study area was expanded to include multiple study areas (Peach et al. 1990, Peach 1993). Peach et al. (1990) captured Reed Warblers (*Acrocephalus scirpaceus*) and Sedge Warblers (*Acrocephalus schoenobaneus*) over 23 years and estimated  $\phi$  and  $p$  from one sampling area and again when a secondary study area was included. Survival probability was 29% higher for Reed Warblers and 54% higher for Sedge Warblers when both study sites were included. However, their comparison involved two small study sites only 80 m apart. I had a total of 11 study sites, with a 3.5 km minimum distance between the main Bitterroot River sites, although paired foothill sites were as close as 0.5 km (Fig. 1). In a separate study, Peach (1993) compared  $\phi$  for five different songbird species from single and multiple study sites and reported that with inclusion of the recaptures from additional study sites,  $\phi$  changed from a decrease of 11% to an increase of 128%, depending on the species. However, direct comparisons between CEMN studies and intensive resighting studies such as ours are difficult because CEMN studies are more likely to violate Cormack-Jolly-Seber model assumptions of equal catchability of individuals and geographic closure (resident birds moving in and out of the netting area) (Thompson et al. 1998).

Other non-passerine studies have effectively used multistate models to estimate survival probabilities, detection probabilities and movement parameters. Spendelov et al. (1995) sampled four large breeding colonies of Roseate Terns (*Sterna dougallii*) and found estimates of apparent survival probabilities increased by 8% as compared to

estimates from a previously studied single colony, with this difference attributed entirely to movement and not mortality. Lindberg et al. (1998) estimated dispersal probabilities and natal and breeding philopatry in a metapopulation of Black Brant (*Branta bernicla nigricans*). These studies benefited from large sample sizes and discreet breeding sites, conditions not generally available for passerines.

The assumption that adult songbird dispersal is a negligible parameter (e.g., Pulliam et al. 1992, Villard et al. 1995) appears widespread in the literature (Koenig et al. 2000) and is often explicit in modeling attempts such as some spatially explicit population models (e.g., Pulliam et al. 1992). Assumptions regarding lack of dispersal stem from evidence of strong site-fidelity. For example, many studies report that adults commonly return to the same territory as the previous year (e.g., Prairie Warbler (*Dendroica discolor*), Nolan 1978; Willow Warbler (*Phylloscopus trochilus*), Tiainen 1983; Painted Bunting (*Passerina ciris*), Lanyon and Thompson 1986; Indigo Bunting (*Passerina cyanea*), Payne and Payne 1990; Savannah Sparrow (*Passerculus sandwichensis*), Wheelright and Mauck 1998; White-eyed Vireo (*Vireo griseus*), Hopp et al. 1999). However, as this study demonstrates, site faithfulness by some in a population tells us little about the proportion of birds that may have dispersed.

*Transients.* – I expected estimates from the transient models (ad hoc and Robson models) to exceed estimates from the dispersal analysis if I did not sample all permanent emigrants in the expanded search or if “transients” that were eliminated from the transient models included individuals other than permanent emigrants. For example, transients eliminated from the analysis may include individuals from the resident population with low survival or recapture probability, especially in systems with

extensive heterogeneity. Without knowing true survival, I am limited in my ability to evaluate the performance of transient models in this study. Nonetheless, transient models did not provide estimates that were consistent with the anticipated patterns and these estimates were less precise because of the reduction in the data set. As discussed, survival estimates from the dispersal analysis were consistently higher than estimates from the core analysis, although the degree of difference in estimates between these analyses was variable. In contrast, estimates of survival probability from the ad hoc models were not consistently higher than estimates from the dispersal analysis; in two of the six comparisons  $\phi$  estimates were lower than  $\phi$  estimates from the dispersal analysis. Estimates from the Robson models were consistently lower than estimates from the dispersal analysis for newly marked individuals, but estimates for previously marked individuals were equal or lower than dispersal analysis estimates in three of the six comparisons. Interestingly, survival estimates for newly marked males were higher or equal to estimates for previously marked birds in 1997 and 1998 and elimination of some of the newly marked birds from the transient models may have lowered survival estimates for the transient models.

Such discrepancies among estimates of survival probabilities makes interpretation challenging. I suggest that use of transient models in the presence of few transients may produce misleading results. I agree with Pradel et al. (1997) that diagnostic analysis about the presence of transients should be performed before using transient models. I am also concerned about the inconsistent pattern of transient model estimates and the elimination of individuals from an analysis. Inappropriately excluding individuals from an analysis results in unnecessary increases in sampling variance. Furthermore, I

question the biological rationale for excluding individuals that are seen only once as transients. Based on Pradel et al. (1997), I estimated 54% of the newly marked females in this study were classified as transients (survival probability of newly marked individuals/survival probability of residents). I believe this number is high, considering that most of these birds were known to breed on the study area. I am not convinced that transient models will increase the accuracy of survival estimates as argued by others (Peach 1993, DeSante et al. 1995, Pradel et al. 1997) when the “transients” eliminated from the analysis may include resident individuals with low survival or capture probabilities. Other researchers are obviously concerned about the definition of transients as a variety of criteria have been used to exclude these birds from the analysis. For his survival analysis, Lawn (1994) included only those individuals known to be residents for the majority of the breeding season. Some CEMN studies define residents as individuals recaptured 7-10 days later within the same season (Peach et al. 1991, Chase et al. 1997, Gardali et al. 2000). Other definitions of residents or transients are certainly possible. Finally, even if transient analysis appropriately identifies and eliminates individuals that permanently emigrate from the sampling area, these models assume that the meaningful population definition for these analyses is individuals that are resident on what may be a very small sampling area. These definitions of “populations” may not be meaningful for management.

I think that transient models may represent an attempt to rectify a sampling problem through analysis and the effectiveness of this approach remains unknown. At minimum I suggest that studies are designed to evaluate the performance of these models. The performance of transient models and the effect of permanent emigration on survival



estimates may be effectively evaluated by estimating survival probability for several different size study areas. Regression analysis of these survival estimates may reveal asymptotic values for estimates when all or most permanent emigrants are included in the study area. Transient models should produce estimates similar to asymptotic values for all scales of the analysis if they appropriately identify and eliminate permanent emigrants from the analysis. Alternatively, I suggest that changes to sampling design may reduce the prevalence and concerns about transients individuals. Passerine population dynamics may be most accurately monitored by sampling individuals during the breeding season.

*Detection probabilities.* – For each year, probabilities of detection,  $p$ , were higher for males than females (Table 3). Males are more territorially vocal and aggressive, making them easier to resight. Female Yellow Warblers are less visible during incubation, although at other times they will respond to playbacks and allow for resighting of bands.

Detection probabilities for the core analysis were higher than for the dispersal analysis because there were more banded birds alive and available to be seen in the expanded search area and the search proficiency was lower. Additionally, as the search area increased, we found more birds that had not been resighted for at least two years post-marking, negatively affecting the detection probabilities. Because field workers were consistently resighting on the core sites throughout the season, I believe we found a high percentage of those that held territories within the boundaries of the core sites (possibly as high as 95% of the males and 85% of the females). Therefore, I suspect that birds that were resighted after being absent for one or more years were more likely to have been temporary emigrants than undetected birds residing within the sites. Studies in

which the authors report that because band status of all known pairs was confirmed, detection probability approached 100% are potentially misleading because they do not consider temporary emigration, and I caution researchers not to confidently assume that because detection probabilities are high, all marked birds are accounted for.

*Comparative life history.* – Even with the expanded search area, my mean survival probability estimates were still relatively low ( $\phi$  for males was 0.49;  $\phi$  for females was 0.41) compared to Yellow Warblers studied elsewhere. Roberts (1971) reported Yellow Warbler apparent survival probability estimates of 0.53 ( $\pm$  0.07). Nichols et al. (1981), using a portion of the data from Roberts (1971), found  $\phi$  was 0.62. The only other mark-resight studies for Yellow Warblers reported a 32.5% return rate for males, but a 90% territory fidelity rate (occupying the same or adjacent territory) among those that did return (Yeserinac and Weatherhead 1997).

My Yellow Warbler survival probabilities appear to be low relative to other North American migratory songbirds. Comparisons among species, however, can be misleading because the same metric for survival probabilities was not always used, results depend on the shape and size of the study site, and investigations involving small study sites in general did not account for dispersal (Barrowclough 1978). For reviews of published survival estimates see Nichols et al. (1981), Karr et al. (1990), Martin and Li (1992), DeSante et al. (1995), and Johnston et al. (1997); most of these reported estimates stem from CEMN studies. For North American passerine populations, few survival probability estimates are from intensive mark-resight studies. Recently, Budnik et al. (2000) estimated survival probabilities for Bell's Vireo (*Vireo bellii*) and found male  $\phi$  was  $0.68 \pm 0.05$  and female  $\phi$  was  $0.47 \pm 0.07$ . Loery (1997) estimated Black-capped

Chickadee (*Parus atricapillus*) mean apparent survival probability to be 0.62 for males and females combined. Finally, Powell et al. (2000) found  $\phi$  for Wood Thrush (*Hylocichla mustelina*) to be  $0.58 \pm .17$ , again for males and females combined.

Although trend analysis from the Breeding Bird Survey does not report declines in Yellow Warbler numbers in Montana (Sauer et al. 1999), my highest  $\phi$  combined with the known seasonal fecundity rate for this population (1.47 to 2.02 young/pair/season), results in a population that appears unsustainable (Tewksbury 1999). Tewksbury (1999) suggests such low growth rates are reflective of high rates of parasitism by Brown-headed Cowbirds (*Molothrus ater*).

*Dispersal quantification approaches.* – Two distinct approaches are commonly used to quantify dispersal – mathematical adjustments and field design alterations. Unfortunately, mathematical adjustments lack knowledge of the underlying dispersal distribution and the pattern of long distance dispersal (Koenig et al. 2000), and there is no universal correction factor. Field designs can be altered by searching for marked birds in either an expanded study area or on secondary study sites, via radio tracking the movements of individuals, or a combination of these (reviewed in Koenig et al. 2000). Dispersal information can then be incorporated into various newly developed modeling approaches (reviewed in Nichols 1996 and Nichols and Kaiser 1999). My study demonstrates the feasibility of combining multiple sites with expanded searches, especially for species restricted to linear habitats. Some argue that dispersal studies are necessarily labor intensive and logistically complex (Moore and Dolbeer 1989), but compared to other techniques (radio and/or satellite tagging), resighting is inexpensive and requires minimal training. Advanced technologies allowing satellite and/or radio

transmitters attached to 5-10 gram warblers are years away at best (Faaborg et al. 1998, W. Cunningham pers. comm.).

In a very different type of study, comparison of genetic markers have been used to analyze population structure and sex-biased dispersal. Recently, Gibbs et al. (2000) studied microsatellite DNA variation among eight northern populations of Yellow Warblers and found evidence for male-biased dispersal – either long distance dispersal or rare episodic instances of high rates of movement. Genetic studies such as these can compare populations that are widely separated geographically and incorporate evidence for long distance dispersal that would otherwise be missed by mark-recapture field studies. Unfortunately, natal and adult dispersal are not distinguished in these studies.

*Conclusions.* – The importance of dispersal information extends beyond issues of survival estimation. Increasingly, in the face of changing landscapes, demographic investigations attempt to assess the source-sink status of one or more populations. By definition, source-sink populations are linked by emigration and immigration, yet movement is often not considered explicitly and direct evidence of dispersal is needed (Faaborg et al. 1998). Landscape structure likely affects movement into and out of habitat patches, and this movement has real consequences regarding persistence in increasingly fragmented landscapes (Faaborg et al. 1998, Walters 1998).

Even though dispersal has received considerable recent attention in the ornithological literature (see Haas 1995, Brawn and Robinson 1996, Koenig et al. 1996, Clarke et al. 1997, Haas 1998, Ferriere et al. 2000, Koenig et al. 2000, Walters 2000), our understanding is limited. Koenig et al. (2000) noted that the problem is not simply the lack of unbiased dispersal data, but also the misconception that the frequency of long

distance dispersal diminishes to insignificance beyond the boundaries of the study area, allowing investigators to be lulled into believing they have a reasonable understanding of fidelity and dispersal. I concur with Koenig et al. (2000) and hope this study will encourage additional passerine dispersal studies.

According to Clobert and Lebreton (1991), the primary weaknesses in estimating survival probabilities with open population mark-recapture studies are that survival probabilities are underestimated by an unknown factor because of dispersal and that survival probabilities are not necessarily applicable to the entire population, especially if investigators choose highly productive study areas. Designing investigations with multiple years, multiple study sites and a dispersal component will allow the use of sophisticated modeling and will provide less biased demographic estimations, avoiding the pitfalls of return rates. Brawn and Robinson (1996) argue that for songbirds, lack of dispersal data is the most prominent missing piece of the songbird demographic puzzle. Studies of dispersal can help address the discrepancy between monitoring programs and demographic studies. I support intensive mark-resight studies that offer the best demographic information possible.

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Appendix I. Adult Yellow Warbler estimates of apparent survival probabilities

( $\phi \pm 1$  SE) for models with  $\Delta AICc < 2.00$  (see Table 1) for the core and dispersal analyses.

Model <sup>a</sup>	1995	1996	1997	1998
<b>CORE ANALYSIS <sup>b</sup></b>				
$\phi(g + t) p(g + T)$ $\Delta AICc = 0.00$				
males	0.49 (0.06)	0.46 (0.05)	0.35 (0.05)	0.37 (0.05)
females	0.42 (0.07)	0.39 (0.06)	0.28 (0.05)	0.31 (0.05)
$\phi(t) p(g + T)$ $\Delta AICc = 0.11$				
males	0.48 (0.06)	0.44 (0.04)	0.33 (0.04)	0.35 (0.04)
females	0.48 (0.06)	0.44 (0.04)	0.33 (0.04)	0.35 (0.04)
$\phi(g + t) p(.)$ $\Delta AICc = 0.28$				
males	0.46 (0.05)	0.47 (0.05)	0.36 (0.05)	0.39 (0.05)
females	0.35 (0.05)	0.36 (0.05)	0.27 (0.05)	0.29 (0.05)
$\phi(g + t) p(g)$ $\Delta AICc = 0.89$				
males	0.45 (0.05)	0.47 (0.05)	0.36 (0.05)	0.39 (0.05)
females	0.36 (0.05)	0.37 (0.06)	0.28 (0.05)	0.30 (0.05)
<b>DISPERSAL ANALYSIS <sup>c</sup></b>				
$\phi(g + t) p(g + T)$ $\Delta AICc = 0.00$				
males	0.59 (0.06)	0.49 (0.05)	0.41 (0.05)	0.48 (0.04)
females	0.51 (0.07)	0.41 (0.06)	0.33 (0.05)	0.40 (0.05)
$\phi(t) p(g + T)$ $\Delta AICc = 1.08$				
males	0.57 (0.06)	0.48 (0.05)	0.39 (0.04)	0.45 (0.04)
females	0.57 (0.06)	0.48 (0.05)	0.39 (0.04)	0.45 (0.04)
$\phi(g + t) p(g + t)$ $\Delta AICc = 1.52$				
males	0.56 (0.06)	0.53 (0.06)	0.41 (0.05)	0.47 (0.04)
females	0.48 (0.07)	0.45 (0.07)	0.34 (0.06)	0.39 (0.05)

<sup>a</sup> Model type:  $\phi$  is apparent survival probability;  $p$  is detection probability;  $g$  is group (male, female),  $t$  is time (year);  $T$  is trend in time;  $(.)$  is no variation;  $+$  is additive effect;  $*$  is interaction effect.

<sup>b</sup> Core analysis data includes all individuals resighted on their original banding site.

<sup>c</sup> Dispersal analysis data includes all individuals resighted on any of the core sites and within the expanded search areas.



Appendix II. Adult Yellow Warbler estimates of detection probabilities

( $p \pm 1$  SE) for models with  $\Delta AICc < 2.00$  (see Table 1) for the core and dispersal analyses.

Model <sup>a</sup>	1996	1997	1998	1999
<b>CORE ANALYSIS <sup>b</sup></b>				
$\phi(g + t) p(g + T)$				
males	0.78 (0.07)	0.84 (0.04)	0.88 (0.04)	0.92 (0.04)
females	0.58 (0.12)	0.65 (0.09)	0.73 (0.08)	0.80 (0.08)
$\phi(t) p(g + T)$				
males	0.78 (0.06)	0.84 (0.04)	0.89 (0.03)	0.92 (0.03)
females	0.51 (0.11)	0.61 (0.08)	0.70 (0.08)	0.77 (0.08)
$\phi(g + t) p(.)$				
males	0.83 (0.03)	0.83 (0.03)	0.83 (0.03)	0.83 (0.03)
females	0.83 (0.03)	0.83 (0.03)	0.83 (0.03)	0.83 (0.03)
$\phi(g + t) p(g)$				
males	0.85 (0.03)	0.85 (0.03)	0.85 (0.03)	0.85 (0.03)
females	0.76 (0.07)	0.76 (0.07)	0.76 (0.07)	0.76 (0.07)
<b>DISPERSAL ANALYSIS <sup>c</sup></b>				
$\phi(g + t) p(g + T)$				
males	0.69 (0.07)	0.78 (0.04)	0.85 (0.03)	0.90 (0.03)
females	0.45 (0.09)	0.56 (0.07)	0.67 (0.07)	0.77 (0.07)
$\phi(t) p(g + T)$				
males	0.69 (0.06)	0.78 (0.04)	0.85 (0.03)	0.91 (0.03)
females	0.41 (0.09)	0.53 (0.07)	0.65 (0.07)	0.75 (0.07)
$\phi(g + t) p(g + t)$				
males	0.74 (0.07)	0.72 (0.07)	0.79 (0.07)	0.92 (0.03)
females	0.51 (0.11)	0.49 (0.11)	0.59 (0.11)	0.82 (0.07)

<sup>a</sup> Model type:  $\phi$  is apparent survival probability;  $p$  is detection probability;  $g$  is group (male, female),  $t$  is time (year);  $T$  is trend in time;  $(.)$  is no variation;  $+$  is additive effect;  $*$  is interaction effect.

<sup>b</sup> Core analysis data includes all individuals resighted on their original banding site.

<sup>c</sup> Dispersal analysis data includes all individuals resighted on any of the core sites and within the expanded search areas.

## CHAPTER 2:

# ARE PATTERNS OF YELLOW WARBLER BREEDING DISPERSAL RELATED TO NEST SUCCESS?

### ABSTRACT

Differentiating between mortality and dispersal remains a challenge to avian researchers. Evidence of breeding dispersal related to nest success can suggest a causal mechanism for dispersal and help distinguish movement from mortality. To assess the relationship between dispersal and reproductive success, 287 male and 149 female adult Yellow Warblers (*Dendroica petechia*) were color-banded and resighted over five breeding seasons at 11 study sites in the Bitterroot Valley, Montana. To document dispersal, during the last two seasons, field assistants and I searched extensively for marked warblers between and surrounding these sites. Additionally, reproductive success in the previous season (1995-1998) was known for many of these marked birds. I compared dispersal distance, dispersal rates, and return rates of successful and unsuccessful males and females. I also assessed dispersal and return in relation to reproductive effort. Results indicate that these Yellow Warblers were not completely breeding site faithful. Median dispersal distance was 123 m for females and 85 m for males. Breeding dispersal appeared to be related to prior nest success for females; unsuccessful females dispersed farther and returned at lower rates than successful females. There were no real differences in dispersal distance, dispersal rates, or return rates between successful and unsuccessful males. Return was not influenced by reproductive effort of males. It was unlikely that female return rate was related to

reproductive effort; however, I could not definitively differentiate between effort and success. I suggest that other unsuccessful females may have dispersed, and this could explain why survival probabilities for females of this population are lower than those of males.

Keywords: breeding dispersal, *Dendroica petechia*, reproductive success, Yellow Warbler

## INTRODUCTION

Although avian dispersal is a critical population parameter (Temple and Wiens 1989, Loery et al. 1997, Koenig et al. 2000), our understanding of year-to-year movement is limited. For songbirds, it is widely believed that dispersal is far greater in the first year of life than in subsequent years, and that adults have strong breeding site fidelity (Greenwood and Harvey 1982). However, because dispersal away from a breeding site is difficult to track, the probability and extent of such movements remain unknown for most species. Additionally, the mechanisms that promote or discourage dispersal in passerines have only recently begun to be studied adequately (e.g., Bollinger and Gavin 1989, Haas 1998, Lindberg 1998). Differences in dispersal patterns between sexes are frequently reported. Site fidelity is often assumed to be strong in territory-establishing males because previous breeding experience may confer a competitive advantage for a breeding territory (Greenwood 1980, Slagsvold and Lifjeld 1990), and knowledge of a particular area may increase a bird's ability to acquire food, escape predators, and reproduce (Wheelwright and Mauck 1998). In most songbird species studied, females are less site

faithful than males, presumably because females are selecting breeding sites based on mate quality foremost, and territory quality either secondarily or indirectly (Greenwood and Harvey 1982, Payne and Payne 1993, Clarke et al. 1997). However, stronger site fidelity has been found in males of some species (reviewed in Clarke et al. 1997).

Many studies suggest that dispersal is related to reproductive success in the previous breeding season (e.g., Nolan 1978, Drilling and Thompson 1988, Bollinger and Gavin 1989, Haas 1998). Recently, Haas (1998) experimentally manipulated the breeding system for American Robins (*Turdus migratorius*) and Brown Thrashers (*Toxostoma rufum*) and found strong support for the “prior experience” hypothesis in which individuals choose breeding sites based on experience in the previous season. Robins and thrashers subjected to human-induced nest failure returned to their previous nesting sites the following year at significantly lower rates than successful breeders, and dispersal distances tended to be greater after both natural and experimental failures than after successful nests. She assumed that a proportion of those that did not return had dispersed. In another example, Bollinger and Gavin (1989) compared the breeding-site fidelity of male and female Bobolinks (*Dolichonx oryzivorus*) at two low-quality sites and one high-quality site. Unsuccessful individuals at the low-quality sites were less likely to return the following year than were successful individuals, and the unsuccessful individuals that did return moved a greater distance between nest sites than those that were successful. A number of other researchers have determined that success in one breeding season resulted in increased likelihood of returning to the same site the next year (e.g., Harvey et al. 1979, Grotto et al. 1985, Gavin and Bollinger 1988, Payne and Payne 1993). However, few birds that disperse farther than the boundaries of the study

site were ever found, and mortality and dispersal remain confounded in most studies (Haas 1998). An alternative explanation for low returns of unsuccessful nesters include the cost of reproduction or extra energy hypothesis, which posits that birds that re-nest within a season expend extra energetic effort which increases mortality (Resnick 1985, Roff 1992, Haas 1998, Lukacs et al. *in review*).

Documenting dispersal is therefore crucial in order to differentiate between movement and mortality. Some argue that dispersal has two components: decision regarding return (i.e. dispersal rate) and decision regarding distance moved (Gratto et al 1985, Clarke et al. 1997). Because the two together determine how individuals in a population are distributed in space and time (Waser and Jones 1983, Clarke et al. 1997), both are important in understanding the biological significance of sex-biased dispersal. Based in part on evidence of between-year dispersal within a population of marked Yellow Warblers (*Dendroica petechia*), I designed a study to locate dispersed breeding birds beyond the boundaries of the study sites. In western Montana, Yellow Warblers breed within linear riparian corridors, and expanded surveys are feasible. The aim of this study was to determine whether breeding dispersal distance, dispersal rates, or return rates were linked to reproductive success in the previous season and whether differences existed between males and females. I also assessed one measure of reproductive effort to determine if this cost influenced the return of males or females.

## **STUDY AREA AND METHODS**

I conducted my research on seven study sites on a combination of public and private lands along the Bitterroot River in western Montana and four smaller sites along

riparian drainages within the western foothills, primarily in the Bitterroot National Forest (Fig.1) (a subset of the sites described in Tewksbury et al. 1998). These core sites averaged 15 ha in size (range 5-20 ha) with elevations of 1050-1350 m. All sites were primarily deciduous riparian habitats. The Bitterroot River sites were dominated by deciduous trees and shrubs, especially black cottonwood (*Populus trichocarpa*) and were surrounded by residential areas, agricultural lands (cultivated and/or grazed by cattle or horses), and deciduous and coniferous forest communities. The foothill sites were dominated by shrubs and deciduous trees, especially quaking aspen (*Populus tremuloides*), and were surrounded by coniferous forests and some grazed lands. Study sites were initially chosen to minimize differences in habitat character among sites, although there was a range in landscape variation surrounding the sites (see Tewksbury et al. 1998).

During the breeding season, Yellow Warblers are the most common species of deciduous riparian areas within the Rocky Mountain West (Tewksbury et al. *in press*). In western Montana, they arrive on the breeding grounds and begin to establish territories during the last two weeks of May, with males generally arriving two to seven days before females (Tewksbury and Cilimburg unpubl. data). They are found in association with streamside shrubs or large deciduous trees, especially black cottonwood, and may also be found within the deciduous vegetation of residential areas (Hutto and Young 1999; Cilimburg unpubl. data).

During the 1995-1998 breeding seasons (approximately 23 May – 1 August), field assistants and I created territory maps of breeding Yellow Warblers on the 11 core sites and target mist-netted adults, often with the help of playback songs and calls. Both

females and males respond to playback songs or calls, though females less so, especially during incubation. Field assistants aged and sexed by plumage all captured birds, and marked individuals with one US Fish and Wildlife Service metal band and a unique combination of three color bands. Over four years, 287 males and 149 females were banded, with over 85% of these from the Bitterroot River sites. As this was part of a larger study (Tewksbury et al. 1998, Tewksbury 1999), field assistants searched for and monitored nests, mist netted, or resighted marked individuals at each core site every one to three days throughout the season. The perimeter of each site (approximately 100-200 m depending on available habitat) was searched for banded birds in 1996 and 1997.

During the 1998 and 1999 seasons, I expanded the resighting area and, together with an assistant, searched for banded individuals within suitable habitat along the Bitterroot River between and surrounding the core sites (Fig. 1). We concentrated our efforts around the sites where the most birds were banded (sites #1, 2, 3, 4, 6). We surveyed about 85-90% of available Yellow Warbler habitat between sites #1-3 during each of these two seasons; surveys around the other sites were less complete (see Fig. 1). For these searches, we systematically traveled sections of the river corridor, sighted individuals and determined the presence or absence of bands and, when present, the color combination. We again used song playbacks to attract pairs and played songs in appropriate warbler habitat when there was no visible or audible activity. As males are commonly located first, we placed extra effort in sighting the female associated with each male. We approached sites by foot whenever possible and used kayaks to access small islands. Resighting time for the expanded dispersal searches totaled approximately 220

hours in 1998 and 380 hours in 1999 and generally occurred between 0600 and 1300 hours. In both years, this resighting occurred from approximately 26 May – 10 July.

Territory centers were used to determine the distance moved between years. We used a *Trimble Geoexplorer* GPS unit to mark exact locations of banded individuals found off the core sites in 1998 and 1999. In 1999, the territory centers for all banded individuals and the boundaries of all core sites were mapped via GPS. From the territory site maps, I digitized the approximate territory center for each bird in 1995-1998, and from these locations, computed straight-line dispersal distances using UTM coordinates.

Tewksbury (1999) collected data for nest success during the 1995-1998 seasons. Nest fates were based on periodic nests checks (every 2-4 days) and fate protocols established by Martin et al. (1996), with nest failure rates estimated using the Mayfield Method (Mayfield 1975, modified by Hensler and Nichols 1981). A bird was considered successful if it was associated with a nest that fledged at least one young within a season. Some of these nests were parasitized by Brown-headed Cowbirds. Pairs infrequently fledged one cowbird young and no natal young (four returning males had this history). For the main analyses, I assumed such situations would not be considered failure by the warbler host and considered these individuals to have been successful. In a separate analysis, I considered whether inference would change if raising a cowbird young alone were considered failure instead of success.

Yellow Warblers produce only one brood per season, yet pairs may renest multiple times following nest failures. Although they usually renested within the same territory, not all nests were located and some pairs may have moved to new territories. To be reasonably assured that those that failed in their last monitored attempt did not



successfully re-nest, I restricted the analysis to those pairs that were followed late into the season (see Martin 1995, Pease and Grysowski 1995). I used 3 July as a cut-off date (less than 5% of all successful nests were initiated after this date), but I also incorporated other resighting information from territorial maps. Using the date after which no successful nests were initiated would have resulted in a sample size too small to run these analyses. Thus, not included in this analysis were pairs in which all nests failed before this date and either no additional nests were found or monitoring was discontinued.

*Data analysis.* – I considered males and females as independent sampling units because in only two cases did a marked pair reestablish in the following season. I assumed that the detection probability (probability of resighting a marked bird, given that it was associated with the population) for successful and unsuccessful individuals did not differ at any given location. Because of sample size limitations, it was necessary to combine data from all years. All tests were two-tailed.

To test for differences between dispersal distributions, I used the two-sample Kolmogorov-Smirnov Goodness of Fit test (Zar 1984). Using a  $\chi^2$  test, I assessed differences in the median dispersal distance for males and females and separately for successful and unsuccessful males and successful and unsuccessful females. To test for differences in return rates based on nest success in the previous season, I used 2 x 2 contingency tables and the Fisher's exact test. Return rate was simply defined as the percentage of birds that returned to the study site on which they were originally banded. I also tested whether the dispersal rate (yes, dispersed versus no, did not disperse) varied with nest success with the Fisher's exact test. *A priori* and as a conservative measure, I arbitrarily defined distance breeding dispersal as between-year movement greater than

700 m (or approximately 10 territories for this population). Thus, movement less than 700 m was not considered dispersal. Additionally, I assessed this relationship at a finer scale, and in a separate analysis, defined dispersal as movement greater than 200 m. Individuals may have knowledge of reproductive success for not only themselves, but also of those in the surrounding territories (Boulinier and Danchin 1997), and beyond this distance (200 m), that information would likely be less well known.

Finally, I was interested in whether reproductive effort influenced rates of return, as a way to assess probable mortality. Because Yellow Warblers commonly reneest many times within a season and because field assistants were rarely certain of finding all nesting attempts, an accurate measure of effort was difficult. However, assuming birds that successfully fledged young early in the season (with limited time to have failed attempts) expended less effort than those that either produced a successful nest later (and presumably failed prior to this) or produced no successful nests (and presumably failed after multiple attempts), comparisons of effort can be made. I used 7 July to split the season and compared both the return of successful individuals with nests completed on or prior to this date to all other individuals. If reneesting is stressful, its effects should be apparent regardless of final nest success or failure, and removing unsuccessful individuals leaves out one group of interest (those that failed) (Haas 1998). Because nest success is confounded with reproductive effort, I also compared return before and after 7 July for only the successful individuals. I again tested these differences for males and females via a 2 x 2 contingency table and the Fisher's exact test.

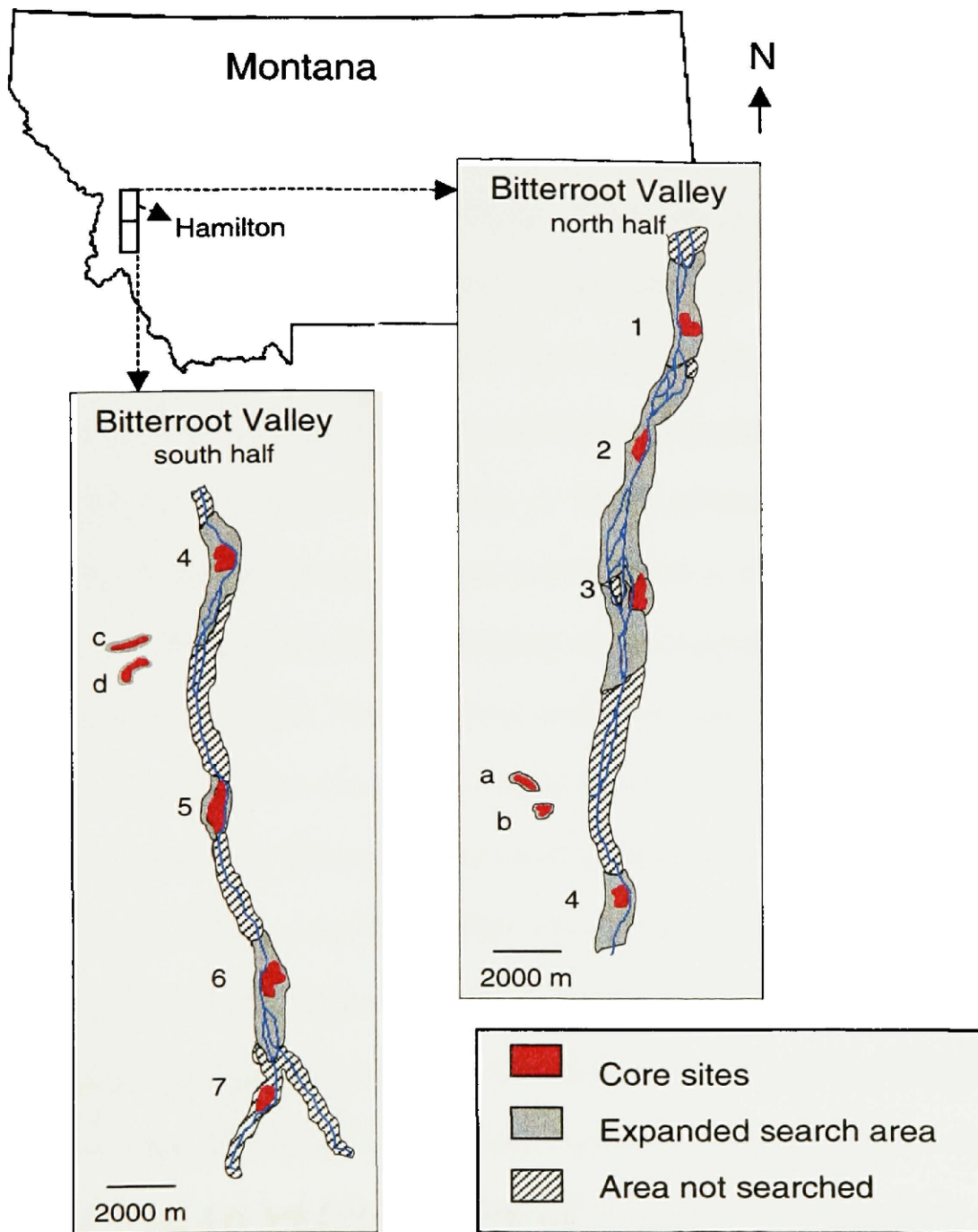


Fig 1. The core sites and expanded search areas within the riparian corridor surrounding the Bitterroot River, Ravalli County, MT. Sites #1 – 7 are the core Bitterroot River sites; sites a – d are the core foothill sites. The core sites were studied 1995-1999; resighting in the expanded search area occurred in 1998-1999.

## Results

Returning female Yellow Warblers dispersed between 13 and 5,862 m; for males the range was 4-24,728 m. Although searches of the linear habitat between and surrounding the core study sites was incomplete (Fig.1), the farthest an individual could have dispersed and been detected was about 45 km. Median dispersal distance for all females was 123 m ( $n = 41$ , mean = 583 m, SE = 226), and for males the median distance was 85 m ( $n = 157$ , mean = 609 m, SE = 193). These medians did not differ significantly ( $\chi^2 = 2.492$ ,  $df = 1$ ,  $P = 0.114$ ), nor did female and male distributions differ (Kolmogorov-Smirnov = 0.869,  $P = 0.437$ ) (Fig. 2). Dispersal data included multiple year moves by some individuals (e.g., dispersal distance 1995 to 1996 and 1996 to 1997).

Of the above 198 cases, I had corresponding nest success data in the previous season for 132 individuals (67%). For females in which nest success was known, median dispersal distance was 162 m ( $n = 32$ ; mean = 710.0 m, SE = 281), for males it was 79 m ( $n = 100$ ; mean = 734 m, SE = 294), and these medians differed significantly ( $\chi^2 = 4.99$ ,  $df = 1$ ,  $P = 0.025$ ). There was a significant difference in the dispersal distributions between females and males (Kolmogorov-Smirnov = 1.902,  $P = 0.001$ ).

In comparisons of dispersal distances with nest success, the median distance for six seasonally unsuccessful females was 3,546 m (range 159-5,862 m, mean = 3,191 m, SE = 1,043), and for 26 successful females it was 113 m (range 22-505 m, mean = 137.5 m, SE = 103;  $\chi^2 = 3.282$ ,  $df = 1$ ,  $P = 0.070$ ). The dispersal distribution of the unsuccessful females was, however, not significantly different than that of successful females (Kolmogorov-Smirnov = 0.566,  $P = 0.906$ ) (Fig. 3A). There was no difference in the median dispersal distance for 32 unsuccessful males (median = 79 m, range 6-

6,055 m, mean = 3191 m, SE = 1043) compared to 68 successful males (median = 82 m, range 15-24,728 m, mean = 1,795 m, SE = 4,960) ( $\chi^2 = 0.000$ ,  $df = 1$ ,  $P = 1.00$ ), but the dispersal distributions differed (Kolmogorov-Smirnov = 2.152,  $P = 1.000$ ) (Fig. 3B). Considering a cowbird fledgling as a failure instead of a success did not alter these results.

For male Yellow Warblers, 42.8% of successful males returned to their study site of origin and 46.6% of unsuccessful males returned, demonstrating that returns were unrelated to an individual's nesting success in the previous year (Table 1; Fisher's exact test,  $P = 0.645$ ). However, more females returned to the study site of origin if successful the previous year (35.1% returned if successful; 6.5% returned if unsuccessful; Table 1; Fisher's exact test,  $P = 0.002$ ). Again, if a cowbird young was considered a failure, this finding did not change.

Comparisons of long distance dispersal rates ( $\geq 700$  m) and their relation to breeding success again showed females were more likely to disperse after failed nest success (Table 2; Fisher's exact test,  $P = 0.002$ ). For males there was also a trend in the same direction (Table 2; Fisher's exact test,  $P = 0.106$ ). When dispersal is defined as movement  $\geq 200$  m, this trend for males did not hold (Table 2; Fisher's exact test,  $P = 0.333$ ), although it did for females (Table 2; Fishers exact test,  $P = 0.023$ ).

For males, there did not appear to be a difference in the return rate for those who successfully nested early in the season (42.0% returned) and those that either successfully nested later in the season or were not successful (45.2% returned; Table 3;  $n = 215$ , Fishers exact test,  $P = 0.789$ ). Nor were there differences in returns for successful males relative to whether they completed their nest early (41.3% returned) or late in the season

(44.2% returned; Table 4;  $n = 149$ , Fisher's Exact test,  $P = 0.741$ ). For females, those with successful nests early in the season returned at a higher rate (40.0%) than all others (22.2%; Table 3;  $n = 125$ , Fishers exact test,  $P = 0.054$ ). When the analysis was restricted to only successful females, there were no significant differences in returns between those that completed nesting early (45.7% returned) and those that completed nesting later in the season (32.1% returned; Table 4;  $n = 88$ , Fisher's Exact test,  $P = 0.261$ ).

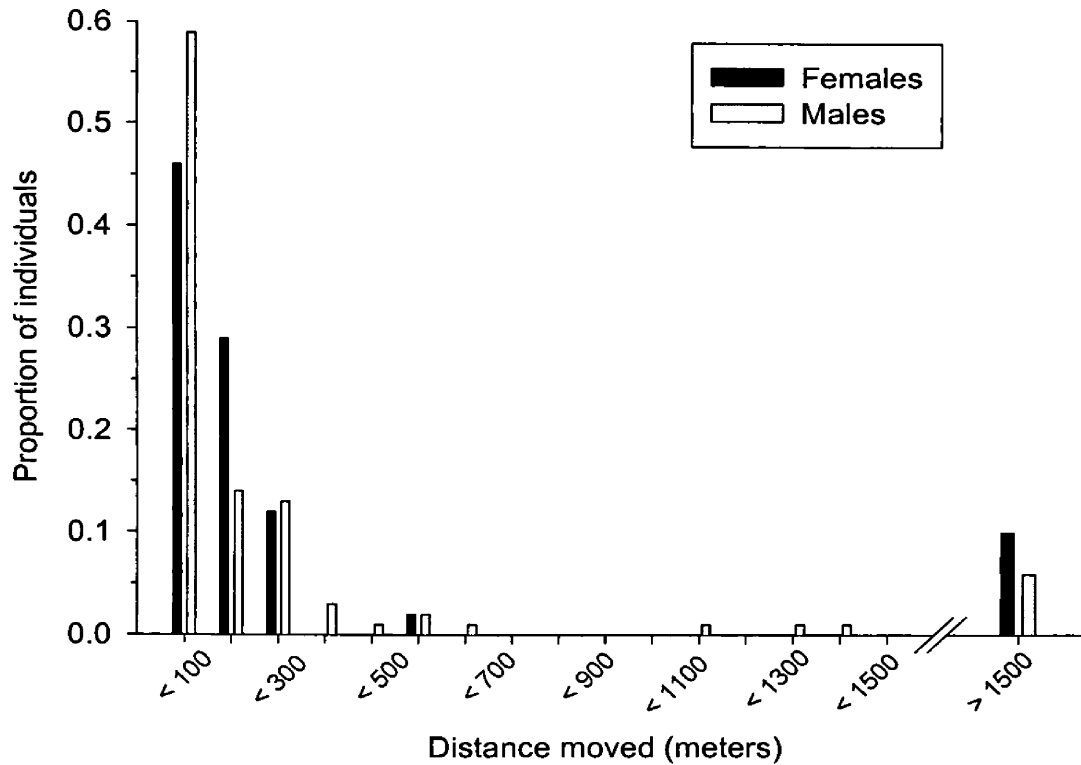


Fig. 2: Distribution of between-year breeding dispersal for adult male ( $n = 159$ ) and female ( $n = 41$ ) Yellow Warblers, 1996–1999, in 100-m increments to 1500 m (range 4–24,728 m). Distance moved is non-cumulative (e.g. "< 300" is between 200 and 300).

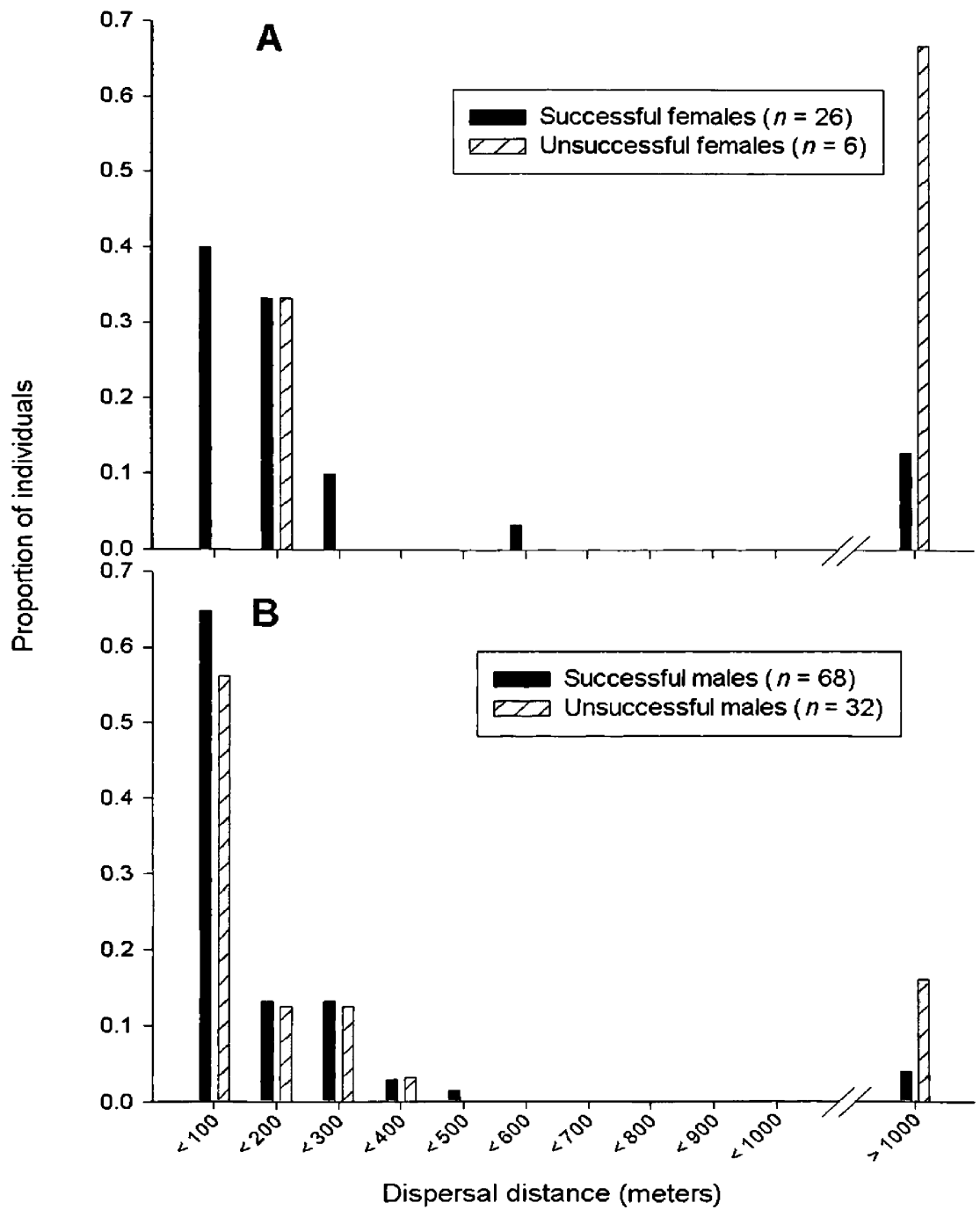


Fig. 3. Comparisons of Yellow Warbler between-year dispersal distributions related to nest success in the previous season for A) females and B) males.



TABLE 1. The percentage of Yellow Warbler males ( $n = 217$ ) and females ( $n = 125$ ) that returned to their original study site between 1996-1999 in relation to nest success in the previous breeding season.

Sex	Nest success	% return	Fisher's exact test
Males	yes	42.8	P = 0.645
	no	46.6	
Females	yes	35.1	P = 0.002
	no	6.5	

TABLE 2. Differences in dispersal in relation to seasonal nest success for Yellow Warblers. The percentage of males ( $n = 100$ ) and females ( $n = 32$ ) that either dispersed or did not disperse between 1996-1999 relative to nest success in the previous breeding season, for two different measures of dispersal. Long distance dispersal is operationally defined as movement  $\geq 700$  m and short distance dispersal is  $\geq 200$  m.

Sex	nest success	% dispersal $\geq 700$ m <sup>a, c</sup>	Fisher's exact test	% dispersal $\geq 200$ m <sup>b, c</sup>	Fisher's exact test
Males	yes	95.6	P = 0.106	22.1	P = 0.333
	no	84.4		31.3	
Females	yes	96.2	P = 0.002	15.4	P = 0.023
	no	33.3		66.7	

<sup>a</sup> Long distance dispersal only ( $\geq$ approximately 10 territories).

<sup>b</sup> Short and long distance dispersal combined.

<sup>c</sup> Distance from territory center.

TABLE 3. Observed return rates of Yellow Warblers that expended low reproductive effort (early successful nesters) versus those that expended greater effort (successful later in the season or not at all), 1996-1999 (males,  $n = 215$ ; females,  $n = 125$ ). The season was split, and 7 July was used as the cutoff date (see STUDY AREA AND METHODS).

Sex	Early success	% return	Fisher's exact test
Males	yes	42.0	P = 0.769
	no	45.2	
Females	yes	40.0	P = 0.054
	no	22.4	

TABLE 4. Observed return rates of successful Yellow Warblers that expended low reproductive effort (early successful nesters) versus those that expended greater effort (successful later in the season), 1996-1999 (males,  $n = 149$ ; females,  $n = 88$ ).

Sex	Early success	% return	Fisher's exact test
Males	yes	41.3	P = 0.741
	no	44.2	
Females	yes	45.7	P = 0.261
	no	32.1	

## DISCUSSION

Although the majority of returning adult Yellow Warblers demonstrated the strong between-year site fidelity considered typical for warblers (i.e. moved less than approximately 10 territories; e.g., Fig. 4A), others were not breeding site-faithful (e.g., Fig. 4B). The additional movement data collected in this study allowed for less biased breeding dispersal distributions. These dispersal distributions reflect those individuals that field assistants and I were able to locate, and undoubtedly there were males and females alive and missed, especially if they returned to territories not within core study sites. Nonetheless, with these data, associations between movement and nest success are evident.

By most measures, female dispersal was strongly related to breeding success. Of the 26 females successful in fledging at least one young the previous year, just one dispersed more than 700 m. Yet of the six unsuccessful females resighted, four dispersed over 3000 m. Although 35% ( $n = 94$ ) of successful females returned to their study site of origin, only 7% ( $n = 31$ ) of those with seasonal nest failure returned. Thus, successful females were almost eight times more likely to return. The low return rate for unsuccessful females, combined with their apparent propensity to disperse far beyond the confines of the study area (for which the four individuals mentioned above are evidence), suggests that some proportion of those females never seen again were dispersers, not mortalities. Even accounting for dispersal, apparent survival estimates for females of this population were relatively low, averaging 0.41 (range  $0.33 \pm 0.05$  to  $0.51 \pm 0.07$  depending on the year; Chapter 1). Detection probabilities were moderate, (range  $0.45 \pm 0.09$  to  $0.77 \pm 0.07$  depending on the year; Chapter 1), indicating that not all surviving

females were resighted. Females are harder to relocate than males, especially when incubating. However, because resighting continued throughout the breeding season on the study sites, field assistants resighted most individuals that returned to those areas. Less time was spent in each area of the expanded searches, and these were, as mentioned, incomplete. Acknowledging that the sample size for unsuccessful females was small and conclusions drawn are necessarily tentative, I suspect that an unknown proportion of unsuccessful females dispersed off the core study areas.

By most measures, male dispersal distance was unrelated to prior breeding success. The exception was the long distance dispersal rate, in which unsuccessful males appeared more likely than successful males to disperse over 700 m. Evidence indicates that some males in this population undertook long dispersals (9.5% moved more than 700 m), yet it remains unclear if this was related to reproductive success or other factors. As with females, there were likely males missed within the expanded search area and males that dispersed even longer distances. I have previously shown (Chapter 1) that estimates of survival probabilities were higher for males than females (mean for males = 0.49, range  $0.41 \pm 0.05$  to  $0.49 \pm 0.06$ ) and that detection probabilities, although variable among years, were relatively high for males in this study (range  $0.69 \pm 0.07$  to  $0.90 \pm 0.03$ ). The finding that dispersal distances tended to be shorter for males than females, together with higher detection probabilities for males, leads me to believe that we failed to resight proportionally more surviving females than males.

A number of other songbird studies have also found evidence of female-biased dispersal (e.g., Drilling and Thompson 1988, Bollinger and Gavin 1989, Roth and Johnson 1993; reviewed in Greenwood and Harvey 1982, Clarke et al. 1997). Fewer

studies, however, demonstrated a difference in male and female return rates associated with prior breeding success. In a long-term study of Blue Tits (*Parus major*), Harvey et al. (1979) showed that females whose nests were depredated moved a greater distance to breed the following year than did successful females, a pattern not evident for males. Lemon et al. (1996) found that for female American Redstarts (*Setophaga ruticilla*), breeding success was a strong predictor of their return to the study area. For males, the duration of time on their territory was a better predictor of return to the study area than was nest success, but whether they returned to their previous territory or not was related to prior success.

A variety of other passerine studies have demonstrated a relationship between return to the study area and reproductive success in the previous season for both sexes. As mentioned, Haas (1998) confirmed this pattern in her study of male and female robins and thrashers. Darley et al. (1977) also found that reproductively successful male and female Grey Catbirds (*Dumetella carolinensis*) returned in greater numbers than those unsuccessful. Gavin and Bollinger (1988) reported that for Bobolinks (*Dolichonyx oryzivorus*) of both sexes, breeding success in one year influenced breeding site location in the year following. In particular, those that fledged more young returned more often than those with fewer fledged young. Holmes and Sherry (1992) found that American Redstarts and Black-throated Blue Warblers (*Dendroica caerulescens*) showed a tendency to return if successful. Jacobsson (1988) found that unsuccessful male Willow Warblers (*Phylloscopus trochilus*) dispersed to new territories at significantly higher rates than successful males, although sample sizes were small.

Nonetheless, songbird nest success and dispersal or return rates do not always follow these patterns. For example, female Cassin's Finches (*Carpodacus cassinii*) have been found to be more site faithful than males (Mewaldt and King 1985). In contrast to Jacobsson (1988), Lawn (1994) reported that the return of older male Willow Warblers was not related to prior breeding success. Payne and Payne (1993) reported that although female Indigo Buntings (*Passerina cyanea*) were more likely to disperse than males, female dispersal was not related to breeding success in the previous year. In contrast to Yellow Warbler females in this study, Drilling and Thompson (1988) found no relationship between the success at the last breeding attempt of the previous year and the likelihood of returning female House Wrens (*Troglodytes aedon*). However, they did find that returning females had produced more offspring in the previous season than non-returning females. In concordance with my results, the reproductive success of male House Wrens was not related to distance moved or return.

An alternative hypothesis to explain the patterns of return observed in this study is that differential returns reflect the energetic stress associated with multiple nesting efforts, and this extra effort results in higher rates of mortality. I found no evidence that extra nesting effort resulted in lower return rates for male Yellow Warblers. For females, there was a difference in return between presumed lower stress individuals (successful early) and presumed higher stress individuals (successful later or not at all). However, when I restricted the analysis to successful females only and then compared return relative to the timing of nest completion, the relationship did not hold. Although Haas (1998) used a similar measure, she had an experimental framework designed to distinguish between dispersal and mortality (see below). I remain unconvinced that those

with extra effort are truly mortalities and not dispersers; the two remain confounded in my study. Nonetheless, increased breeding effort and decreased nesting success together may affect both adult breeding dispersal and survival (Anders et al. 1997, Payne and Payne 1993).

Although life history theory predicts that the energetic stress of reneating would have associated costs (Resnick 1985, Roff 1992), this remains difficult to demonstrate. Haas (1998) showed that the cost of reproduction hypothesis did not explain differential returns in American Robins and Brown Thrashers (assuming that reneating was correlated with reproductive costs). She was able to rule out this competing hypothesis because individuals that nested once per season returned at rates indistinguishable from those that nested repeatedly. However, Lukacs et al. (*in review*) compared the survival probabilities of breeding versus non-breeding male and male versus female Orange-crowned Warblers (*Vermivora celata*) and found that the lower survival rates for breeding males was consistent with the cost of reproduction explanation. They were unable to rule out dispersal, but did note that non-breeding males are generally thought to have higher dispersal and would be expected to show lower survival (not higher) if significant levels of dispersal were occurring. Lacking evidence of sex-biased dispersal, they also suggest lower female survival probabilities reflect true differences in mortality (via a cost of reproduction), but acknowledge this could be due to differences in dispersal (permanent emigration away from the study area).

I have previously shown (Chapter 1) that although model-based estimates of apparent survival probabilities varied among years, they were consistently higher for males than for females. In light of higher rates of dispersal for unsuccessful females

versus unsuccessful males, further assessment of Yellow Warbler nesting attempts may help to clarify if there is a detectable cost to reproductive effort. Again, differentiating between dispersal and mortality remains a challenge.

The reasons for differences in male and female dispersal and return patterns remain open to speculation. As mentioned, males may be more constrained in their abilities to disperse. Drilling and Thompson (1988) noted that dispersing males risk either not locating a suitable territory or being expelled from this new territory when the previous owner returns. Females, however, are thought to settle based, at least in part, on male attractiveness, and this has been demonstrated for Yellow Warblers (Yesernac and Weatherhead 1997).

In summary, further studies that focus on locating dispersed birds are necessary to understand the influence of prior experience on year-to-year songbird movement. As this study shows, searching for marked songbirds in an extended area can be a successful technique for documenting dispersal, especially for birds breeding in linear or otherwise limited areas, and I hope this encourages further dispersal studies. Dispersal should not be considered a negligible parameter. As Haas (1998) suggested, evidence that breeding dispersal may be linked to reproductive success ties these two demographic parameters together and has important implications for the management of bird populations. Dispersers may originate disproportionately from low quality habitats (Bollinger and Gavin 1989, Holmes et al. 1996), and additional studies of dispersal could lead to better understanding of source-sink dynamics.



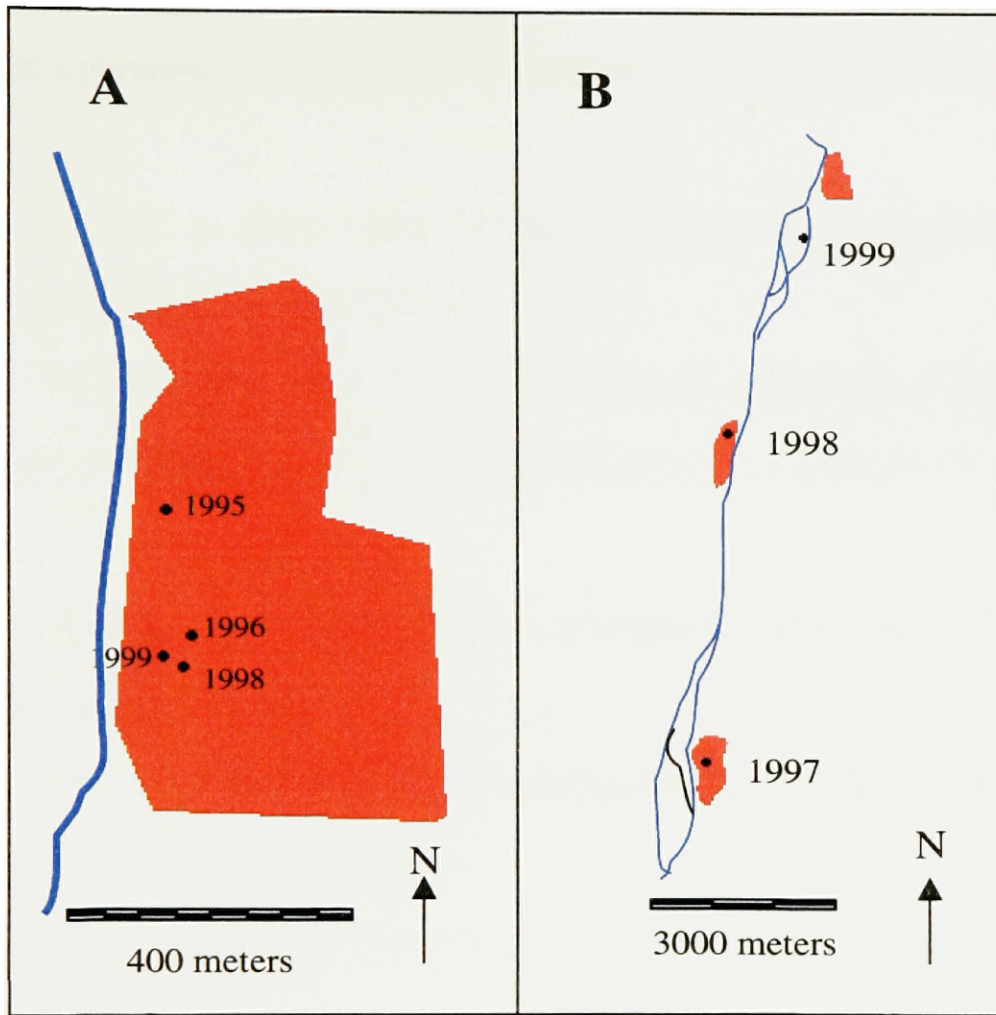


Fig. 4 (A). Breeding territories for one male at Bitterroot River site #1 (not seen in 1997), demonstrating strong site-fidelity. (B) Breeding territories for one female in three consecutive years, demonstrating dispersal (darkened plots are Bitterroot River study sites # 1-3).

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